

Floral vasculature of *Phaseoleae* (*Papilionaceae*)

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INTRODUCTION

Bentham and Hooker (1862—1867) and de Dalla Torre and Harms (Englerian system; 1900—1907) have classified the tribe *Phaseoleae* into six subtribes: (1) *Glycineae* B. & H. (*Glycininae* E.), (2) *Erythrineae* B. & H. (*Erythrinae* E.), (3) *Galactieae* B. & H. (*Galactiinae* E.), (4) *Dioclieae* B. & H. (*Diocleinae* E.), (5) *Euphaseoleae* B. & H. (*Phaseolinae* E.), and (6) *Cajaneae* B. & H. (*Cajaninae* E.). In order to trace the phylogeny in this taxon, study of somatic chromosomes have been taken up. Cytological and xylotomical studies of the taxon (Datta and Saha, 1970 a, b) have revealed that (1) *Euphaseoleae* (*Phaseolinae*) are the most primitive subtribe, (2) within this subtribe *Phaseolus calcaratus* Roxb. is a primitive species and *P. mungo* L. is one of the most advanced species. (3) *Vigna* and *Dolichos* have evolved from *Phaseolus*, (4) *Cajaneae* and *Dioclieae* are related to *Euphaseoleae*, whereas *Glycineae*, *Erythrineae* and *Galactieae* have evolved in different lines and have advanced considerably.

Importance of floral anatomy for tracing phylogeny has been maintained by Fisher (1928), Bancroft (1935), Mathews (1941), Rao (1951), Just (1952), Eames (1953) and others. The present paper is an attempt to find out the possible trends of evolution in *Phaseoleae*.

MATERIALS AND METHODS

The following species were selected from the six tribes:

Species	Sample voucher No.
1. <i>Glycineae</i> (<i>Glycininae</i>):	
i) <i>Clitoria ternatea</i> L.	E. B. herb. Phas. 1/68.
ii) <i>Glycine max</i> Marril. (= <i>G. soja</i> , S. & Z.)	E. B. herb. Phas. 2/68.
2. <i>Erythrineae</i> (<i>Erythrinae</i>):	
i) <i>Butea monosperma</i> (Lam.) Kuntze	E. B. herb. Phas. 19/68.
(= <i>B. frondosa</i> Wall.)	

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| ii) <i>Erythrina variegata</i> L.
(= <i>E. indica</i> Lam.) | E. B. herb. Phas. 3/68. |
| 3. <i>Galactieae</i> (<i>Galactiinae</i>): | |
| i) <i>Spatholobus roxburghii</i> Benth. | Camb. (Tundi)
C. U. herb. 25.12.85. |
| 4. <i>Dioclieae</i> (<i>Diocleinae</i>): | |
| i) <i>Canavalia enciformis</i> (L.) DC. | E. B. herb. Phas. 20/68 |
| 5. <i>Euphaseoleae</i> (<i>Phaseolinae</i>): | |
| i) <i>Dolichos lablab</i> L. | E. B. herb. Phas. 5/68. |
| ii) <i>D. axillaris</i> E. Mey. | E. B. herb. Phas. 21/68. |
| iii) <i>D. baumannii</i> Harms. | E. B. herb. Phas. 22/68. |
| iv) <i>Phaseolus mungo</i> L. | E. B. herb. Phas. 7/68. |
| v) <i>P. aureus</i> Roxb. | E. B. herb. Phas. 6/68. |
| vi) <i>P. calcaratus</i> Roxb. | E. B. herb. Phas. 8/68. |
| vii) <i>Pachyrrhizus erosus</i> (Linn.)
Urban. | E. B. herb. Phas. 23/68. |
| viii) <i>Vigna cylindrica</i> Skeels | E. B. herb. Phas. 9/68. |
| 6. <i>Cajaneae</i> (<i>Cajaninae</i>): | |
| i) <i>Cajanus cajan</i> (Linn.) Mill.
(= <i>C. indicus</i> Spreng.) | E. B. herb. Phas. 16/68. |

The seeds of many species were collected from a local nursery and they were grown in the University garden and identified properly. Some of the species were kindly supplied by Dr A. K. Ghosh, Head of the Department of Botany, Maharaja Bir Bikram College, Agartala. Flower buds at fully differentiated condition were fixed in formalin-propiono-alcohol (Johansen, 1940), microtomed at 10–15 μ (both transverse and longitudinal), embedded in paraffin, de-waxed and stained with crystal violet. Permanent slides, thus prepared, were examined and figures were drawn with camera lucida with IX eyepiece and 10 objective, at a magnification of 300 or with IX eyepiece and 0 objective at a magnification of 35.

