VESSELS IN LATE METAXYLEM

OBSERVATIONS
Leucojum vernum (Fig. 1 a, b)

Root : Length - 1423.50 \( \mu \text{m} \) to 2409.00 \( \mu \text{m} \), average length - 1805.75 \( \mu \text{m} \) (The figures represent an average of 15-20 measurements); diameter - 43.80 \( \mu \text{m} \) to 65.70 \( \mu \text{m} \), average diameter - 54.78 \( \mu \text{m} \); lateral wall thickening spiral; end walls slightly oblique, rarely very much so; perforation plate reticulate; vessels with one end transverse and other slightly oblique, but both with reticulate plates occur occasionally.

Scape : Vessels absent

Leaf : Vessels absent

Amaryllis reginae (Fig. 1 c, d, e)

Root : Length - 1314.00 \( \mu \text{m} \) to 2682.75 \( \mu \text{m} \), average length - 1817.70 \( \mu \text{m} \); diameter - 65.70 to 76.65 \( \mu \text{m} \), average diameter - 71.17 \( \mu \text{m} \); lateral wall thickening spiral-scalariform; end walls much oblique, plate scalariform; rarely sub-terminal in position; rarely perforation plate with vertical and oblique bars; number of bars 8-30, often inter-connected.
Scape : Vessels absent
Leaf : Vessels absent

Amaryllis vittata (Fig. 1 f, g)

Root : Length - 1040.25 \( \mu m \) to 1971.00 \( \mu m \), average length - 1511.10 \( \mu m \); diameter - 76.65 \( \mu m \) to 87.60 \( \mu m \), average diameter - 82.12 \( \mu m \); lateral wall thickening spiral-scalariform; end walls mostly very oblique, plate scalariform, rarely slightly oblique, prominently reticulate; sometimes, vessel with one end wall slightly oblique with reticulate plate, and other much oblique with scalariform plate and with scalariform lateral wall thickening noted; number of bars 15-28.

Scape : Vessels absent
Leaf : Vessels absent

Crinum latifolium (Fig. 2 a, b)

Root : Length - 2956.50 \( \mu m \) to 4818.00 \( \mu m \), average length - 3668.25 \( \mu m \); diameter - 87.60 \( \mu m \) to 109.50 \( \mu m \), average diameter - 98.55 \( \mu m \); lateral wall thickening spiral-scalariform; end walls much
oblique; perforation plate scalariform, number of bars 11-30.

Scape : Vessels absent
Leaf : Vessels absent

**Crinum pratens** (Fig. 2 c)

Root : Length - 1588.70 µm to 2562.40 µm, average length - 2003.85 µm; diameter - 65.70 µm to 76.65 µm, average diameter - 71.17 µm; lateral wall thickening spiral-scalariform; end walls much oblique, perforation plate scalariform; number of bars 16-31.

Scape : Vessels absent
Leaf : Vessels absent

**Zephyranthes grandiflora** (Fig. 2 d, e)

Root : Length - 985.50 µm to 1971.00 µm, average length - 1478.25 µm; diameter - 54.15 µm to 76.65 µm, average diameter - 65.70 µm; lateral wall thickening scalariform; end walls transverse, plate reticulate, rarely oblique with scalariform plate (number of bars 10-15); vessel with one
end wall transverse and other oblique with similar variations in plate also observed.

Scape: Vessels absent
Leaf: Vessels absent

Zephyranthes texana (Fig. 2 f, g)

Root: Length - 810.30 μm to 1752.00 μm, average length - 1401.60 μm; diameter - 54.75 μm to 65.70 μm, average diameter - 60.22 μm; lateral wall thickening spiral-scalariform; end walls transverse, plate reticulate, rarely oblique with scalariform plate (number of bars 8-16), vessel with one end transverse and other oblique with similar variation in perforation plate noted.

Scape: Vessels absent
Leaf: Vessels absent

Haemanthus multiflorus (Fig. 3 a)

Root: Length - 1916.25 μm to 2847.00 μm, average length - 2343.30 μm; diameter - 76.65 μm to 87.60 μm, average diameter - 82.12 μm; lateral wall thickening spiral-scalariform; end walls oblique, plate scalariform; number of bars 8-34.
Scape: Vessels absent

Leaf: Vessels absent

*Clivia miniata* (Fig. 3 b, c, d)

Root: Length - 1314.00 μm to 2135.25 μm, average length - 1784.00 μm; diameter - 43.80 μm to 65.70 μm, average diameter - 54.75 μm; lateral wall thickening scalariform often inter-connected, reticulate; end walls oblique, plate scalariform, rarely reticulate; number of bars 14-30.

