Floral vasculature and trichomes of common Indian
Scrophulariaceae

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Abstract

The floral anatomy of 24 species of Scrophulariaceae was studied. The results show that although, clear anatomical bases to differentiate taxa are absent, the P en nell classification of subfamilies is strongly supported.

INTRODUCTION

Bentham and Hooker (1873) classified the family Scrophulariaceae into three series, Pseudosolaneae, Antirrhinideae and Rhinantheideae. Wettstein's classification (1897) retained the same major groups (subfamilies Pseudosolaneae, Antirrhinideae and Rhinantheideae). But P en nell (1935) drops the group Pseudosolaneae. The outstanding differences between these three exhaustive treatments are in the positions and delimitations of tribes under the subfamilies. Major groups in these classifications, given below, provide idea of the basic differences.

\begin{tabular}{|c|c|c|}
\hline
\textbf{Bentham & Hooker} & \textbf{Wettstein} & \textbf{P en nell} \\
(1873) & (1897) & (1935) \\
\hline
\textbf{A. Pseudosolaneae} & \textbf{A. Pseudosolaneae} & \textbf{A. Antirrhinoideae} \\
Leucophylleae & Verbasceae & Gratioleae \\
Aptosimeae & Aptosimeae & Verbasceae \\
Verbasceae & & Leucophylleae \\
\hline
\textbf{B. Antirrhinideae} & & \\
Calceolarieae & Hemimerideae & Cheloneae \\
\hline
\textbf{H. Hemimerideae} & & \\
Antirrhineae & Calceolarieae & Collinsieae \\
Cheloneae & Antirrhineae & Antirrhineae \\
Manuleieae & Cheloneae & \\
Gratioleae & Manuleae & \\
\hline
\textbf{C. Rhinantheideae} & & \\
Digitaleae & Gratioleae & Digitalear \\
Gerardieae & Selagineae & Veronicae \\
Euphrasieae & & Buchnerae \\
\hline
\end{tabular}
Hence is the present attempt to examine the controversies on the basis of vascular traces of flowers, utility of which has been emphasised by different authors (Fisher, 1928; Bancroft, 1935; Mathews, 1941; Just, 1952; Puri, 1951; Eames, 1953, 1961).

Floral anatomy of discrete genera of the family has been studied (Sopobia and Vandellia by Krishna Iyengar, 1937, 1940 a, b; Scoparia by Raghavan and Srinivasan, 1941; Bacopa by Safeesulla and Govinda, 1950; Veronica by Saunders, 1934; Angelonia and Striga by Srinivasan (V. K.), 1940; Srinivasan (A. R.), 1964; Hartl, 1956, etc.). The present investigation is for comparison between different genera and species.

**MATERIAL AND METHODS**

24 species mentioned below (arranged according to Wettstein, 1897) are included in the present study. Plants were mostly collected from Calcutta and its suburbs and some from the herbarium of Calcutta University and from Botanical Survey of India (Western and Eastern Circles). All specimens were compared with those of the Herbaria of Calcutta University and Botanical Survey of India at Shibpur (Calcutta) for identification. Nomenclatures were corrected by consulting Raizada (1958) and Pennell (1935).

Flower buds, two to three days before anthesis, were fixed in formalin-propionic acid-alcohol (Johansen, 1940), washed, dehydrated and

<table>
<thead>
<tr>
<th>Species</th>
<th>Collector, source</th>
<th>Locality</th>
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<tbody>
<tr>
<td>A. Sub-family Pseudosolaneae</td>
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<td></td>
</tr>
<tr>
<td>1. Tribe Verbascaceae</td>
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<td></td>
</tr>
<tr>
<td>1) Verbascum virgatum Stokes</td>
<td>Agharkar, S.N.; C.U.</td>
<td>Calcutta</td>
</tr>
<tr>
<td>B. Sub-family Antirrhinoaee</td>
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<td></td>
</tr>
<tr>
<td>1. Tribe Hemimeridea</td>
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<td></td>
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<tr>
<td>1) Angelonia grandiflora C. Morr.</td>
<td>Serop 18(10); C.U.</td>
<td>Unknown</td>
</tr>
<tr>
<td>2. Tribe Calceolarieae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Calceolaria mexicana Benth.</td>
<td>Dep Serop 2; C.U.</td>
<td>Darjeeling (W. Bengal)</td>
</tr>
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<td>III. Tribe Antirrhinoaee</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Linaria bipartita Willd.</td>
<td>Banerjee, S.N.; C.U.</td>
<td>Calcutta</td>
</tr>
<tr>
<td>2) Antirrhinum majus L.</td>
<td>Deb Scorp 3; C.U.</td>
<td>Calcutta</td>
</tr>
<tr>
<td>IV. Tribe Cheiloneae</td>
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</tr>
<tr>
<td>2) Wightia speciosissima (D. Don) Merr. =Wightia gigantea Wall.</td>
<td>Deb Scorp 5; C.U.</td>
<td>Punjab</td>
</tr>
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<td>6. V. Tribe Manuleae</td>
<td></td>
<td></td>
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<tr>
<td>1) Sutiera glandulosa Roth.</td>
<td>Deb Scorp 6; C.U. (B.S.I.)</td>
<td>Poona</td>
</tr>
</tbody>
</table>
Floral vasculature of *Scrophulariaceae*

VI. Tribe *Grateoleae*

1) *Mazus japonicus* (Thumb.) Kuntze  
   = *Mazus rugosus* Loure.  
2) *Lindenbergia indica* (L.) Kuntze  
   = *Lindenbergia urticaefolia* Lehm.  
3) *Broma monoica* (L.) Pennell  
   = *Bacopa monoica* (L.) Wettst.  
   = *Herpestis monoica* (L.) H.B. & K.  
4) *Pagesia dianthera* (Swartz) Pennell  
   = *Herpestis chamaedroides* H.B. & K.  
5) *Torentia fournieri* Linden  
6) *To rentia vagans* Roxb.  
7) *Lindernia crustacea* (L.) Mueller  
   = *Vandella crustacea* (L.) Benth.  
8) *Lindernia ciliata* (Colsm.) Pennell  
   = *Bonnaya brachiata* Link & Otto  
9) *Lindernia multiflora* (Roxb.) Mukherjee  
   = *Vandella multiflora* D. Don. Gen.

C. Sub-family *Rhinanthoideae*

I. Tribe *Digitaleae*

1) *Scoparia dalcis* L.  
2) *Veronica himalensis* D. Don. Prod.  
3) *Digitalis purpurea* L.

II. Tribe *Gerardieae*

1) *Alectra arvensis* (Benth.) Merrill  
   = *Alectra indica* Benth.  
2) *Centranthera nepalenis* D. Don  
   = *Centranthera hispida* Hk. f. non R. Br  
3) *Striga gesneroides* (Willd.) Watke  
   = *Striga oromanchoides* (R. Br.) Benth.