OBSERVATION

All the species of the tribe studied possess a *Phaseolus* type (unihiate) of vascular organisation (as shown by Moore, 1936), but they show difference in details of nature of branching of vascular traces when studied critically.

Subtribe *Glycineae*:

Ten large common bundles for perianth, stamen and disc separate out gradually from the central stele at different levels. They divide tangentially to produce ten external bundles (five sepal-midrib traces and five petal-midrib + sepal-lateral cords alternately) and ten large internal bundles, stamen-disc cords (Fig. 1). The petal-midrib + sepal-lateral cords ten larger (stamen-disc cords). Of these ten perianth traces, five sepal-mi-

continue undivided for a long distance after which it divides to produce one petal-midrib trace and two sepal-lateral traces, supplying sepal margins (Fig. 17). Sepal-midrib traces branch later. No sepal lateral commissural trace is found. The stamen-disc cords divide tangentially to produce ten disc traces and ten stamen traces. The central vascular bundles orient into one dorsal and two to three marginal traces of the ovary.

In *Clitoria ternatea* (Fig. 1) the common bundles for perianth, stamen and disc remain undivided for a short distance (Table 1); whereas in *Glycine max* (Fig. 2) this undivided portion is considerably long, about seven times longer than the former. The disc traces of *C. ternatea* are feeble, branching immediately after origin in the swellings at the bases of the stamens for a short distance. *G. max* may also be distinguished by the separation of the hypanthium (having petal, stamen and disc traces) from the ovary at a level below the branching of the perianth traces. Here the disc is annular, but very short, arising from hypanthium. The staminal column forms a continuous tube at the base without separation of the odd stamen. The style is hollow in both the species having one dorsal and two marginal traces. The upper part of the style is solid having a single trace. The stigma is non-vascular in *G. max*; while in *C. ternatea* the vascular trace continues almost upto the tip.

Subtribe *Erythrineae*:

Ten large common bundles divide tangentially into ten outer perianth traces and ten inner stamen disc cords shortly after origin. Sepal-midrib traces branch immediately after origin (Fig. 17). Petal-midrib sepal-lateral cords also divide immediately to produce a petal-midrib trace and two sepal-lateral traces each (Fig. 17). Disc traces are very short and comparatively feeble in both the species. In *Erythrina variegata* (Figs. 4, 5) disc traces divide into a large number of minute branches immediately after origin while in *Butea monosperma* (Fig. 3) the identity of disc traces is lost within a short distance. The ovary in both the species is situated on a long stalk having three traces (two marginal and one dorsal) in *Butea* and a ring of bundles in *Erythrina*. The ovary of *Butea* is surrounded by profuse hairs. In *E. variegata* the ovary is separated first from the hypanthium. Disc is represented by ten low inward protrusions of the hypanthium. In the middle part of the ovary of *Erythrina*, bundles orient into one dorsal, two marginal and two lateral branches. Three traces continue in the hollow cylindrical style without fusion. The stigma is non-vascular.

