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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 Pennell classification of subfamilies is strongly supported.

INTRODUCTION

Bentham and Hooker (1873) classified the family *Scrophulariaceae* into three series, *Pseudosolaneae, Antirrhinideae* and *Rhinanthideae*. Wettstein's classification (1897) retained the same major groups (subfamilies *Pseudosolaneae, Antirrhinoideae* and *Rhinanthoideae*). But Pennell (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.

Bentham & Hooker (1873)	Wettstein (1897)	Pennell (1935)
A. *Pseudosolaneae*	A. *Pseudosolaneae*	A. *Antirrhinoideae*
Leucophylleae	*Verbasceae*	*Gratioleae*
Aptosimeae	*Aptosimeae*	*Verbasceae*
Verbasceae	B. *Antirrhinoideae*	*Leucophylleae*
B. *Antirrhinideae*	*Hemimerideae*	*Cheloneae*
Calceolarieae	*Calceolareae*	*Collinsieae*
H. *Hemimerideae*	*Antirrhineae*	*Antirrhineae*
Antirrhineae	*Cheloneae*	B. *Rhinanthoideae*
Chelomeae	*Manuleae*	*Digitaleae*
Manuleieae	*Gratioleae*	*Veroniceae*
Gratioleae	*Selagineae*	*Buchnereae*
C. *Rhinanthideae*	C. *Rhinanthoideae*	*Euphrasieae*
Digitaleae	*Digitaleae*	
Gerardieae	*Gerardieae*	
Euphrasieae	*Rhinantheae*	

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 (*Sopubia* and *Vandellia* by Krishna Iyengar, 1937, 1940a, b; *Scoparia* by Raghavan and Srinivasan, 1941; Bacopa by Safeeulla 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 Eeastern 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

Species	Collector, source	Locality
A. Sub-family *Pseudosolaneae*		
I. Tribe *Verbasceae*		
1) *Verbascum virgatum* Stokes	Agharkar, S.N.; C.U.	Calcutta
B. Sub-family *Antirrhinoideae*		
I. Tribe *Hemimerideae*		
1) *Angelonia grandiflora* C. Morr.	Scrop 18(10); C.U.	Unknow
II. Tribe *Calceolarieae*		
1) *Calceolaria mexicana* Benth.	Dep Scrop 2; C.U.	Darjeelin (W. Bengal)
III. Tribe *Antirrhineae*		
1) *Linaria bipartita* Willd.	Banerjee, S.N.; C.U.	Calcutta
2) *Antirrhinum majus* L.	Deb Scorp 3; C.U.	Calcutta
IV. Tribe *Cheloneae*		
1) *Russelia equisetiformis* Schlecht. Cham. = *Russelia juncea* Zucc.	Deb Scrop 4; C.U.	Calcutta
2) *Wightia speciosissima* (D. Don) Merr. = *Wightia gigantea* Wall.	Deb Scorp 5; C.U.	Punjab
6 V. Tribe *Manuleae*		
1) *Sutera glandulosa* Roth.	Deb Scorp 6; C.U. (B.S.I.)	Poona