III. Tribe *Rhinanthae*

1) *Pedicularis furfuracea* Wall. Cat.  

Collector, source  |  Locality  
--- | ---  
Deb Scrop 7; C.U.  |  Calcutta  
Dep Scrop 9; C.U.  |  Garia (W. Bengal)  
Dep Scrop 10; C.U.  |  Garia (W. Bengal)  
Dep Scrop 11; C.U.  |  Ballygunje (Calcutta)  
Dep Scrop 12; C.U.  |  Ballygunje (Calcutta)  
Dep Scrop 13; C.U.  |  Ballygunje (Calcutta)  
Dep Scrop 14; C.U.  |  Ballygunje (Calcutta)  
Dep Scrop 15; C.U.  |  Ballygunje (Calcutta)  
Deb Scrop 16; C.U.  |  Ballygunj (Calcutta)  
Agharkar, S.N.; C.U.  |  Mussoori  
Deb Scrop 17; C.U.  |  Darjeeling (W. Bengal)  
Ghosh, S.N.; C.U.  |  Assam Hill  
Campell 9867; C.U.; C.U.  |  Manbhum (W. Bengal)  
Khan, S.N.; C.U.  |  Mysore  
Agharkar, S.N.; C.U.  |  Cholam  

embedded in paraffin in usual procedures. Paraffin blocks were microtomed at 15 µ thickness, and serial sections (T. S. & L. S.) were dewaxed, stained with crystal violet, dehydrated and mounted in Canada balsam. Dry old specimens were swelled by boiling in water, cleared in equal proportion of ammonium hydroxide and hydrogen peroxide (conc.) for 24 hours, washed in running water for an hour and then treated as a fresh material.

The specimens have been cited according to procedure recommended by Stern and Chamber (1960).
The family generally possesses centripetal inflorescence (centrifugal in Cheloneae), sometimes compound or with solitary flowers. Bracteoles are generally two. Ebracteolate genera are Angelonia, Linaria, Antirrhinum, Sutera, Mazus, Lindenbergia, Torenia, Lindernia, Scoparia, Veronica, Pedicularis, etc.

Sepals are always connate, generally numbering five. Calyx is generally 5-partite or deeply 5-lobed (campanulate in Mazus, Lindenbergia, Alectra; campanulate and 3–4 lobed in Wightia; 4-partite in Scoparia and Calceolaria, 2-lipped in Torenia), imbricate or quincuncial. In the species having five sepals, the position of the external sepal lobe or lobes is anterior in Verbasum, Angelonia, Antirrhinum, Russelia, Lindenbergia, Lindernia, Centranthera, while it is posterior in Linaria, Wightia, Mazus, Pagesia, Brama, Horenia, Veronica, Digitalis, Alectra and Striga. Corolla is generally tubular, excepting Angelonia. It is rotate in Verbasum, Scoparia and Veronica, campanulate in Alectra and Brama, and declined in Digitalis. Tubes are generally slenderly cylindrical, spurred in Linaria, saccate in Antirrhinum, incurved in Russelia and Centranthera, narrow at base having nectar glands in Pedicularis, short in Mazus. Stamens are generally four in number, included and didynamous. The number is five in Verbasum, two in Veronica (posterior-lateral pair, and Calceolaria (lateral pair). Filaments are distinctly short in Angelonia, exerted in Wightia and Veronica. Stigma is minute (Linaria, Russelia, Calceolaria), capitate (Verbasum, Lindenbergia), subcapitate (Veronica), 2-lobed (Antirrhinum, Sutera, Brama, etc.), 2-lamellate (Mazus, Torenia, Lindernia, etc.), distinct (Pedicularis, Digitalis, and many species of Gasteoleae), truncated (Scoparia), linguiformis (Centranthera, Alectra), entire (Striga, Pagesia), or dilated (Wightia).

Although the vascular anatomy of flowers of Scrophulariaceae follows a common plan, distinguishable characters are also available in many species and genera. Sepals are supplied by sepal-midrib traces and sepal-lateral commisural strands. A sepal-midrib trace generally forms a cord with a stamen trace. A petal-midrib trace forms a cord with a sepal-lateral commisural strand. The number of stamen traces varies from five to four, of which one or two are often vestigial. Number of disc traces, if present, is variable. Minor variations are noticed in the ovarian traces.

Receptacle

The receptacular vascular bundles generally form a continuous cylinder, circular in transection, with external phloem and internal endarch xylem. In Calceolaria mexicana, six to seven discrete bundles form a cir-
Figs. 1—11. Camera lucida drawings of transections of flower buds showing vascular traces. 1. Verbascum virgatum; 2 & 3. Calceolaria mexicana showing two vestigial stamen traces; 4 & 5. Linaria bipartita showing one vestigial stamen trace; 6 & 7. Majus japonicus; 8—10. Lindenbergia indica; 11. Paeonia dianthera. (B. S. T. — bent end of store; D — disc trace; DT — dorsal trace of carpel; OV. W. — ovary wall trace; P — petal midrib; PSLCL — petal + sepal lateral + carpel lateral cord; SB — sepal bundle; SL — sepal lateral trace; SLCT — sepal lateral commissural strand; SM — sepal midrib; SS — sepal stamen cord; SSDCC — sepal + stamen + dorsal carpel trace cord; SSVC — sepal + stamen + ventral carpel trace cord; ST — stamen trace; VC — ventral commissural trace of carpels; VST — vestigial stamen trace)
Fig. 23. Graphical representation of different floral traces of the 1st 12 species, drawn according to relative lengths and distances. The distance between the origin of the lowest perianth traces and the orientation of ovarian traces has been divided into 100 parts. Taking this distance as equal to 100 divisions, the other distances (e.g. of internodes, levels of branching, levels of fusion, etc.) have been calculated.
Fig. 24. Graphic representation of different floral traces of the next lot of 12 species, drawn according to relative lengths and distances, as in Fig. 23
cular ring. In *Mazus japonicus* the cylinder is divided into two arches below. In *Lindernia multiflora*, the 5-angled pedicel contains four bundles which gradually coalesce into a cylinder, circular in transection.

**Bracteoles**

Each member receives a single trace. In *Verbascum virgatum*, the two bracteole traces originate fused with two sepal-midrib traces and diverge into the bracteolar protrusions. In *Brama monnierii* two traces come out from two corners of a triangular and continuous vascular cylinder of a triangular pedicel and supply the two bracteoles. In *Alectra arvensis* the single bracteolar trace branches immediately into four to five bundles. They arise markedly below the perianth of *Centranthera nepalensis* and branch immediately. In *Striga gesneroides*, they arise slightly below the perianth.