Subtribe *Galactieae*:

Ten common bundles from the compact stele of *Spatholobus roxburghii*, by tangential division produce ten smaller (perianth bundles) and

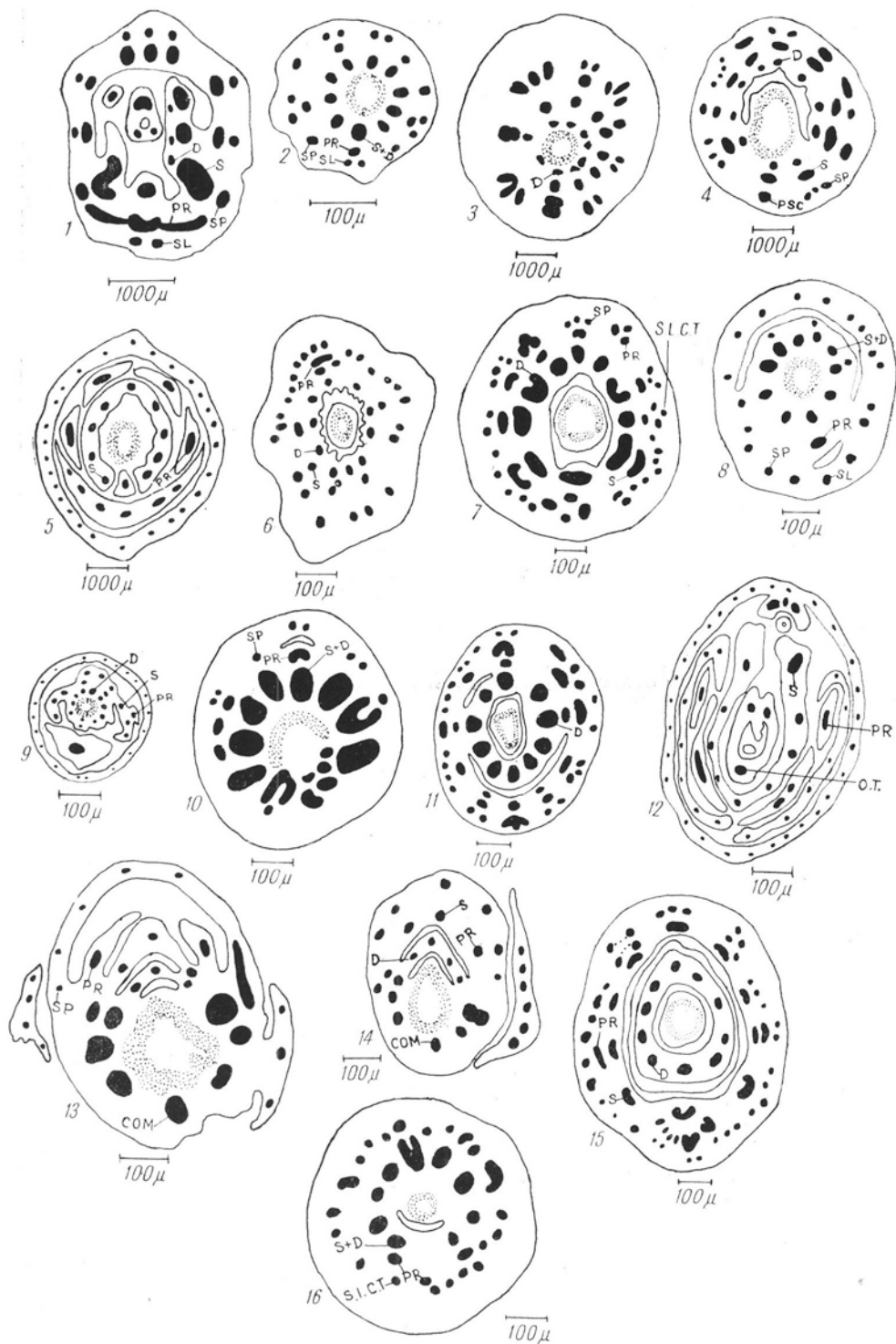
drib traces (Fig. 17) divide into three, and the petal-midrib + sepal-lateral cords (Fig. 17) divide into three, two sepal-lateral and one petal-midrib traces, resulting into 25 sepal and 5 petal traces. Massive stamen disc cords divide tangentially at a slightly higher level into ten stamen traces and ten prominent disc traces (Fig. 6). Disc traces move inwardly and branch in some inward protrusions encircling the ovary but attached with the staminal column which is a complete tube at the base. The central stele organise into one midrib and two marginal traces of the ovary.