Species	Collector, source	Locality
VI. Tribe *Grateoleae*		
1) *Mazus japonicus* (Thumb.) Kuntze = *Mazus rugosus* Lour.	Deb. Scrop 7; C.U.	Calcutta
2) *Lindenbergia indica* (L.) Kuntze = *Lindenbergia urticaefolia* Lehm.		
3) *Brama monnieri* (L.) Pennell = *Bacopa monnieri* (L.) Wettst. = *Herpestis monniera* (L.) H.B. & K.	Dep Scrop 9; C.U.	Garia (W. Bengal)
4) *Pagesia dianthera* (Swantz) Pennell = *Herpestis chamaedroides* H.B. & K.	Deb Scrop 10; C.U.	Garia (W. Bengal)
5) *Torentia fournieri* Linden	Deb Scrop 11; C.U.	Ballygunje (Calcutta)
6) *Torenia vagans* Roxb.	Deb Scrop 12; C.U.	Ballygunje (Calcutta)
7) *Lindernia crustacea* (L.) Mueller = *Vandellia crustacea* (L.) Benth.	Deb Scrop 13; C.U.	Ballygunje (Calcutta)
8) *Lindernia ciliata* (Colsm.) Pennell = *Bonnaya brachiata* Link & Otto	Deb Scrop 14; C.U.	Ballygunje (Calcutta)
9) *Lindernia multiflora* (Roxb.) Mukherjee = *Vandellia multiflora* D. Don. Gen.	Deb Scrop 15; C.U.	Ballygunje (Calcutta)
C. Sub-family *Rhinanthoideae*		
I. Tribe *Digitaleae*		
1) *Scoparia dulcis* L.	Deb Scrop 16; C.U.	Ballygunj (Calcutta)
2) *Veronica himalensis* D. Don. Prod.	Agharkar, S.N.; C.U.	Mussouri
3) *Digitalis purpurea* L.	Deb Scorp 17; C.U.	Darjeelin (W. Bengsl)
II. Tribe *Gerardieae*		
1) *Alectra arvensis* (Benth.) Merrill = *Alectra indica* Benth.	Ghosh, S.N.; C.U.	Assam Hill
2) *Centranthera nepalensis* D. Don = *Centanthera hispida* Hk. f. non R. Br	Cambell 9867; C.U.	Manbhum (W. Bengal)
3) *Striga gesneroides* (Willd.) Vatke = *Striga oronbranchoides* (R. Br.) Benth.	Khan, S.N.; C.U.	Mysore
III. Tribe *Rhinantheae*		
1) *Pedicularis furfuracea* Wall. Cat.	Agharkar, S.N.; C.U.	Cholan

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).