**Calyx**

(a) Species without fusion of sepal-main and stamen traces:

The connate calyx (in most of the genera) or almost free sepals (in *Angelonia grandiflora*) are supplied altogether by 10 bundles, five sepal-main (or sepal-midrib) bundles and five sepal (commisural) + petal cords alternating them. These cords (absent in *Wightia speciosissima*) bifurcate radially into the outer commisural strand and the inner petal-midrib bundle. The commisural strands bifurcate tangentially to supply the adjacent sepals as sepal-laterals. This condition is common in *Verbascum virgatum* (Verbasceae), *Angelonia grandiflora* (Hemimerideae), *Russelia equisetiformia* and *Wightia speciosissima* (Cheloneae), *Brama monnierii* and *Pagesia dianthera* (Gratioleae), and almost all members of *Rhinanthoideae* (Scoparia dulcis, *Veronica himalensis*, *Digitalis purpurea*, *Centranthera nepalensis*, *Striga gesneroides* and *Pedicularis furfuracea* (Figs. 22, 23 & 24).

(b) Species with sepal-main + stamen cord:

In most of the remaining species examined (*Linaria bipartita* and *Antirrhinum majus* of Antirrhineae; *Sutera glandulosa* of *Manuelae*; *Mazus japonicus*, *Lindenbergia indica*, *Torenia fournieri*, *T. vagans*, *Lindernia crustacea*, *L. ciliata* and *L. multiflora* of Gratioleae; *Alectra arvensis* of Gerardieae), sepal-midrib bundles are fused below with five stamen bundles (sepal-midrib + stamen cord).
An extreme type of adhesion is noticed in *Calceolaria mexicana* (Calceolarieae) where eight cords (two formed by adhesion bundles of sepal-main and stamen with the commisural bundles of ventral traces of a carpel, two formed by adhesion of bundles of sepal-main and stamen with dorsal carpellary traces and four formed by petal-midrib with sepal-lateral commisural strand and carpel-lateral traces) arise first. They divide to produce inner eight carpellary bundles and outer four sepal-main + stamen cords and four sepal-lateral + petal-midrib cords (Figs. 2, 8, 9, 23 & 24).

The number of such basal bundles varies according to species. It is 10 in *Verbascum*, *Angelonia*, *Linaria*, *Antirrhinum*, *Russelia*, *Wightia*, *Sutera*, *Brama*, *Pagesia*, *Torenia*, *Lindernia*, *Digitalis*, *Alectra*, *Centranthera*, *Striga* and *Pedicularis*; eight in *Calceolaria*, *Scoparia* and *Veronica*. The proportional lengths of the adhesion cords and sepal-lateral commisural strands have been given in Figs. 23 & 24.

The level of branching of sepal-midrib traces varies in different species. It is highest in *Scoparia dulcis* and lowest in *Verbascum virgatum* (Figs. 23 & 24) while in the different species of *Torenia* and *Lindernia* and in *Striga gesneroides*, the midrib bundle is unbranched (Fig. 24).

The height of the sepal-lateral commisural strand also differs, highest in *Alectra arvensis*, lowest in *Wightia speciosissima*, absent in *Russelia equisetiformis*, *Sutera glandulosa* and *Digitalis purpurea* (Figs. 23 & 24).

### Corolla

Petals and stamens form a single tube. A petal is supplied by a single trace (petal-midrib trace) which generally arise fused with the sepal-lateral commisural strand. The height of such a cord varies according to species, highest in *Lindenbergia indica* and lowest in *Pagesia dianthera*, absent in *Wightia speciosissima* (Figs. 23 & 24). In *Calceolaria mexicana* the petal-midrib bundles form cords with sepal-lateral commisural strands and carpel-lateral bundles (Fig. 2). The number of petal-midrib traces (or their adhesion cords) varies according to species, five in *Verbascum virgatum* (Fig. 1), *Angelonia grandiflora*, *Linaria bipartita*, *Antirrhinum majus*, *Russelia equisetiformis*, *Wightia speciosissima*, *Sutera glandulosa*, *Brama monnierii*, *Pagesia dianthera*, *Torenia* species (Figs. 15 & 18), *Lindernia* species, *Digitalis purpurea*, *Alectra arvensis*, *Centranthera nepalensis*, *Striga gesneroides* and *Pedicularis furfuracea*, while four in *Calceolaria mexicana*, *Scoparia dulcis* and *Veronica himalensis*. The level of branching of petal traces varies according to species, highest in *Alectra arvensis* and lowest in *Linaria bipartita* (Figs. 23 & 24). The lowest lateral branches of each petal midrib trace act as lateral traces. The midrib traces branch out further in the lobes.
Androecium

The corolla tube receives traces for stamens, alternating with the petal-midrib traces. Stamen traces arise independent of sepal traces in Verbascum virgatum, Angelonia grandiflora, Russelia equisetiformis, Wightia speciosissima, Brama monnieri, Pagesia dianthera, Scoparia dulcis, Veronica himalensis, Digitalis purpurea, Centranthera nepalensis, Striga gesneroides and Pedicularis furfuracea. In these species, the distance between traces for sepals and stamens, relative to the length of axis, is longest in Russelia equisetiformis and shortest in Centranthera nepalensis. In Calceolaria mexicana the stamen traces form fusion bundles (cords) with sepal and carpel traces. In the remaining species, the stamen traces form cords with the sepal-midrib traces. The relative length of the cord is highest in Torenia vagans and Sutera glandulosa and lowest in Antirrhinum majus (Figs. 23 & 24). One vestigial stamen trace is common in the family (absent in Verbascum virgatum having five fertile stamens and in Scoparia dulcis having four fertile stamens). Two vestigial stamens are found in Calceolaria mexicana and Veronica himalensis. Lengths of vestigial stamen traces (relative to axes) vary according to species, longest being in Lindernia crustacea (Figs. 23 & 24). The position of the vestigial stamen trace, where present, is always against the external calyx-lobe, regardless of anterior or posterior position of the latter.

On the basis of stamen traces, the species may be classified into the following four categories:

(a) Species with five fertile stamens:

Verbascum virgatum has five functional stamens (as reported by Fernald, 1950) and five distinct stamen traces having no adhesion with traces of other whorls. Each bold stamen trace bifurcates, one branch remaining in the corolla-stamen tube and discontinuing immediately and the other branch supplying the sessile connectives. The latter divides again in the connective to supply the two anther-lobes (Fig. 1).

(b) Species with four fertile stamens and one staminode:

Species including Angelonia grandiflora, Antirrhinum majus, Wightia speciosissima, Russelia equisetiformis, Digitalis purpurea (Fig. 20), Alectra arvensis, though have four functional stamens, possess five traces for stamens. The fate of the trace for staminode differs according to species. In Russelia equisetiformis, it is quite long continuing upto the level of anther base of fertile stamens. In Wightia speciosissima and Angelonia
grandiflora, it is comparatively short, and discontinue much below the level of separation of normal filaments from the corolla tube. In Alectra arvensis it continues up to the level of anther lobes and Antirrhinum majus it is extremely short. Arber (1932) states that in Digitalis purpurea the fifth stamen is represented by a small ephemeral protrusion without a vascular strand. The present study reveals a clear vestigial strand. The present study reveals a clear vestigial stamen trace in the corolla tube but not in the protrusion. In Angelonia grandiflora, Wightia speciosissima and Russelia equisetiformis it is distinct from the sepal midrib trace, while in Antirrhinum majus and Alectra arvensis, it forms an adhesion bundle with the sepal-midrib trace. In all these species the staminode trace gradually becomes narrow in the staminode, and does not produce any branch.