Subtribe *Dioclieae*:

Wavy continuous stele is found in stalk. From wavy stele twelve large bundles are produced at the same level, of which two pairs on two sides of the abaxial bundle fuse together ultimately to form ten large bundles (Fig. 7). These ten common bundles for perianth, stamen and disc divide tangentially to produce outside five sepal-midrib traces (Fig. 17) and five petal-midrib + sepal-lateral cords. The inner ten large bundles are the stamen-disc cords. These two rings of traces continue unbranched for a long distance. The first tangential division indicated in stamen disc traces occurs long before the branching of the perianth traces. The stamen disc traces divide tangentially into inner ten disc traces and outer ten stamen traces. Disc is very massive and prominent and becomes separated very early from the outer hypanthium. The sepal-midrib traces branch almost at the same level as the division of the stamen-disc cord.

EXPLANATION OF FIGURES

Figs. 1—16: Camera lucida drawing (diagramatic) of transections of floral axis of *Phaseoleae* showing distribution of different traces. 1, *Clitoria ternatea* Linn.; 2, *Glycine max* Merril. (showing sepal-lateral traces and stamen-disc. cords etc.); 3, *Butea monosperma* (Lam.) Kuntze (showing petal-sepal cords, etc.); 4 & 5, *Erythrina variegata* Linn. (showing petal-sepal cords etc.); 6, *Spatholobus roxburghii* Benth.; 7, *Canavalia enciformis* (Linn.) DC. (showing sepal-lateral commissural traces etc.); 8, *Dolichos axillaris* E. Mey. (showing stamen-disc cords, sepal-lateral traces etc.); 9, *Dolichos baumanii* Harms. (showing sepal-lateral traces etc.); 10, *Dolichos lablab* Linn. (showing stamen-disc cords etc.); 11, *Pachyrrhizus erosus* Linn. (showing sepal-lateral traces etc.); 12, *Phaseolus aureus* Roxb.; 13, *Phaseolus calcaratus* Roxb. (showing common traces etc.); 14, *Phaseolus mungo* L.; 15, *Vigna cylindrica* Skeels; 16, *Cajanus cajan* (Linn.) Mill sp. (Abbreviations: COM = common trace; SP. = sepal-midrib trace; SL. = sepal-lateral trace; PR. = perianth trace; S.L.C.T. = sepal-lateral-commisural trace; S. = stamen trace; D. = disc trace; S + D = stamen-disc cords; P.S.C. = petal-sepal cords and O.T. = ovarian trace).