Scape: Vessels absent

Leaf: Vessels absent

*Pancratium verecundum* (Fig. 3 e, f)

Root: Length - 1423.50 μm to 2244.75 μm, average length - 1742.50 μm; diameter - 54.75 μm to 65.70 μm, average diameter - 60.25 μm; lateral wall thickenings spiral-scalariform; end walls nearly transverse or oblique, plate scalariform; number of bars 4-10.

Scape: Vessels absent

Leaf: Vessels absent
Hymenocallis speciosa (Fig. 3 g, h, i)

Root : Length - 1533.00 µm to 2518.00 µm, average length - 2036.70 µm; diameter - 76.65 µm to 87.60 µm, average diameter - 82.12 µm; lateral wall thickening scalariform with inter-connections; end walls transverse, rarely slightly oblique, plate reticulate; rarely oblique perforation plate with vertical and transverse bars noted.

Scape : Vessels absent

Leaf : Vessels absent

Hymenocallis tenuiflora (Fig. 3 j, k)

Root : Length - 1073.10 µm to 2409.00 µm, average length - 1511.10 µm; diameter - 131.40 µm to 143.35 µm, average diameter - 136.80 µm; lateral wall thickening scalariform often inter-connected; end walls transverse, rarely oblique, plate reticulate.

Scape : Vessels absent

Leaf : Vessels absent
**Eucarhis grandiflora** (Fig. 4 a)

Root : Length - 1971 μm to 3339.75 μm, average length - 2649.90 μm; diameter - 43.80 μm to 65.70 μm, average diameter - 54.15 μm; lateral wall thickening spiral-scalariform; end walls oblique, plate scalariform, bars inter-connected; number of bars 6-15.

Scape : Vessels absent

Leaf : Vessels absent

**Eurycles sylvestris** (Fig. 4 b, c)

Root : Length - 760.50 μm to 1204.50 μm, average length - 952.65 μm; diameter - 54.75 μm to 65.70 μm, average diameter - 60.22 μm; lateral wall thickening scalariform, bars inter-connected; end walls oblique, plate reticulate, rarely vessels with vertical and oblique bars on end wall plate occur.

Scape : Vessels absent

Leaf : Vessels absent
Lyco|ris radiata (Fig. 4 d, e)

Root : Length - 1445.90 μm to 2321.40 μm, average length - 1784.85 μm; diameter - 65.70 μm to 87.60 μm, average diameter - 76.65 μm; lateral wall thickening scalariform with the bars interconnected; end walls oblique, plate scalariform; number of bars 10-20.

Scape : Vessels absent

Leaf : Vessels absent

Curculigo orchioides (Fig. 4 f)

Root : Length - 1971.00 μm to 3723.00 μm, average length - 3076.95 μm; diameter - 43.80 μm to 54.75 μm, average diameter - 48.12 μm; lateral wall thickening scalariform-reticulate; end walls very oblique, perforation plate scalariform, number of bars 60-70.

Leaf : Vessels absent
<table>
<thead>
<tr>
<th>S.No.</th>
<th>Name of the plant</th>
<th>Length of the vessel (μm)</th>
<th>Diameter of the vessel (μm)</th>
<th>Lateral wall thickening</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Minimum</td>
<td>Maximum</td>
<td>Average</td>
</tr>
<tr>
<td>1</td>
<td><em>Leucocrum versum</em></td>
<td>1423.50</td>
<td>2409.00</td>
<td>1805.75</td>
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<td>2</td>
<td><em>Amurcule regale</em></td>
<td>1314.00</td>
<td>2682.75</td>
<td>1817.70</td>
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<td>1040.25</td>
<td>1971.00</td>
<td>1511.10</td>
</tr>
<tr>
<td>4</td>
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<td>2596.50</td>
<td>4818.00</td>
<td>3688.25</td>
</tr>
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<td>5</td>
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<td>2562.40</td>
<td>2003.05</td>
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<tr>
<td>6</td>
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<td>985.50</td>
<td>1971.00</td>
<td>1478.25</td>
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<td>7</td>
<td><em>Zephyranthes texana</em></td>
<td>810.30</td>
<td>1752.00</td>
<td>1401.60</td>
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<td>8</td>
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<td>2847.00</td>
<td>2343.30</td>
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<td>2135.25</td>
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<tr>
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<td>16</td>
<td><em>Calyclic ariboles</em></td>
<td>1971.00</td>
<td>3723.00</td>
<td>3076.95</td>
</tr>
</tbody>
</table>