(c) Species with four fertile stamens without clear staminode:

Species, including Linaria bipartita (Fig. 5), Sutera glandulosa, Mazus japonicus (Figs. 6 & 7), Lindenbergia indica (Fig. 10), Brama monnieri, Pagesia dianthera (Fig. 12), Torenia fournieri (Fig. 17), T. vagans (Fig. 19), Lindernia crustacea, L. ciliata, L. multiflora, Centranthera nepalensis, Striga gesneroides, Pedicularis furfuracea (Fig. 22), have four functional stamens, but five stamen traces. The fifth (vestigial) stamen trace becomes narrow at the end and discontinues. In Scoparia dulcis, the fifth trace is absent. Sepal + stamen cord is absent in Brama monnieri, Pagesia dianthera, Centranthera nepalensis, Striga gesneroides, Pedicularis furfuracea and Scoparia dulcis. In other species of this group the stamen trace arises jointly with the sepal midrib trace. Relative lengths of the sepal stamen cords and vestigial stamen traces (where present) varies according to species (Figs. 23 & 24).

(d) Species with two functional stamens:

Veronica himalensis and Calceolaria mexicana are the two species where only two fertile stamens are observed. In the former, a posterio-lateral pair and in the latter (Fig. 3), the lateral pair are developed into normal stamens. In Calceolaria mexicana, four stamen traces remain fused below with sepal-midrib traces, of which two remain fused with the dorsal carpellary traces and two with the two ventral commisural traces of carpels. The carpellary traces are separated above from the sepal-stamen cords. In Veronica the four stamen traces originate free from adhesion. In both the species two or the four stamen traces are vestigial.
Disc

Disc is present in *Verbascum virgatum*, *Russelia equisetiformis*, *Lindenbergia indica*, *Brama monnierii*, *Pagesia dianthera*, *Torenia fournieri*, *T. vagans*, *Lindernia crustacea*, *L. ciliata*, *L. multiflora*, *Veronica himalensis*, *Digitalis purpurea*. It is absent in other species studied here. The number of disc traces varies according to species. It is 10—12 in *Verbascum virgatum*, indefinite in *Russelia equisetiformis*, 8—10 in *Lindenbergia indica*, 4—5 in *Brama monnierii*, ± 16 in *Pagesia dianthera*, 12—16 in *Torenia species*, 12—16 in *Lindernia crustacea* and *L. ciliata*, 8 in *L. multiflora*; 3—4 in *Digitalis purpurea*, 4—5 in *Veronica himalensis*. In *Verbascum virgatum* and *Russelia equisetiformis*, the disc traces originate directly from the stele, below the organization of carpellary traces. In *Lindernia species*, *Brama monnierii*, *Pagesia dianthera*, *Torenia species* and *Lindenbergia indica*, the traces for disc and carpel originate at the same level from the stele. Traces for disc and ovary arise fused in *Veronica himalensis* and *Digitalis purpurea*. Height of disc traces, relative to length of axis, varies according to species (Figs. 23 & 24).

Gynaeecium

Generally, after departure of the staminal traces, vascular tissue of the axial stele organizes into four broad bundles (two dorsal bundle-complexes, here mentioned as dorsal trace and two ventral complexes formed by fusion of two ventral bundles of adjacent carpels, placento-parietal bundles of R a o, 1953, but here mentioned as commisural ventral strands) and four narrow lateral bundles.

The patterns of vascular orientation encountered in the present study are of the following categories:

1. Species with eight basal traces: two commisural ventral strands enter the septum producing minor peripheral branches

In *Mazus japonicus* and *Lindenbergia indica* of *Grateoleae*, eight parietal bundles (two commisural ventral, two dorsal and four lateral) are found. The amphicribral commisural ventral strands are typical placento-parietal bundles, producing peripheral branches supplying ovary wall and enter the septum to supply the ovules. The number of bundles in the middle part of the ovary wall is ± 10 in *M. japonicus* (Fig. 7) and 28—30 in *L. indica*. 
ovary wall. This central cylinder divides into two arches towards the
placentae of two chambers. The hollow style is supplied by two dorsal
traces.

Both Veronica himalensis and Scoparia dulcis, highly reduced in other
characters, have a single branch produced from one commisural ventral
strand. Both the species have eight peripheral bundles at the base. S.
dulcis has a hollow style supplied by two dorsal traces, which fuse in
the upper solid part. Henslow (1891) also mentions of a single trace
entering the septum of V. spicata.

Under Gerardiaeae, Alectra arvensis, Centranthera nepalensis and Stri
ga gesneroides have a similar plan of eight peripheral bundles and a sin
gle branch supplying the septum. In A. arvensis the wall bundles become
branched into ± 16 bundles, in C. nepalensis 10—12 bundles and in S.
gesneroides ± 16 bundles. The style of A. arvensis is solid, having a loose
transmission tissue without any vascular trace. The styles of C. nepalen
sis and S. gesneroides are hollow, supplied by four traces.

5. Species with four basal bundles: one of the commisural ventral bundles
producing a septal branch

Pedicularis furfuracea (Rhinantheae) has two dorsal and two com
misural ventral bundles and a single septal trace at base. Lateral traces
are absent. Dorsal traces branch (Fig. 22) at a higher level. The middle
part of the ovary wall contains 26—30 bundles. Each of the commisural
ventral bundles divides into two ventral traces within a short distance.
The hollow style is supplied by two dorsal traces.

Epidermis and trichomes

The epidermis of the pedicel possesses thick cuticle in Verbascum
virgatum, Angelonia grandiflora, Torenia fournieri, Lindernia crustacea,
Scoparia dulcis, Veronica himalensis, Alectra arvensis, Striga gesneroides
and Pedicularis furfuracea.

Attention of all workers on floral anatomy of Scrophulariaceae has
naturally been drawn by the strikingly diverse nature of trichomes. The
trichomes encountered may be classified into the following types (Fig. 25):

A — A group of basal cells, two rows of cells (2—4 in each row) for
ming a supporting stalk and a bunch of elongated terminal glandular
cells.

B — A small basal cell, two supporting cells (lower long, the upper
subterminal small) and elongated terminal glandular cells (as report
Fig. 25. Trichome types of flowers of Scrophulariaceae

C — A small basal cell, 3—5 cells (more or less equal) forming a supporting stalk and four elongated glandular cells arranged in two tiers at the apex.