Figs. 1—16

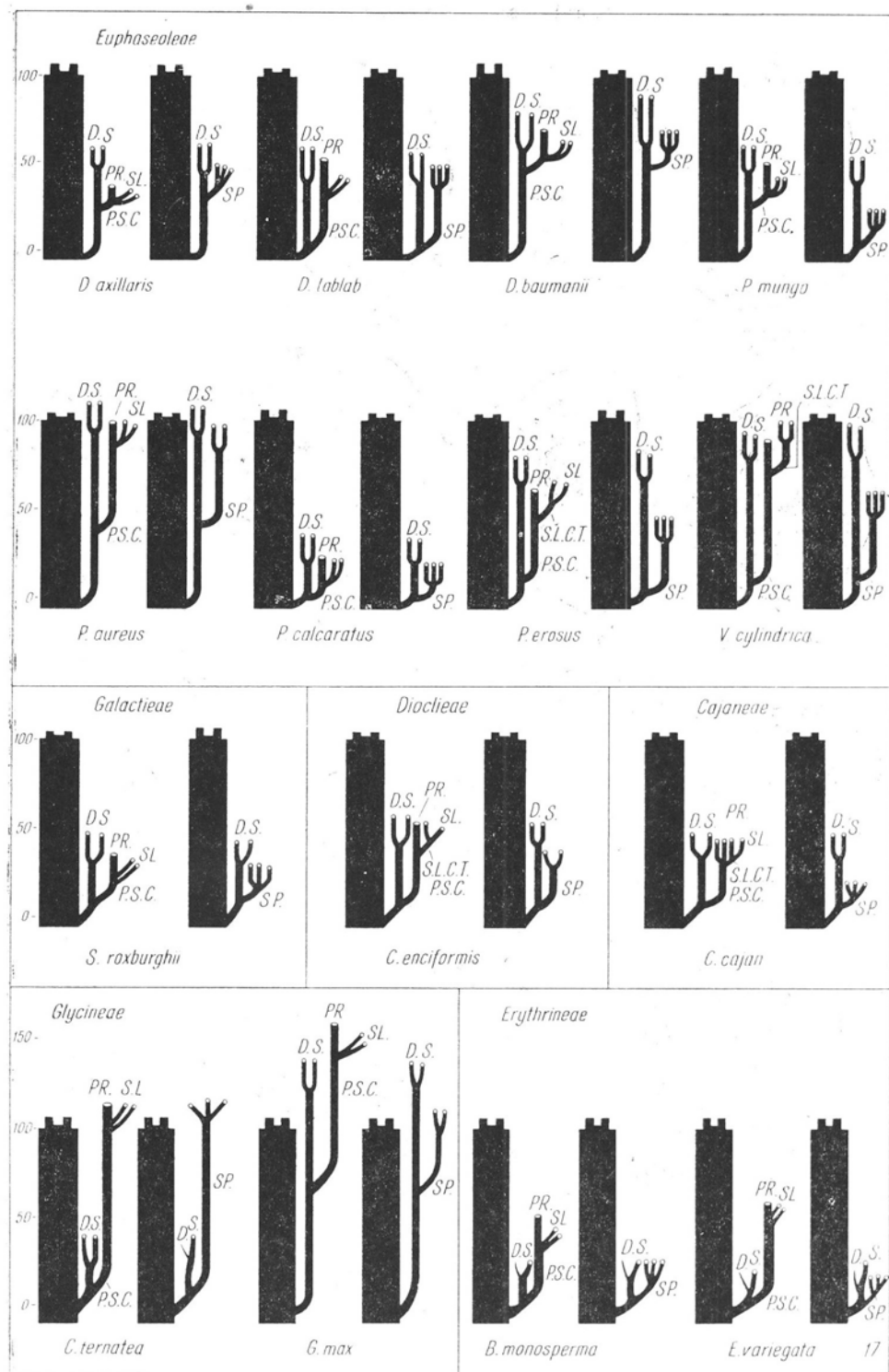


Fig. 17: Graphic diagram of floral vasculature of *Phaseoleae* (S.P. = sepal midrib traces, P.R. = perianth trace, P.S.C. = petal-sepal cord, D = disc traces, S = stamen traces, S.L. = sepal-lateral traces, S.L.C.T. = sepal-lateral commissural trace).

The petal-midrib + sepal-lateral cords divide into sepal-lateral commissural traces moving outwards and the inner petal-midrib traces. Commissural traces (Fig. 17) divide radially into two sepal-lateral traces within a short distance. Petal traces and stamen traces are included in a common column or tube separated from outer calyx tube. The staminal column (9 + 1) separates from corolla tube at a higher level.

Inner most central stele becomes more compact and organises into three traces of the ovary, one for midrib and two marginal.

Petal-midrib traces divide at the level where disc and the staminal column separate and all petals are distinguished. Traces passing through the filaments supply the connective where it becomes tangentially dilated and produce two lateral branches supplying the two anther lobes.

Subtribe *Euphaseoleae*: (Figs. 8—15)

In this subtribe eight species have been studied. From the central stele ten large common bundles separate and from them ten perianth traces are separated either after a very long distance (*Dolichos axillaris* (Fig. 8), *D. baumanii*, *Phaseolus mungo* and *P. aureus*) or within a very short distance (*Dolichos lablab*, *Phaseolus calcaratus*, *Pachyrrhizus erosus* and *Vigna cylindrica*). The ten inner large bundles are stamen-disc cords of the ten perianth traces, five sepal-midrib traces (Fig. 17) branch within a very short distance after origin (*D. axillaris*, *D. baumanii*, *P. mungo* and *P. calcaratus*) or after a long (Fig. 17) distance (*D. lablab*, *P. aureus*, *Pachyrrhizus erosus* and *Vigna cylindrica*). Petal-midrib + sepal-lateral cords are either long (*D. lablab*, *P. aureus*, *Pachyrrhizus erosus* and *V. cylindrica*) or very short (*D. axillaris*, *D. baumanii*, *P. calcaratus* and *P. mungo*, Fig. 17). Stamen-disc cords give stamen traces and disc traces, after branching.