Table 1. Late metaxyle vessels in the root of Amaryllidaceae and Hypoxidaceae
Fig. 1. Late metaxylem vessel elements in root:

a, b - *Leucojum vernum*;  c, d, e - *Amaryllis reginae*;
f, g - *Amaryllis vittata*. 
Fig. 2. Late metaxylem vessel elements in root:

a, b - *Crinum latifolium*;  c - *Crinum pratense*;
d, e - *Zephyranthes grandiflora*;
f, g - *Zephyranthes texana*. 
Fig. 3. Late metaxylem vessel elements in root:

a - *Haemanthus multiflorus*;  b, c, d - *Clivia miniata*;

e, f - *Pancratium verucundum*;

*g, h, i - Hymenocallis speciosa*;

*j, k - Hymenocallis tenuiflora.*
FIG. 3
Fig. 4. Late metaxylem vessel elements in root:

a - Eucharis grandiflora;  b, c - Eurycles sylvestris;  d, e - Lycoris radiata;

f - Curculigo orchioides.
VESSELS IN LATE METAXYLEM

DISCUSSION
The vessels occur only in the roots and are absent from the rest of the organs of the plant in all the species studied. In addition, the vessels in the roots do not show a high degree of specialization. They are of the least length in *Eurycles* (760.50 µm). Generally, the vessels in this genus are comparatively the shortest amongst all the genera studied. Both the species of *Zephyranthes* have the vessels of a little greater length (810.30 µm and 985.50 µm). However, species of the same genus show a great disparity in vessel length, e.g., *Crinum*, *Amaryllis* and *Hymenocallis*. It is more marked with respect to the species of *Crinum*. *Crinum latifolium* has the metaxylem vessel length nearly double to that of *Crinum pratense*. The rest of the plants fall in between these two ranges.

That the longer vessels are generally narrower is not always true with respect to the species studied, for, *Crinum latifolium* which has the maximum length of the vessel (4818.00 µm) also has it very broad (109.50 µm). The shorter vessels of *Eurycles* are rather very narrow. This would testify that the increase in width of the vessel does not go hand in hand with the decrease in length of the vessel. On an average, a third of the species have very narrow vessels (65.75 µm), while the highest diameter is noted in *Hymenocallis tenuiflora* (143.35 µm).
The vessels have mostly multiperforate end wall plates. A monoperforate condition is not observed in any of the plants studied. The plates are mostly oblique except in both the species of *Zephyranthes* and *Hymenocallis*. Even then species of both the genera show one endwall with transverse plate and other with a slightly oblique one. Very oblique plates are noted in at least fifty percent of genera studied (*Haemanthus, Clivia, Pancretium, Eucharis, Euryales, Lycoris, Curculigo*). The number of bars is a maximum of 35 in amaryllid taxa, while it is up to even 70 in *Curculigo*. However, majority of the plants have fewer bars. Furthermore, the number of bars in different vessels in the same species varies widely e.g., *Haemanthus*, which has some with as few as 8 bars and others with as many as 35. The reduction in the number of bars is accompanied by the development of reticulation especially in *Hymenocallis, Leucojum* and *Zephyranthes*. It is worthy of note that when the plate is reticulate the end walls are either transverse or slightly oblique.

Observations on the vessels would indicate that the evolution of decrease in plate length and number of bars is not synchronous with a decrease in length or increase in diameter. Development of reticulate plate has proceeded quite early as is shown by *Euryales*. This plant which has the vessels which are rather narrow has the endwalls very
oblique but the plate is reticulate. *Zephyranthes* which has rather medium-sized vessels which are also rather narrow, has transverse plates. It is *Crinum latifolium* which has the longest vessels that are rather broad but have very oblique plates with a large number of bars. These examples are noted to bring home the point that the vessel evolution with respect to the length, the diameter, the type of plate etc. has not been synchronous.

The lateral wall thickening by and large is scalariform or spiral-scalariform. It is only very rarely that the metaxylem vessel has spiral lateral walls e.g., *Leucojum*. There are no vessels where pits are observed. A perusal of the data on lateral wall thickening in the different species further testifies the contention that the development of the lateral wall thickening has not kept pace with the other characters namely length, width and features of the plate. The evolutionary progress with respect to these four characters is at different rates or degrees so that one does not find a single species where all the advanced features are noted or most of them are characteristic.