C₁ — Same as C, but two glandular elongated cells at the tip, instead of four.

D — A small basal cell, one elongated supporting cell and two terminal glandular cells.

E — A small thick-walled basal cell, a row of thick-walled cells forming a stalk and three to four terminal glandular cells, more or less obovate.

F — A group of basal cells, a small sub-basal cell in the stalk base, a row of 3—5 cells in the supporting stalk, and three to four elongated glandular terminal cells.

G — A basal cell, a supporting stalk of three cells (the lowest and the middle long and equal, the uppermost or subterminal very small) and two elongated glandular cells gradually poducing thick walls.

H — A basal cell, a gradually narrowing supporting stalk of 4—6 cells, and a single terminal glandular cell.

I — A large basal cell, a short stalk of two flattened small cells and a bunch of about four elongated terminal glandular cells.

J — Similar to I, but the lower stalk cell narrow towards base, and the bunch of terminal cells larger (having about 6 elongated glandular cells).
K — A basal cell, a single short supporting cell, and a dome of glandular cells (8—10).

L — A basal cell, and about three glandular cells forming a triangular structure, one of the glandular cells supporting it.

M — A basal cell, a stalk of 4—5 cells, and a glandular dome of 10—12 cells.

N — A group of basal cells and a thick walled pointed large cell.

O — A single thick-walled basal cell and a thick-walled pointed large cell.

P — A single thick-walled basal cell, a stalk of 2—7 thick-walled cells and a thick-walled pointed large terminal cell.

Q — A dendroid type of trichome having all thick-walled cells and pointed terminal cells.

R — A basal cell and a globular cell.

R₁ — A group of globular cells (formed by transformation of some of the epidermal cells) partly embedded in the epidermal cells.

S — A basal cell and a thick rosette of elongated glandular cells directly on the basal cell.


Calyx contains N and H types on the abaxial surface of *V. virgatum*, B, C and A on the adaxial surface of *A. grandiflora*, H on the abaxial surface of *C. mexicana*, F and R₁ common on the abaxial surface and K on the adaxial surface of *A. majus*, D and D₁ on the adaxial surface (near mid-vein) of *R. equisetiformis*, O, P and Q densely distributed on abaxial surface of *W. speciosissima*, D and J on the margin of *Sutera glandulosa*, I on the abaxial surface of *M. rugosus*, P and G on the abaxial surface of *Lindenbergia indica*, S and R on the outer surface of *Pagesia dianthera*, R₁ on the abaxial surface of *T. vagans*, L on both the surfaces *L. crustacea*, S on the adaxial surface of *L. ciliata*, F and S on the inner surface of *L. multiflora*, B and C on both the surfaces of *V. himalensis*, H₁ on abaxial surface of *D. purpurea*, O and P on both the surfaces of *Alectra arvensis*, P, N and E on the abaxial surface of *C. nepalensis*,
R₁ and H on the abaxial surface of *Striga gesneroides*, R₁ on the abaxial surface of *P. furfuracea*. Trichomes are very rare in *Brama monnieri*, *Scoparia dulcis*, and absent in *Linaria bipartita* and *T. fournieri*.

On corolla, B type occurs in *C. mexicana* generally on the folded regions of pouches, mainly on the abaxial surface, F type on the outer surface of *A. majus*, H on the adaxial surface of *R. equisetiformis*, I and R on the abaxial surface of *M. japonicus*, H₂ (unicellular) on the adaxial surface of *Pagesia dianthera* and on the abaxial surface of *T. vagans*, L on the adaxial surface of *Lindernia crustacea*, M on the abaxial surface of *L. ciliata*, a few F and S on the adaxial surface of *L. multiflora*, H₁ on the adaxial surface of *D. purpurea*, B and C on both the surfaces of *Veronica himalensis*, O and P on both the surfaces of the corolla of *Alectra arvensis*, E on the abaxial surface of *C. nepalensis*, H on the outer surface of *Striga gesneroides* and R₁ on the abaxial surface of *P. furfuracea*. Trichomose on corolla surface is almost absent in *V. virgatum*, *A. grandiflora*, *Linaria sp.*, *W. speciosissima*, *S. glandulosa*, *Lindenbergia indica*, *Brama monnieri* and *T. fournieri*.


**DISCUSSION**

Taxonomy of the species:

The sub-family *Pseudosolaneae* of *Bentham and Hooker* (including tribes *Leucophylleae*, *Aptosimeae* and *Verbascaceae*) and of *Wettstein* (including *Verbascaceae* and *Aptosimeae*) was thought to be distinct, primitive and related to *Solanaceae*, for their five stamens, absence of zygomorphy, etc. But *Pennisell* (1935) concludes that these characters
in Scrophulariaceae are all derived, and unrelated to Solanaceae. Hence Pennell drops the “super group” Pseudosolaneae, and places the species under Antirrhinoideae. In the present study, all five staminal traces are noticed in most of the species of the family. Clear zygomorphy is absent in Antirrhinoideae also.

In formulating the new classification, Pennell makes the first cleavage into Antirrhinoideae and Rhinantheoideae, distinguished by the relative positions of corolla lobes, the former having external posterior (upper) lobes overlapping in the bud and the latter having external anterior (lower) lobes overlapping in the bud. The character of external anterior lobes, according to Pennell, tends to be associated with much specialization of flower and specialized habits of root-parasitism. Therefore, of these two groups, Rhinantheoideae is more evolved. For this redefinition of the subfamilies, a few genera of original Rhinantheoideae (e.g. Digitalae) have been transferred to Pennell’s Antirrhinoideae. Similarly some genera of Cheloneae (Antirrhinoideae) have been transferred to Buchneae (Rhinantheoideae). The study of vasculature does not provide any clear basis of distinction of the subfamilies.

Floral vasculature aiding taxonomy:

If one wants to classify species purely on the basis of vascularization pattern, number of stamen traces will appear to him as a good basis. Verbasum virginatum can be distinguished by five stamen traces supplying five fertile anthers. The common type, four fertile and one vestigial traces, is found in all other species studied here, excepting Scoparia dulcis, Veronica himalensis and Calceolaria mexicana, having four stamen traces. Within these three again, Scoparia dulcis has four fertile traces, while the other two have two fertile and two vestigial. Such a classification is no doubt artificial, and is incompatible with the views of all taxonomists. According to Carlquist (1969), presence of vascular bundles should be interpreted as functional structures related to actual physiological activity, not merely as vestiges that do not function but have not yet been lost.