OBSERVATION

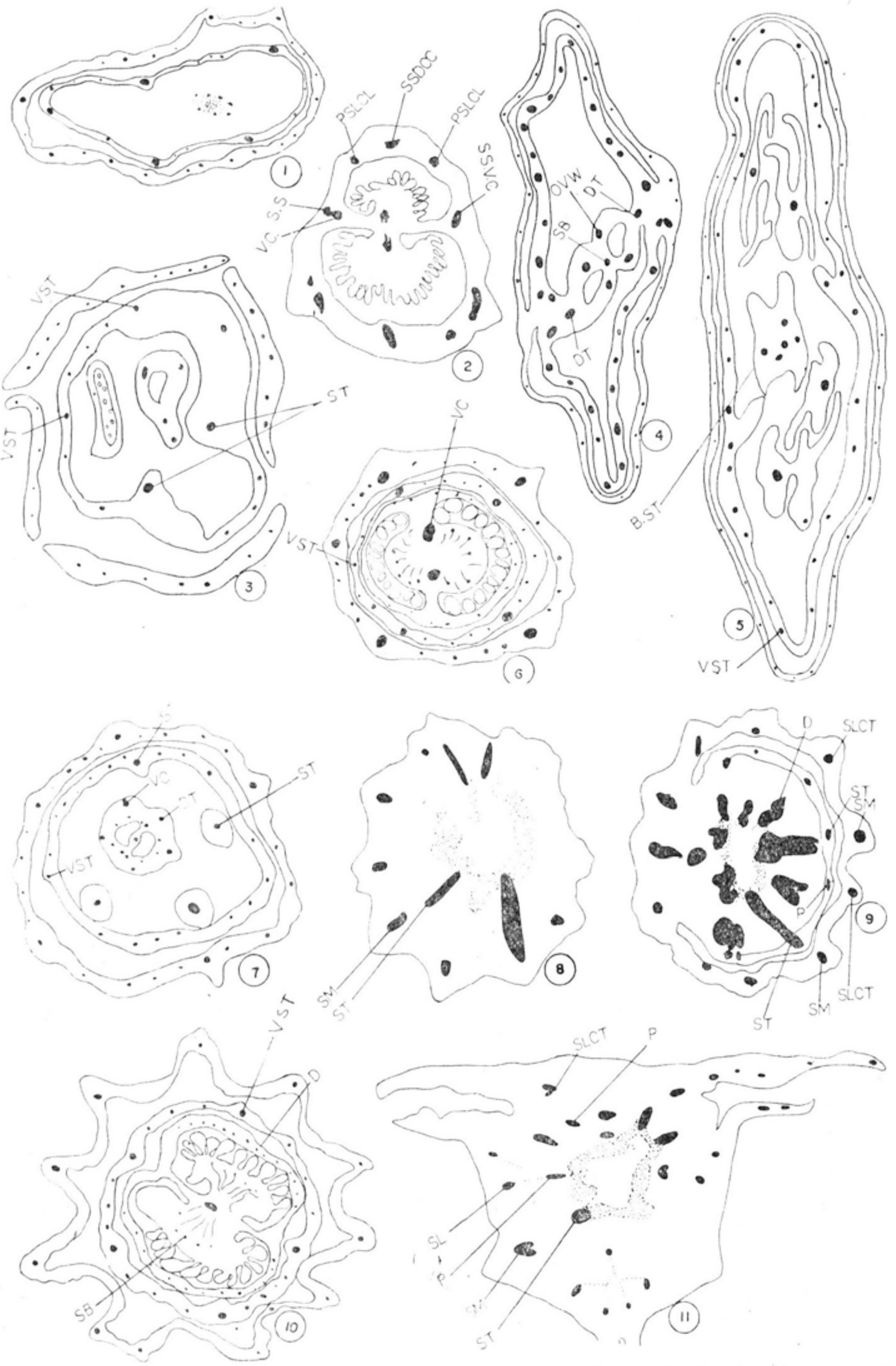
The family generally possesses centripetal inflorescence (centrifugal in *Cheloneae*), sometimes compound or with solitary flowers. Bracteoles are generally two. Ebracteolate genera are *Angelonia, Linaria, Antirrhinum, Sutera, Mazus, Lindenbergia, Torenia, Lindernia, Scoparia, Veronica, Pedicularis,* 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 *Verbascum, 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 *Verbascum, 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 *Verbascum,* two in *Veronica* (posterio-lateral pair) and *Calceolaria* (lateral pair). Filaments are distinctly short in *Angelonia,* exerted in *Wightia* and *Veronica.* Stigma is minute (*Linaria, Russelia, Calceolaria*), capitate (*Verbascum, Lindenbergia*), subcapitate (*Veronica*), 2-lobed (*Antirrhinum, Sutera, Brama,* etc.), 2-lamellate (*Mazus, Torenia, Lindernia,* etc.), distinct (*Pedicularis, Digitalis,* and many species of *Grateoleae*), truncated (*Scoparia*), linguiformis (*Centranthera, Alectra*), entire (*Striga, Pagesia*), or dilated (*Wightia*).