A perusal of Table 1 indicates that the vessels in Amaryllidaceae are at a very low level of evolution. That they do not occur in any other organ of the plant amongst
the species studied, is also worthy of note. The different genera, while showing variations in level or degree of specialization in a way, do not indicate a single plant which can be picked as the most highly evolved with respect to vessel structure amongst the taxa studied. Inhibitions exist with respect to one or the other characters. All the same, amongst the sixteen species of the present account *Eurycles* appears to have comparatively more evolved vessels.

It may also be noted that vessel structure does not support Hutchinson's placement of the tribes early or later in his treatment of the Amaryllidaceae. *Crinum* treated later under the tribe Crineae shows very long vessels whereas *Leucojum* treated under the first tribe Galantheae has them comparatively shorter in length.

The present observations on vessel structure mostly conform with those of Cheadle (1969). According to him, the vessels in the Amaryllidaceae are to be found in the root system alone. The vessels in the Tecophilaeaceae and the Hypoxidaceae are as primitive as those in the Amaryllidaceae (cf. Cheadle, 1969; the present account). In the material of *Alstroemeria* there was none with roots. Hence, no observations could be made. The stem of the species has no vessels; none in the leaf as well.
A comparison of the vessel structure in the presumed putative allies of the Amaryllidaceae may be attempted here. Bessey (1915), Wettstein (1935) and Engler and Diels (1936) believe that the amaryllids evolved out of liliaceous ancestors and are the progenitors of the more advanced family, the Iridaceae. Hutchinson (1973), on the other hand, emphasizes that the amaryllids and the irids are parallelly derived from the liliaceous ancestors. While Cheadle's exhaustive studies on the three families have led him to arrive at certain conclusions of considerable phylogenetic significance, the above views have somehow escaped his attention. His papers make no comment in regard to them.

The Liliaceae present a mixed picture of evolutionary specialization of vessels amongst the many tribes of the family. In some tribes, e.g., Dianelleae, Asparageae, Asphodeleae, Convallarieae etc. not only the vessels are of a specialized type with simple plates in the root, but they occur in the stem and even in the leaf. However, in the latter two organs, the vessels are with multiperforate plates. These are the tribes which contemporary phylogenists like Takhtajan (1980) and Dahlgren and Rasmussen (1983) separate out from the family and elevate to the rank of families. It is interesting to note that there do exist a number of tribes in the lilies with the
level of specialization of the vessels of the same order as or lower than that of the amaryllids.

In the Iridaceae, the vessels in most genera are more or less at the same level of specialization as the amaryllids and only rarely do they extend into the stem and the leaf, e.g., *Sisyrinchium* (Cheadle, 1963).

This leads one to venture that from the primitive liliaceous or the so called "proto-liliaceous" stocks, the Amaryllidaceae and the Iridaceae have evolved parallely testifying the contention of Hutchinson (1973). Probably, the stocks were with very primitive vessels or possibly none at all, and the vessel evolution in both these derivative groups has remained at more or less the same level with an exception of *Sisyrinchium* of the Iridaceae. If the irids were derivative from the amaryllids, the vessel structure should have been of a comparatively higher order. In fact, the state of the vessel structure precludes an amaryllid origin for the irids.

The above resume, would lead one to surmise that probably the lilies are a more heterogeneous assemblage of taxa. Contemporary taxonomists do subscribe to this view and separate traditional lily tribes into distinct families as related earlier. In these, vessel development has
advanced into the stem and into the leaf. One may as well infer that the lilies, amaryllids and the irids are collateral parallel developments from the protoliliaceous stocks. It is particularly interesting to note that in the sharply circumscribed lilies, the amaryllids and the irids, vessel structure and evolution is rather synchronous with occasional or rare variants or exceptions which one should expect. Thus, there is greater truth in the Hutchinson's view or the further modified one put forth here in regard to the affinities of the three major liliifloral families. It must be reiterated that the view of Engler and Diels, Bessey and Wettstein stands negated in the light of vessel evolution.

Another point that emerges from the study on vessels is in regard to the rather controversial position of the tribes Agapantheae, Allieae and Gilliesieae. It may be recalled that Hutchinson transfers these three tribes to the Amaryllidaceae holding the fundamental character of the inflorescence as more important than the position of the ovary in taxonomic alignments. The three tribes have an umbellate inflorescence as the traditional amaryllids but have a superior ovary as against the inferior one in the latter.
The vessels in the three tribes are far more advanced than the amaryllids precluding, nay even negating their transfer to the amaryllids. There exist several other features that not only militate the transfer of these tribes to the amaryllids and their retention within that family, but emphasize that they are best treated in two or even three independent taxa of the order of family (cf. Takhtajan, 1980; Dahlgren and Rasmussen, 1983). Traub (1975) erects an order Alliales for the allium group.