Presence of cords formed by fusion of sepal midrib traces and stamen traces may also appear as a clear character for classification. But this character also is absent in genera of both the subfamilies, e.g. Verbasum, Angelonia, Russelia, Wightia, Brama, Pagesia and Scoparia of Antirrhinoideae (of Pennell); and Veronica, Digitalis, Centranthera, Striga and Pedicularis (of Pennell). Grateoleae, a primitive tribe of Pennell’s Antirrhinoideae, thus, is characterized by both presence and absence of the cord. In the Rhinantheoideae, all tribes, primitive or advanced, have some genera without this cord. This suggests a polyphyletic evolution in
the family, this cord appearing at the ends of the different evolutionary branches and sub-branches.

Similar to adhesion, cohesion of traces, e.g. sepal-lateral commisural trace, is common in this family. This commisural trace is absent in *Russelia equisetiformis*, *Sutera glandulosa* and *Digitalis purpurea*.

Although, for broad classification of the family, clear distinction in vasculature of flowers is absent, characters supporting Pennell’s classification are available. For example the position of *Scoparia dulcis* appears more natural near *Brama* and *Pagesia* of *Antirrhinoideae* (as in Pennell’s), than with *Digitalis* of *Rhamnithoideae* (as in other systems). The reasons are: *Scoparia*, *Brama* and *Pagesia* are characterized by (1) absence of sepal-midrib + stamen trace cord (also in *Digitalis*), (2) short petal-midrib + sepal-lateral cord (also in *Lindernia*), (3) presence of sepal-lateral commisural strands (absent in *Digitalis*), (4) distinct and parallel anther cells, (5) turgid long capsules, (6) external upper corolla lobe, (7) free sepals. *Digitalis* can be distinguished from *Scoparia* by (1) absence of sepal-lateral commisural strands, (2) longer petal-midrib + sepal-lateral cords, (3) external lower corolla lobes, (4) divericate anther cells, (5) long terminal racemes and ovate capsules having septicidal dehiscence. The vascular patterns of carpels of *Scoparia, Digitalis, Torenia*, genera of *Gratiolae* and *Veronica* are of the same plan. But *Digitalis* differs by the presence of 20—24 bundles on the ovary wall, in contrast to eight in others. The position of the vestigial or lost stamen traces is posterior in *Digitalis, Veronica, Scoparia, Torenia, Brama, Pagesia* and *Mazus*, while it is anterior in *Lindenbergia* and *Lindernia* species. Therefore, this trace provides no clue to classification.

The separation of *Digitalis* and *Veronica* under *Digitaleae* and *Veronicaceae* finds justification in (1) the presence of two fertile and two vestigial stamen traces without adhesion in *Veronica*, and four fertile and one vestigial stamen traces without adhesion in *Digitalis*, (2) ovary wall having eight bundles in *Veronica himalensis* and 20—24 in *Digitalis purpurea*; (3) a fusion of two traces in the upper part of style of *Veronica*, a feature absent in *Digitalis*; (4) corolla being declined in *Digitalis*, rotate in *Veronica*; (5) stamens being two posteriolateral, with exerted anthers in *Veronica*, and four included in *Digitalis*; (6) anther lobes being parallel and confluent in *Veronica*, divergent in *Digitalis*, (7) stigma being sub-capitate in *Veronica* and distinct in *Digitalis*.

Placement of *Sutera* (Manuleae of older systems) under *Grateooleae* by Pennell seems more natural. *Sutera glandulosa* has carpellary traces very similar to that of *Brama monnieri*, having eight basal traces, two entering into the septum and discontinuing in the upper ovary. The stamen traces of *S. glandulosa* corresponds perfectly with that of *Linaria, Mazus, Lindernia, Brama, Pagesia, Torenia* and *Lindenbergia* of *Grateooleae*. 

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*Floral vasculature of Scrophulariaceae* 73
Though Pennell has placed *Calceolaria* under *Cheloneae* (near *Russelia* and *Wightia*), on the basis of external morphological characters, vascular supplies of flowers differ markedly; (1) *Calceolaria mexicana* has vestigial traces and two traces for fertile stamens, fused with traces of perianth and carpels, while the species of *Cheloneae* have one sterile and four fertile traces distinct from outer and inner whorls. (2) The eight carpel traces of *C. mexicana* at first arise fused with the staminal and perianth traces, while in *Cheloneae*, the lateral bundles and ventral fusion bundles arise free from adhesion. (3) In *Calceolaria* the septum is primarily supplied by a single trace which divides into two, while in the species of *Cheloneae*, two prominent traces enter the septum, each of which may further divide (as in *Russelia*). (4) Number of traces for sepals and petals are ten and five respectively in *Cheloneae*, while it is eight and four in *Calceolaria*.

Evolutionary status of tribes and subfamilies

From the evolutionary point of view, cohesion, adhesion, reduction or elimination of traces are generally accepted as advanced characters (Eames, 1931, 1953; Manning, 1940; Puri, 1951; Tepfer, 1953 and many other authors). Of course, Carlquist (1969) has pointed out that the directions of evolution does not follow the same plan always. Evolution may accompany freedom and elaboration of traces as well. Correlation of external and anatomical characters may be helpful to get definite clues on evolution.

Pennell's conclusions on phylogeny show that (1) *Rhinanthoideae* are advanced over *Antirrhinoideae* for specialized habits of root parasitism. (2) *Psedosolanae* of previous taxonomists (*Verbasceae* and *Leucophylleae* of Pennell) are not primitive, but derived and more evolved than *Gratiolea* of *Antirrhinoideae*. (3) *Gratiolea*, for their simple inflorescence, opposite leaves, many seeded capsule and reticulate seed coat seem to be most primitive. (4) *Antirrhineae* (tribe) are among the most highly evolved tribe of *Scrophulariaceae* for elaborate zygomorphy of corolla, attended by pouches or spurs for the nectar, the remarkably modified capsule dehiscence and scattered phyllotaxy. (5) *Digitaleae* are primitive and *Euphrasieae* are most advanced among the tribes of *Rhinanthoideae*. This sequence is found in all other classifications also. (6) *Cheloneae* are more advanced than *Verbasceae* and *Gratioleae*.

Following paragraphs representing combinations of characters in groups mentioned above will help in understanding their degree of specialization.