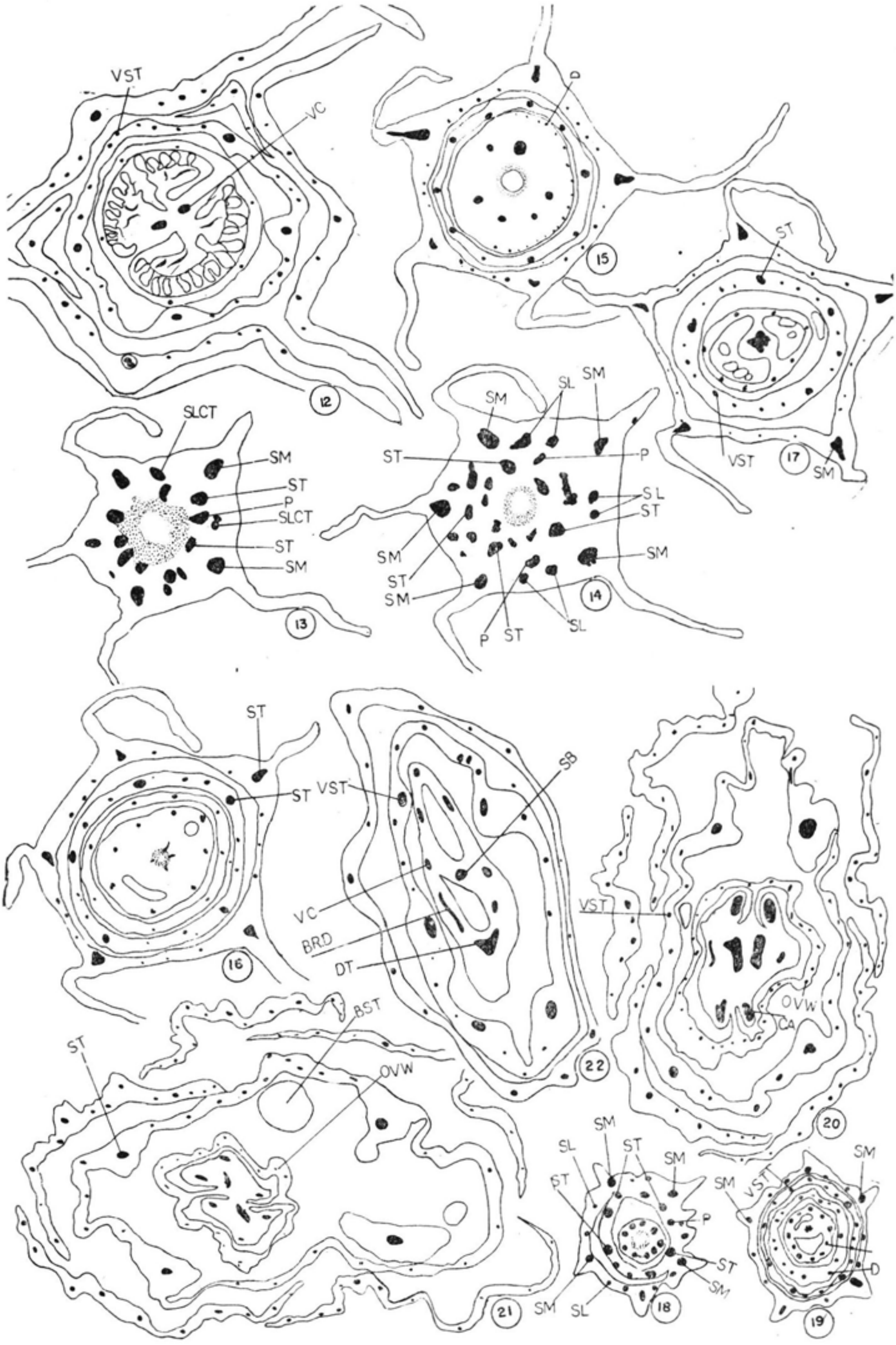
Although the vascular anatomy of flowers of *Scrophulariaceae* follows a common plan, distinguishable characters are also available in many species and genera. Sepals are supplied by sepal-midrib traces and sepal-lateral commisural strands. A sepal-midrib trace generally forms a cord with a stamen trace. 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. Pagesia 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* — septal bundle; *SL* — sepal lateral trace; *SLCT* — sepal lateral commisural 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 commisural trace of carpels; *VST* — vestigial stamen trace)



Figs. 12—22. Camera lucida drawings of transections of flower buds showing vascular traces. *12. Pagesia dianthera, 13—17. Torenia fournieri, 18—19. T. vagans; 20—21. Digitalis purpurea; 22. Pedicularis furfuracea.* (*CA* — central arches, *BR. D.* — branching of dorsal trace of carpel. Other indications as in the previous plate)

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 of the axis 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 monnieri* 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 monnieri* 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 *Manuleae; Mazus japonicus, Lindenbergia indica, Torenia fournieri, T. vagans, Lindernia crustacea, L. ciliata* and *L. multiflora* of *Grateoleae; 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* (*Calceclarieae*) 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 monnieri, 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 upto 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 monnieri, 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 monnieri,* ± 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 monnieri, 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).