Commissural strands for sepal-lateral traces may be absent (*D. axillaris*, Fig. 8, *D. lablab*, Fig. 10; *D. baumanii*, Fig. 9; *P. mungo*, Fig. 14; *P. aureus*, Fig. 12; and *P. calcaratus*, Fig. 13) or present (*Pachyrrhizus erosus*, Fig. 11; and *Vigna cylindrica*, Fig. 15). The stamen-disc cord may be short (*Dolichos axillaris*, *D. baumanii*, *P. mungo* and *P. calcaratus* Fig. 13) or long (*D. lablab*, *P. aureus*, *Pachyrrhizus erosus* and *Vigna cylindrica*). The central stele becomes more compact and ultimately organised into three traces of the ovary, one dorsal and two marginal. In *Pachyrrhizus erosus* (Fig. 11) the style is almost solid having a loose parenchymatous transmission tissue at the centre but three traces are recognised throughout the style and at the lower part of the stigma lobes. Terminal part of the stigma is non-vascular. In *Dolichos lablab* the style is hollow and flat. The three traces are visible in the lower part of the style.

The style is hollow and cylindrical in *D. axillaris*, *D. baumanii*, *Vigna cylindrica* and the species of *Phaseolus*. Stigma portion is generally non-vascular.

Species	Distance			
	Origin of com. & pr.		Origin and branching of Sp.	
	Mea. μ	Rd.	Mea. μ	Rd.
1	2	3	4	5
<i>Glycineae</i>				
<i>Clitoria ternatea</i>	60	8.66	735	106.52
<i>Glycine max</i>	90	69.20	50	38.40
<i>Erythrineae</i>				
<i>Butea monosperma</i>	350	7.10	350	7.10
<i>Erythrina variegata</i>	75	3.17	155	6.50
<i>Galactieae</i>				
<i>Spholobus roxburghii</i>	150	15.50	45	4.60
<i>Dioclieae</i>				
<i>Canavalia enciformis</i>	180	8.30	480	22.27
<i>Euphaseoleae</i>				
<i>Dolichos axillaris</i>	1110	37.50	120	4.00
<i>D. baumanii</i>	765	52.40	135	9.10
<i>Euphaseoleae</i>				
<i>D. lablab</i>	45	8.82	150	29.41
<i>Phaseolus aureus</i>	260	44.80	230	39.40
<i>P. calcaratus</i>	20	4.50	20	4.50
<i>P. mungo</i>	135	30.00	30	6.66
<i>Pachyrrhizus erosus</i>	165	16.40	180	17.90
<i>Vigna cylindrica</i>	105	16.20	390	30.20
<i>Cajaneae</i>				
<i>Cajanus cajan</i>	225	10.78	45	2.15

Abbreviation: com. = common trace, pr. = perianth trace, sp. = sepal-midrib trace, PSC = petal-sepal cord, p. = petal, sl. = sepal-lateral traces, St. = stamen traces, D = disc traces, S.L.C.T. = Sepal-lateral-commisural-trace, Mea. = measurement and Rd. = Relative distance.

Subtribe *Cajaneae*: *Cajanus cajan*

Ten large common bundles divide tangentially to form ten perianth traces and ten larger stamen disc cords. Disc is prominent (Fig. 16). The sepal-midrib traces later branch immediately (Fig. 17). The petal-midrib + sepal-lateral cords are very long which divide to form petal midrib traces inside and short commisural traces outside (Figs. 16 and 17). The central stele becomes more compact and form one midrib trace and two marginal traces of the ovary at the level where all floral parts are differentiated. Style is hollow, cylindrical, slightly flattened, marginal traces fuse to form two bundles on two sides of the canal. In the upper part of the style only the fusion bundles are noticeable.