In *Gratioleae* sepal-stamen cord, sepal-petal cord, sepal-lateral commisural traces are common (Table 1). One stamen trace is either
Table 1
Combination of advanced characters showing degree of advancement

<table>
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<tr>
<th>Sep. St. cord present (+)</th>
<th>Sep. Pet. cord well marked (+)</th>
<th>Disc. absent (+) or traces reduced (+)</th>
<th>Per. + St. Carp. Cord. Present</th>
<th>No. of Vest. St. trace (+/trace)</th>
<th>No. of lost St. traces (+/trace)</th>
<th>Vest. trace reduced (+)</th>
<th>D + Ov. traces fused</th>
<th>Perianth trace lost</th>
<th>S. tr. unbranched</th>
<th>Ovary wall traces ± unbranched (not 8-10)</th>
<th>Cohesion of S. L. trac. prominent (+)</th>
<th>Very strong (+)</th>
<th>Total + signs (degree of advancement)</th>
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**GRATEOLEAE**

*Pagesia*  
*Brama*  
*Torenia fournieri*  
*Lindenbergia indica*  
*Lindernia crustacea*  
*Torenia vagans*  
*L. multiflora*  
*L. ciliata*  
*Suteria glandulosa*  
*Scoparia dulcis*  
*Mazus japonicus*  

Floral vasculature of Scrophulariaceae
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vestigial or absent. Vestigial traces show gradation of reduction (Figs. 23 & 24). Disc is generally present, absent in a few species. Perianth traces are branched or unbranched (in sepals). Ovary traces are generally eight, two ventral (commisural), two dorsal and four lateral. Highly branched ovary wall traces are found in Pagesia and Sutera. For the presence of only a single advanced character (one vestigial stamen trace), Pagesia dianthera seems to be the most primitive species. Brama monnieri is slightly advanced for having two such characters (single vestigial stamen trace and unbranched carpel traces). Mazus japonicus appears as the most advanced species for the highest number of advanced characters. Table 1 shows that the species of Grateoleae have a range of one to nine such advanced characters.

Verbascum virgatum is distinct from Grateoleae for the absence of all cords, vestigial or aborting stamen trace, etc. Only two advanced characters (reduced branching of carpel traces and short sepal lateral commissural traces) are present. Angelonia grandiflora (not mentioned by Pennell), placed under Hemimerideae (Antirrhinoideae) of Bentham and Hooker, may be characterized by absence of disc and presence of a highly reduced vestigial stamen trace. Species of Cheloneae show a range of one to twelve plus (+) signs, which may be regarded as indications of degrees of advancement.

The two species of Antirrhineae have fairly large number of advanced characters, but lack in the cohesion of sepal lateral traces. Similarly, another advanced species, Digitalis purpurea, may be distinguished by two primitive features, absence of sepal-stamen cords and sepal-lateral commissural strands. Veronica hisalensis, one of the most advanced species, is without adhesion of sepal and stamen traces. Actually all species of Rhinanthoideae are without cohesion of traces for sepals and stamens.

Figure 26 shows the range of the gradation of suposed advanced characters. This figure shows that the plan of advancement, on the basis of those characters, does not oppose the conclusions of Pennell. Grateoleae appears to be the most primitive tribe, Antirrhineae stands as one of the fairly advanced groups, Rhinanthoideae are more advanced than Antirrhinoideae and Verbascum is not so primitive as is found in the older classifications. Investigation with more species will certainly show a better correlation.

Trends of evolution of floral vasculature

Measurements of unbranched portions of midribs of petals and sepals, petal-sepal cords, sepal-lateral commissural strands, sepal-stamen cords, vestigial stamen traces, height of disc traces in relation to the total height of the floral axis (Table 2). The table also represent gradiations of
advancement based on arbitrary equal divisions of the measurements. Mean of these seven gradations has been calculated (column 10 of Table 2).

For further analysis it will be convenient to concentrate on *Grateoleae*, of which the largest number of species has been studied. Fig. 27 shows that the mean values of advanced characters (Table 2, column 10; shown in A of the Fig.) fit perfectly with the order of arrangement of species of *Grateoleae* in Table 1 on the basis of the number of + signs. But the characters when considered individually (represented as A — mean of total advanced characters, B — height of petal + sepal main bundles, C — sepal lateral commisural trace, D — sepal lateral petal cord, E — vestigial stamen trace, F — sepal stamen cord, G — height of disc), correlation is imperfect. Of course, most of the characters of *Brama monnieri* and *Pagesia dianthera* appear as comparatively less advanced while those of *Mazus, Scoparia, Sutera* and *Lindernia* are generally most evolved. This suggests that the general trends of evolution are of reduction and fusion of traces, though certain species may lag in some of the trends. Thus the family is an array of different trends of evolution involving both reduction and fusion of traces. For example, *Torenia fournieri*, unreduced in most of the characters, has remarkably reduced perianth trace branches. Cohesion of sepals is very short or absent in *Scoparia dulcis* and *Sutera glandulosa*, the two very highly reduced advanced species. Absence of adhesion of traces for sepals and stamens in *Scoparia* is also a contrasting character among all other trends of reduction and fusion.
Table 2

Arbitrary gradations of the heights of different traces, relative to the heights of the floral axis
(Expressed in percentage; height of the axis = 100)

<table>
<thead>
<tr>
<th>Species</th>
<th>Unbranched part of sepal-midrib trace</th>
<th>Unbranched part of petal trace</th>
<th>Sepal lateral + petal cord</th>
<th>Sepal lateral commisural trace</th>
<th>Sepal midrib stamen cord</th>
<th>Vestigial stamen trace</th>
<th>Height of disc</th>
<th>Total of 7 gradations (Col. 2–8)</th>
<th>Mean of 7 gradations</th>
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<tr>
<td><em>Verbascum virgatum</em></td>
<td>1</td>
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<td>1</td>
<td>2</td>
<td>1</td>
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<td>11</td>
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<td>1</td>
<td>2</td>
<td>7</td>
<td>6</td>
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<td>10</td>
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<td>6</td>
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<td>3</td>
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<td>5</td>
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<td>3</td>
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<td>4</td>
<td>7</td>
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<td>4</td>
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<td>3</td>
<td>4</td>
<td>3</td>
<td>7</td>
<td>1</td>
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<td>10</td>
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</tbody>
</table>

Explanation of the Columns:

Column 2: Arbitrary gradation of the length of the unbranched part of the sepal midrib, relative to flower axis. (6) more than 250% or unbranched; (5) 200.1—250%; (4) 150—200%; (3) 100.1—150%; (2) 50.1—100% (1) 0—50%

Column 3: Arbitrary gradation of the length of the unbranched part of petal trace, relative to axis length. (4) 300.1—400%; (3) 200.1—300%; (2) 100.1—200%; (1) 0—100%

Column 4: Gradations of the length of the sepal lateral-petal cord, relative to axis length. (1) Cord absent, (2) Cord very short to 20% of axis; (3) Cord 21—40%; (4) Cord 41—60%; (5) Cord 61—80%

Column 5: Gradations of the length of the sepal lateral commissural trace, relative to axis length. (1) 0—50%; (2) 50.1—100%; (3) 100.1—150%; (4) 150.1—200%; (5) 200.1—250%; (6) 250.1—300%; (7) 300.1—350%

Column 6: Gradation of the sepal midrib-stamen cord length, relative to axis length. (1) no cord, distance between sepal midrib origin and stamen trace origin more than 25% of axis; (2) no cord, distance less than 25%; (3) cord present, length 1—25%; (4) cord length 26—50%; (5) cord length 51—75%; (6) cord length 76—100%

Column 7: Gradation of the vestigial stamen trace length, relative to axis length. (1) All 5 traces present, none vestigial; (2) 1 vest., length 600.1—700%; (3) 1 vest., length 500.1—600%; (4) 1 vest., length 400.1—500%; (5) 1 vest., length 400.1—500%; (6) 1 vest., length 200.1—300%; (7) 1 vest., length 100.1—200%; (8) 1 vest., length 0.1—100% (9) 1 trace absent, no vestigial; (10) 1 trace absent+1 or 2 vestigial.