Gynaecium

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 Rao, 1953, but here mentioned as commisural ventral strands) and four narow 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 *Gerardieae*, *Alectra arvensis*, *Centranthera nepalensis* and *Striga gesneroides* have a similar plan of eight peripheral bundles and a single 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. nepalensis* 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 commisural 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) forming 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 reported by Schrock and Palser, 1967, in *Collinsia*).

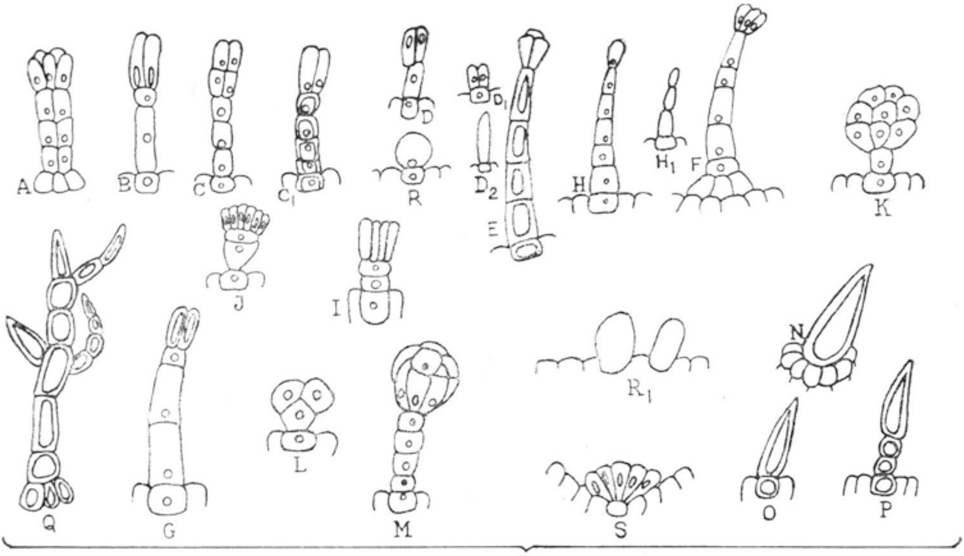


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Fig. 25. Trichome types of flowers of *Scrophulariaceae*

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

C_1 — 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.

R_1 — 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.

Excepting *Linaria bipartita*, all species of *Scrophulariaceae* studied have different degrees of pubescens on floral organs. The pedicel possesses 2—3-celled, N or H type of trichome in *Verbascum virgatum*, *Calceolaria mexicana*, *Angelonia grandiflora*, thin-walled 5—7 celled P, H and E in *Antirrhinum majus*, densely pubescent with O, P and Q types in *Wightia speciosissima*, D and J types in *Sutera glandulosa*, I in *Mazus japonicus*, P in *Lindenbergia indica*, R_1 in *Torenia vagans*, F and S in *Lindernia multiflora*, B and C in *Veronica himalensis*, non-glandular multicellular in *Digitalis purpurea*, R_1 and D in *Alectra arvensis*, N and E in *Centranthera nepalensis*, R in *Striga gesneroides*. Hairs are absent in the pedicel of *Russelia equisetiformis*, *Linaria bipartita*, *Brama monnieri*, *Pagesia dianthera*, *Torenia fournieri*, *Lindernia crustacea*, *Pedicularis furfuraecea*, (very rare in *L. ciliata*, *Scoparia dulcis*).

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 R_1 common on the abaxial surface and K on the adaxial surface of *A. majus*, D and D_1 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*, R_1 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*, H_1 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*,

R_1 and H on the abaxial surface of *Striga gesneroides*, R_1 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*, H_2 (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*, H_1 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 R_1 on the abaxial surface of *P. furfuracea*. Trichomse on corolla surface is almost absent in *V. virgatum*, *A. grandiflora*, *Linaria* sp., *W. speciosissima*, *Su. glandulosa*, *Lindenbergia indica*, *Brama monnieri* and *T. fournieri*.