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Origin of PSC separation of p. & sl.		Origin of Pr. separation of St. & D		Length of S.L.C.T.		Origin of com. orientation of ovarian trace	
Mea. μ	Rd.	Mea. μ	Rd.	Mea. μ	Rd.	Mea. μ	Rd.
6	7	8	9	10	11	12	13
720	104.34	120	17.39	0	0	690	100
100	76.92	70	54.60	0	0	130	100
1400	28.50	350	7.10	0	0	4900	100
1035	43.65	100	4.22	0	0	2365	100
120	12.50	165	17.10	0	0	960	100
750	34.50	755	35.34	45	2.09	2155	100
135	4.50	315	10.60	0	0	2955	100
120	8.10	135	9.10	0	0	1478	100
150	29.41	165	32.35	0	0	510	100
270	46.50	285	49.10	0	0	580	100
40	9.00	70	15.90	0	0	440	100
30	6.66	45	10.00	0	0	450	100
345	34.40	480	47.70	75	7.4	1005	100
390	60.40	450	62.00	105	16.3	645	100
525	25.18	480	23.02	30	1.4	2085	100

DISCUSSION

It is evident from the graph (Fig. 16) showing the nature of branching of disc-stamen and perianth bundles, that the *Euphaseoleae* Benth. & Hook. (*Phaseolinae* E.) have a common characteristic, i.e. the branching of sepal-midrib traces or petal-midrib + sepal-lateral cords is always below the plane of division of stamen-disc cords into traces for disc and stamens. This character is also found in *Cajanus* (*Cajaneae*), and *Spatholobus* (*Galactieae*). This proves a relationship among the subtribes *Euphaseoleae*, *Cajaneae* and *Galactieae*. *Canavalia enciformis* (*Dioclieae*) also shows more or less similar branching, slight difference being in level of branching of the disc-stamen cord and petal-sepal cord. *Vigna cylindri-*

ca, *Cajanus cajan*, *Canavalia enciformis* and *Pachyrrhizus erosus* are characterized by prominent sepal-lateral commissural strands which show a degree of specialization.

Among the species of *Euphaseoleae*, *Phaseolus calcaratus* has got the shortest common bundles directly arising from stele, cords of traces for different whorls and unbranched portions of midrib traces for perianths. If this condition is regarded as most primitive (because *P. calcaratus* has represented the most primitive karyotype), *P. aureus* and *P. mungo* are more advanced, *P. aureus* being the highest evolved species of the genus for its longest cords and common traces. *Pachyrrhizus* is characterized by the presence of sepal-lateral commissural strands and by a long distance between the branching of stamen-disc cords and of the petal-sepal cords. *Vigna cylindrica* on the other hand is characterised by the close approximation of the levels of division of these two cords and the presence of long sepal-lateral commissural strands. In *Dolichos* also the distance between the planes of division of these cords and sepal-midrib traces is much reduced like in *Vigna*; but the absence of sepal-lateral commissural strand distinguishes *Vigna* from *Dolichos*.

If the increase in length of the common bundles or cords is regarded as the trend of evolution, *Cajanus*, *Canavalia* and *Spatholobus* should be regarded as comparatively primitive taxa related to the lowest species of *Euphaseoleae*, e.g. *P. calcaratus*. The structure of the floral traces of both *Canavalia* and *Cajanus* are very similar and both are characterized by the presence of the sepal-lateral commissural strands. *Spatholobus* has got a very close similarity with *P. calcaratus*. All these facts suggest a close relationship of *Diocleae*, *Galactieae* and *Cajaneae* with *Euphaseoleae* as concluded by cytological studies. *Erythrina variegata* and *Butea monosperma* though do not show long common bundles and common traces, represent a specialization in highly reduced disc traces, stamen-disc cords and the unbranched portions of the sepal-midrib traces. In *Clitoria* and *Glycine* (*Glycineae*) the common bundles have become considerably long. Particularly in *G. max* the common bundles and cords for disc and stamen and for perianths are longest, proving a very advanced condition of the species. These findings on vascular anatomy of the flowers corroborate, in general the results obtained from the cytological xylotomical investigation (Datta and Saha, 1970a & b).