Column 8: Gradation of the height of disc, relative to axis length. (6) disc absent, (5) 0.1—20%; (4) 20.1—40%; (3) 40.1—60%; (2) 60.1—80%; (1) 80.1—100%

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Fig. 27. *Grateoleae* — histogram showing comparison of degrees of specialization of characters. A — column 10 of Table 2, mean value of all gradations of characters; B — total of gradations of the length of unbranched portions of sepal- and petal- main-traces, i.e. total of columns 2 and 3 of Table 2; C — length gradation of sepal lateral commisural traces, column 5 of table 2; D — length gradation of sepal lateral petal cord (column 4 of table 2); E — length gradation of vestigial stamen traces, column 4 of table 2; F — length gradation of sepal stamen cord, column 6 of table 2; G — height gradation of disc traces, column 8 of table 2.

On the whole, *Grateoleae* are a primitive group, as described by Pennell. Among the species of *Grateoleae*, the fundamental common trend is the reduction or loss of a stamen trace. There are three major trends, (1) the reduction of all traces, but no cohesion or adhesion (as in *Scoparia dulcis*), (2) fusion of traces, with less reduction (culminated in *Sutera glandulosa*), (3) both fusion and reduction of traces (culminated in *Lindernia* species and *Mazus japonicus*). *Angelonia grandiflora* shows reduction of stamen and disc traces only, but without a tendency of fusion of traces. *Verbascum virgatum* represents slight fusion (only the sepal laterals) and slight reduction of traces. In *Cheloneae* the fundamental strong trend is the reduction of traces. The fusion of bundles probably gradually appear in the most evolved species like *Calceolaria mexicana*. The two species of *Antirrhinae* are characterized by reduction of disc
mainly and by adhesion of perianth and stamen traces. No cohesion and no reduction of other traces is noticed. All species of Rhinantheoideae lack adhesion of sepal and stamen traces and the reduction, particularly of stamen and disc traces (not fusion) is the main trend.

Trichomes of flowers and demarcation of species

The distribution of trichome types does not show any clear relation. Even in the same genus (like Torenia), variation of types of trichomes and patterns of distribution is noticed. Still, a glance on the description of types and distribution of them shows that the tribe Grateoleae has a preponderance of glandular trichomes. Cheloneae possesses some glandular types with long non-glandular supporters and many purely non-glandular types. Buchnerae and Pedicularis shows preponderance of non-glandular thick-walled trichomes.

This fact suggests that the trichomes show a broad trend of evolution from purely glandular types (like S, D, R or L) to glandular types with short non-glandular stalk (D, I and J). All these types are common in Grateoleae. K and M with multicellular globular glandular heads probably represent a different line. The next change is probably in further proliferation of the non-glandular stalk (as in A, B, C, C, E, F, H and G). These types are found in Angelonia and Antirrhineae. The next step covers dendroid or simple multicellular or unicellular thick-walled non-glandular trichomes (e.g. O, P, Q and N), which are common in Buchnerae and Cheloneae. Further critical study of trichomes, including their developmental anatomy in different organs, vegetative and reproductive, may reveal definite trends of evolution.

SUMMARY

Investigation into some important aspects of floral anatomy of 24 species of Scrophulariaceae reveals that although clear anatomical bases of distinguishing flowers of different taxa are absent, reasons supporting the classification of Penne11 are available. For example, position of Scoparia dulcis in Grateoleae appears more natural than in Digitaleae. Transposition of Sutera (Manuleae) of Benth and Hooker under Grateoleae is supported by the nature of the traces of stamens and carpels. Separation of Digitalis and Veronica and their placement under two tribes by Penne11 finds justification in their distinct patterns of staminal and carpellary bundles. Floral vasculature of Calceolaria mexicana is distinct from that of Wightia speciosissima and Russelia equisetiformis of Cheloneae. Placement of Calceolaria mexicana under Cheloneae by Penne11 seems therefore unnatural.
Plan of advancement of floral structures supports fairly the classification of Penneill. Grateoleae appears as the most primitive tribe. Antirrhineae are fairly advanced. Rhinanthsoids are more evolved than Antirrhinoideae. Verbascum is not so primitive as is found in older classifications.

Particular types of trichomes are preponderant in flowers of particular tribes. Their distribution patterns seem to be species specific. Correlation of trichome types with the evolution of taxa within the family suggests a gradual change from purely glandular to non-glandular dendroid or unbranched or unicellular thick-walled types.

Acknowledgement

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Unerwienie i owłosienie pospolitych indyjskich gatunków z rodziny

Serophulariaceae

Streszczenie

Badania niektórych istotnych aspektów budowy kwiatów 24 gatunków Serophulariaceae wykazały, że chociaż brak wyraźnych anatomicznych podstaw wyróżniających kwiaty różnych taksonów, to jednak przeprowadzone obserwacje anatomiczne popierają klasyfikację Pennella. Wydaje się na przykład, że umieszczenie Scoparia dulcis w Gratioleae jest bardziej naturalne niż w Digitaleae. Charakter śladów pręcikowych i owocolistkowych popiera przeniesienie gatunku Sutera (Manu
eleae, wg Bentham a i Hookera) do Gratioleae. Oddzielnie Digitalis i Veronica i umieszczenie ich w odrębnych plemionach przez Pennella, znajduje uzasadnienie w odrębnych ukладach wiązek pręcikowych i owocolistkowych. Natomiast unerwienie kwiatowe Calceolaria mexicana różni się od unerwienia kwiatowego Wightia speciosissima i Russelia equisetiformis z Cheloneae, umiejscowienie przez Pennella Calceolaria mexicana w Cheloneae jest więc nienaturalne.

Stopień ewolucyjnego zaawansowania struktur kwiatowych popiera silnie klasyfikację Pennella. Gratioleae wydają się być najprymitywniejszym plemieniem. Antirrhineae są ewolucyjnie zaawansowane, a bardziej od nich zaawansowane są Rhinanthoideae. Verbascum nie jest tak prymitywnym gatunkiem, jak to wynika z dawniejszych klasyfikacji.

W poszczególnych plemionach występują na kwiatach określone typy włosów, układ ich rozmieszczenia jest gatunkowo specyficzny.

Korelacja typu włosów z ewolucją taksonów w obrębie rodziny sugeruje stopniowe przejście od czysto gruczołowatych do niegruczołowatych, dendroidalnych albo nierozgałęzionych lub do jednokomórkowych, grubościennych typów włosów.