On stamens, N occurs on the connective of *Verbascum virgatum*, long pointed multicellular hairs on the adaxial surface of *Angelonia grandiflora*, H on the abaxial surface of filaments of *C. mexicana*. Trichomes are almost absent on the stamen of *Linaria bipartita*, *Antirrhinum majus*, *Russelia equisetiformis*, *W. speciosissima*, *Sutera glandulosa*, *Mazus japonicus*. *Lindenbergia*, *indica*, *Brama monnieri*, *Pagesia dianthera*, *Torenia* species, *Lindernia* species, *Scoparia dulcis*, *Veronica himalensis*. *D. purpurea*, *Alectra arvensis*, *Striga gesneroides*, *Centranthera nepalensis*, *P. furfuracea*.

On carpels, C_1 occurs on the ovary wall of *Angelonia grandiflora*, R_1 on the ovary wall of *C. mexicana*, R_1 on the ovary wall of *T. fournieri*, H_1 on the ovary wall of *D. purpurea*, D on ovary wall of *Alectra arvensis*. Trichomes are absent in *V. virgatum*, *Linaria bipartita*, *A. majus*, *R. equisetiformis*, *W. speciosissima*, *Sutera glandulosa*, *Mazus japonicus*, *Lindenbergia indica*, *Brama monnieri*, *Pagesia dianthera*, *T. vagans*, *Lindernia* species, *Scoparia dulcis*, *Veronica himalensis*, *Centranthera nepalensis*, *Striga gesneroides*, *P. furfuracea*.

DISCUSSION

Taxonomy of the species:

The sub-family *Pseudosolaneae* of Bentham and Hooker (including tribes *Leucophylleae*, *Aptosimeae* and *Verbasceae*) and of Wettstein (including *Verbasceae* and *Aptosimeae*) was thought to be distinct, primitive and related to *Solanaceae*, for their five stamens, absence of zygomorphy, etc. But Pennell (1935) concludes that these characters in *Scrophularianceae* 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 *Antirrhinideae* also.

In formulating the new classification, Pennell makes the first cleavage into *Antirrhinoideae* and *Rhinanthoideae*, 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, *Rhinanthoideae* is more evolved. For this redefination of the subfamilies, a few genera of original *Rhinanthoideae* (e.g. *Digitaleae*) have been transferred to Pennell's *Antirrhinoideae*. Similarly some genera of *Cheloneae* (*Antirrhinoideae*) have been transferred to *Buchnereae* (*Rhinanthoideae*). 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. *Verbascum virgatum* 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 vestigal. 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. *Verbascum*, *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 *Rhinanthoideae*, 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 *Rhinanthoideae* (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) divaricate 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 *Veroniceae* 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 subcapitate in *Veronica* and distinct in *Digitalis.*

Placement of *Sutera* (*Manuleae* of older systems) under *Grateoleae* 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 *Grateoleae.*

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) *Psedosolaneae* of previous taxonomists (*Verbasceae* and *Leucophylleae* of Pennell) are not primitive, but derived and more evolved than *Gratioleae* of *Antirrhinoideae*. (3) *Gratioleae*, 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 *Grateoleae* 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

1	2 Sep.-St. cord present (+) strong adhesion (++)	3 Sep.-Pet. cord — well marked (+)	4 Disc absent (++) or traces reduced (+) (i.e. no. 5)	5 Per.+St.+Carp. Cord — present	6 No. of Vest St. trace (+/trace)	7 No. of lost St. traces (++/trace)	8 Vest. trace reduced (+)	9 D+OV. traces fused	10 Perianth trace lost	11 S. tr. unbranched	12 Ovary wall traces ± unbranched (not 8—10)	13 Cohesion of S.L. trac. prominent (+) very strong (++)	14 Total+signs (degree of advancement)
GRATEOLEAE													
Pagesia					+								1
Brama					+						+		2
Torenia fournieri	+				+					+	+	+	5
Lindenbergia indica	++	+			+							+	5
Lindernia crustacea	+				+		+			+	+	+	6
Torenia vagans	+	+			+					+	+	+	6
L. multiflora	+				+		+			+	+	+	6
L. ciliata	+	+			+		+			+	+	+	7
Sutera glandulosa	++	+	++		+		+						7
Scoparia dulcis			++			++			++		+	+	8
Mazus japonicus	+	+	++		+		+				+	++	9

Table 1 (Cont.)