Baker (1879) has placed *Butea* under *Galactieae* along with *Spatholobus*. But the nature of floral vasculature clearly suggests a relationship between *Butea* and *Erythrina*, the stamen-disc cord being shorter than unbranched trace portions for perianths, while it is longer in *Spatholobus* as in *Euphaseoleae*. The classifications of Bentham and Hooker (1862) and De Dalla Torre and Harms (1900—7) get support in the floral anatomy.

SUMMARY

Fifteen species of the *Phaseoleae* have been selected for the study of floral vasculature and they belong to the subtribes *Glycineae*, *Erythrineae*, *Galactieae*, *Dioclieae*, *Euphaseoleae* and *Cajaneae*. The findings of the vascular anatomy of the flowers corroborate in general, with the results obtained from the cytological and xylotomical investigations. Following conclusions are drawn from this part of observation:

(1) Among the species of *Euphaseoleae*, *Phaseolus calcaratus* has got the least fusion of bundles and early branching (i.e. the shortest common bundles, cords and unbranched portions of midrib traces). If this condition is regarded as most primitive, *P. aureus* and *P. mungo* are comparatively advanced.

(2) If longer fusion, i.e. increase in length of the common bundles or cords is regarded as a trend of advancement, *Cajanus*, *Canavalia* and *Spatholobus* are more primitive than the lowest evolved species of *Euphaseoleae*, e.g. *P. calcaratus*.

(3) *Erythrina variegata* and *Butea monosperma* though do not show long common bundles and common traces, represent a line of evolution having highly reduced disc-traces, stamen-disc cords and the unbranched portions of the sepal-midrib traces.

(4) In *Clitoria* and *Glycine* the common bundles have become considerably long. Particularly in *G. max*, the common bundles and cords for disc and stamen and for perianths are longest, proving a very advanced condition of the species.

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Unerwienie kwiatów u Phaseoleae (Papilionaceae)

Streszczenie

Wybrano 15 gatunków *Phaseoleae* celem zbadania unerwienia ich kwiatów. Gatunki te należą do podplemion *Glycineae*, *Erythrineae*, *Galactineae*, *Dioclieae*, *Euphaseoleae* i *Cajaneae*. Wyniki badań unerwienia są w zasadzie zgodne z wynikami otrzymanymi z badań cytologicznych i ksyłotomicznych. Z przeprowadzonych badań nad unerwieniem kwiatów można wyciągnąć następujące wnioski:

1. Wśród gatunków *Euphaseoleae*, *Phaseolus calcaratus* posiada najmniej zrośnieć wiązek i wykazuje wczesne rozgałęzienie (a więc najkrótsze wspólne wiązki, sznury i nie rozgałęzione części śladów nerwu głównego). Jeśli ten stan przyjmie się za najbardziej pierwotny to *Ph. aureus* i *Ph. mungo* są względnie zaawansowane.
2. Jeśli dłuższe zrośnięcia, a więc wzrost na długości wspólnych wiązek i sznurów przyjmujemy jako właściwość wtórną, to *Cajanus*, *Canavalia* i *Spatholobus* będą bardziej pierwotne niż niżej ewolucyjnie zaawansowane gatunki *Euphaseoleae*, np. *Ph. calcaratus*.
3. *Erythrina variegata* i *Butea monosperma*, chociaż nie wykazują długich wspólnych wiązek i wspólnych śladów, przedstawiają linię ewolucyjną mającą wysoce zredukowane ślady dysków oraz sznury dysków przecikowych i nie podzielone części śladów nerwów głównych działek.
4. U *Clitoria* i *Glycine* wspólne wiązki są znacznej długości. Zwłaszcza u *G. max* wspólne wiązki i sznury dla dysków i przecików i dla okwiatu są najdłuższe, co wskazuje, że pod tym względem gatunki te są wyraźnie ewolucyjnie zaawansowane.