1	2	3	4	5	6	7	8	9	10	11	12	13	14
VERBASCEAE													
Verbascum sp.											+	+	2
HEMIMERIDEAE													
Angelonia grandiflora			++		+		+						4
CHELONEAE													
Russelia equisetiformis					+								1
Wightia speciosissima			++		+		+						4
Calceolaria mexicana	+	+	++	+	++	++			++			+	12
ANTIRRHINEAE													
Linaria bipartita	+	+	++		+								5
Antirrhinum majus	+	+	++		+		+						6
DIGITALEAE													
Digitalis purpurea		+	+		+		+	+					5
VERONICEAE													
Veronica himalensis		+	+		++	++		+	++			+	10
BUCHNEREAE													
Centranthera nepalensis			++		+		+					+	5
Alectra arvensis			++		+							++	5
Striga gesneroides		+	++		+				+				5
EUPHRASIEAE													
Pedicularis furfuracea			++		+		+					+	5

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 commisural 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 commisural strands. *Veronica himalensis,* 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 gradiation 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 commisural 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

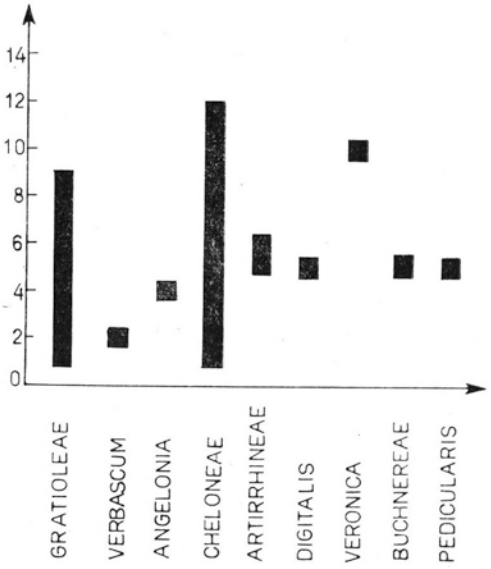

Fig. 26. Histogram range of specialization grades (as shown in Table 1) of the tribes of *Scrophulariaceae*

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)

Species 1	Unbranched part of sepal-midrib trace 2	Unbranched part of petal trace 3	Sepal lateral + petal cord 4	Sepal lateral commisural trace 5	Sepal midrib stamen cord 6	Vestigial stamen trace 7	Height of disc 8	Total of 7 gradations (Col. 2—8) 9	Mean of 7 gradations 10
Verbascum virgatum	1	1	2	1	2	1	3	11	1.57
Angelonia grandiflora	1	1	2	1	2	7	6	20	2.86
Calceolaria mexicana	2	2	3	2	4	10	6	28	4.00
Linaria bipartita	2	1	3	1	4	6	6	23	3.28
Antirrhinum majus	3	2	3	1	3	7	6	25	3.57
Russelia equisetiformis	3	2	2	1	1	6	1	16	2.29
Wightia speciosissima	1	1	1	1	1	7	6	18	2.57
Sutera glandulosa	2	2	3	1	5	7	6	26	3.71
Mazus japonicus	3	2	3	5	4	7	6	30	4.29
Lindenbergia indica	2	1	5	1	6	6	2	23	3.29
Brama monnieri	2	1	2	1	1	4	1	12	1.71
Pagesia dianthera	1	1	2	1	2	4	1	12	1.71
Torenia fournieri	6	3	2	1	4	2	1	19	2.71
T. vagans.	6	2	3	2	5	6	1	25	3.57
Lindernia crustacea	6	1	3	1	4	8	1	24	3.43
L. ciliata	6	2	3	4	3	7	1	26	3.71
L. multiflora	6	1	2	1	4	7	3	25	3.57
Scoparia dulcis	5	3	2	1	1	9	6	27	3.86
Veronica himalensis	4	2	4	1	2	10	1	24	3.43
Digitalis purpurea	2	2	3	1	1	—	1	17	2.43
Alectra arvensis	4	4	2	7	3	6	6	32	4.57

Table 2 (Contd.)

1	2	3	4	5	6	7	8	9	10
Centranthera nepalensis	1	1	2	4	2	—	2	19	2.71
Striga gesneroides	6	3	3	1	1	6	3	23	3.28
Pedicularis furfuraceae	1	1	2	2	2	7	6	21	3.00

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 gradiation 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 commisural 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 57—75%; (6) cord length 76—100%

Column 7: Gradation of the vestigal 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%; (5) 1 vest., length 300.1—400%; (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%

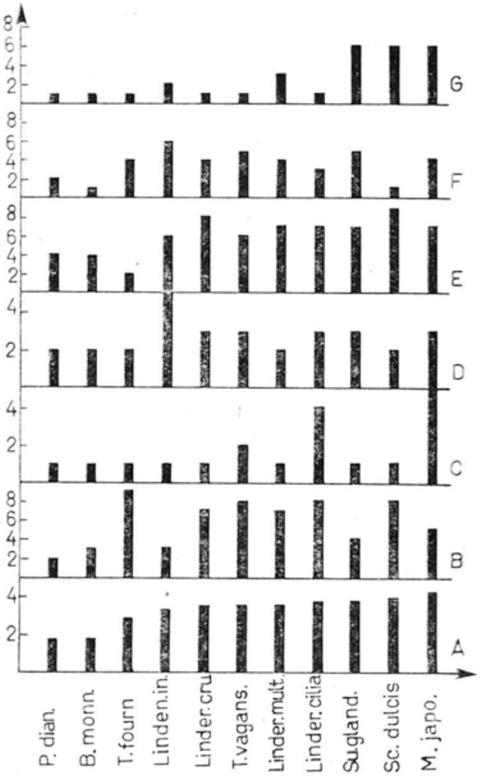

Fig. 27. *Grateoleae* — histogram showing comparison of degrees of specialization of characters. A — column 10 of Table 2, mean value of all gradations of characters; B — total of gradations of the length of unbranched portions of sepal- and petal-main-traces, i.e. total of columns 2 and 3 of Table 2; 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 *Rhinanthoideae* 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. *Buchnereae* 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_1, 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_1, 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 *Buchnereae* 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 Pennell are available. For example, position of *Scoparia dulcis* in *Grateoleae* appears more natural than in *Digitaleae*. Transposition of *Sutera (Manuleae* of Bentham 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 Pennell 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 Pennell seems therefore unnatural.

Plan of advancement of floral structures supports fairly the classification of Pennell. *Grateoleae* appears as the most primitive tribe. *Antirrhineae* are fairly advanced. *Rhinanthoideae* 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.

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Unerwienie i owłosienie pospolitych indyjskich gatunków z rodziny Scrophulariaceae

Streszczenie

Badania niektórych istotnych aspektów budowy kwiatów 24 gatunków *Scrophulariaceae* 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 (Manuleleae,* wg Benthama i Hookera) do *Grateoleae*. Oddzielnie *Digitalis* i *Veronica* i umieszczenie ich w odrębnych plemionach przez Pennella, znajduje uzasadnienie w odrębnych układach wiązek pręcikowych i owocolisktowych. 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 Pannella. *Grateoleae* wydają się być najprymitywniejszym plemieniem. *Antirrhineae* są ewolucyjnie zaawansowane, a bardziej od nich zaawansowane są *Rhinanhoideae*. *Verbascum* nie jest tak prymitywnym gatunkiem, jak to wynika z dawniejszych klasyfikacji.

W poszczególnych plemionach występują na kwiatach określone typy włosków. Układ ich rozmieszczenia jest gatunkowo specyficzny.

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