Floral morphology of certain species of the Papilionaceae with a special reference to stamen adelphy

A.S. Al-Nowaihi
E-mail: abdelsalamalnowaihi@hotmail. com

Karima A. Hamed
E-mail: karimahamed@hotmail. com

and

Magdy M. Mourad

Botany department, Faculty of Science Ain Shams University, Cairo – Egypt

AL- Nowaihi, A.S.; Hamed, K. and Mourad M. M. 2001. Floral morphology of certain species of the Papilionaceae with a special reference to stamen adelphy. ***Taeckholmia*** **21(1)**: 153-172.

***Key word*:** Floral morphology, stamen adelphy.

The floral morphology of the three papilionaceous species: *Ononis vaginalis* Vahl , *Dolichos lablab* L. and *Crotalaria aegyptiaca* Benth. was studied to trace the organ vascularization. Vascular complexes to the sepals, the petals and the stamens were recorded in the three species. Three cases of stamen adelphy were met with viz. monadelphy, diadelphy and pseudomonadelphy. In the latter case a basal fenestration in the staminal tube exists as an access to successful insect pollination. A foliar nature was determined for the nectary disc where present. In the three species the carpel is supplied by the basic number; one dorsal and two ventral traces.

Introduction

Floral morphological studies, particularly those on floral vasculature provided clues to the understanding of a number of taxonomic and phylogenetic querries. Some comprehensive publications remain good promotors to several workers to follow such approach. A salient one appeared as early as 1891, when Henslow studied the vascular system of the floral organs for the interpretation of the flower. Since then subsequent publications bearing a more or less similar objective appeared in the first half of the 20^{th} century and raised the importance of the vascular pattern as playing a great role in morphological interpretation (Puri, 1951; Eames, 1961; Carlquist, 1970; Sattler, 1972; Tucker, 1972; Sporne, 1985).

The Papilionaceae *s.str.* represents a good material for such studies on grounds of its unique papilionaceous corolla, the frequent tendency towards the fusion of stamens and the occasional presence of an intrastaminal nectary disc. Relying on the floral morphology, several scholars reached acceptable solutions to a number of taxonomic and phylogenetic problems. Parallel to this the architecture of the papilionaceous flower in relation to entomophily was a corner stone for studies in pollination biology and the literature so dealing is rather voluminous to be reviewed here. However, studies bearing

Received 9 January 2001. Revision accepted 25 August 2001.

on taxonomic and phylogenetic considerations in this family are exemplified by the work of Moore (1936 a & b); Polhill (1976), Tucker (1987, 1989), Shrire (1989), Schutte (1998) and Rodriguez-Riaňo *et al* (1999), and those on the floral biology are exemplified by the works of Westerkamp (1993, 1996, 1997 a&b), Ladd (1994) and Westerkamp and Weber (1999).

The present work is planned to investigate the floral morphology of *Ononis vaginalis*, *Dolichos lablab* and *Crotalaria aegyptiaca* through the mode of organ vascularization and also to show variations in the stamen adelphy which may be accompanied by an intrastaminal nectary disc.

The selected species exhibit different cases of adelphy with occasional presence of an intrastaminal nectary disc. Visual examination of the flowers shows three cases and one sub-case (Fig.1). In *Ononis vaginalis* the stamens are monadelphous with the staminal tube closed and not accompanied by nectary disc. In *Dolichos lablab* the stamens are diadelphous below, monadelphous above with basal fenestration and accompanied by a nectary disc. In *Crotalaria aegyptiaca* two cases are investigated; the first case is a flower with monadelphous stamens and the staminal tube is opened, and the second case is a flower with ten distinct stamens. In both cases the nectary disc is lacking.

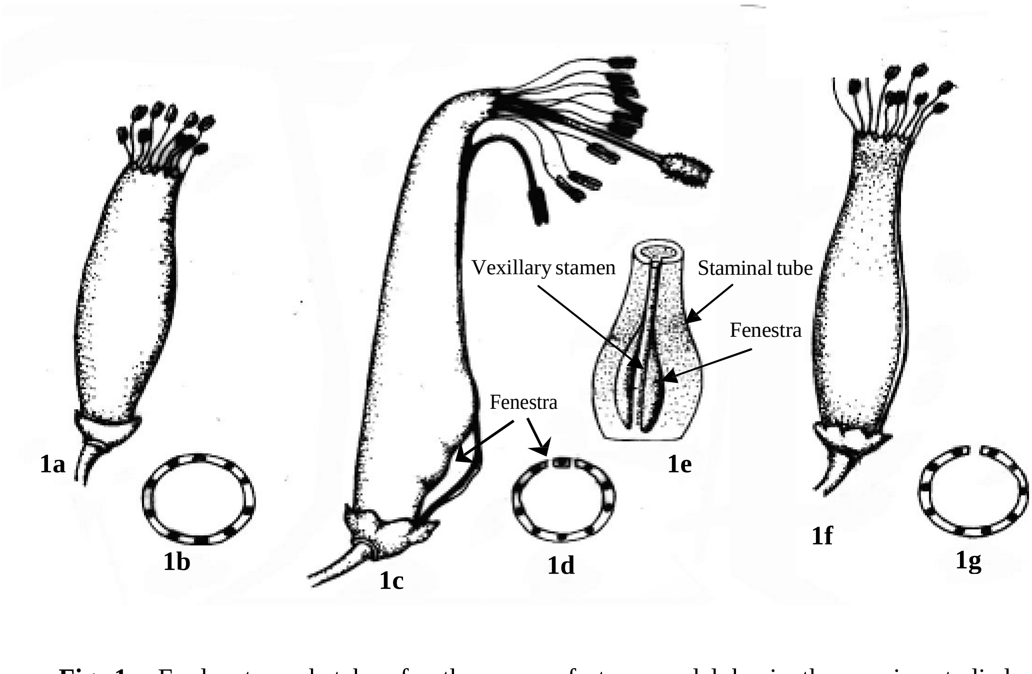


Fig. 1. Explanatory sketches for the cases of stamen adelphy in the species studied.
1 a & b. Monadelphous, staminal tube closed *(Ononis vaginalis)*,
2 c, d & e. Pseudo monadelphous with basal fenesrtration *(Dolichos lablab)*,
3 f & g. Monadelphous, staminal tube opened *(Crotalaria aegytiaca).*

Material and Methods

For the investigation of floral vascularization, flower buds were fixed in F.A.A, embedded in paraffin wax, serially microtomed at 10-12 μ, dehydrated and stained with erythrosine and crystal violet according to the conventional methods (Johansen, 1940). Photographs were taken on kodak TMAX 100 film and supplemented by explanatory drawings of the same magnification. The term “trace” is applied when the vascular strand is still in the receptacular tissue. The term “bundle” is applied when the supply departs from the receptacle and enters the body of the concerned organ.

Observations

Ononis vaginalis **(Fig.2)-**The receptacle supply is more or less siphonostele (Fig.1a), which at a higher level differentiates into ten vascular stubs. Five of these form the sepal median traces and the other five represent conjoint sepal laterals (Fig. 2 b & c). Each of the conjoint sepal lateral splits to give two lateral traces supplying two adjacent sepals (Fig.1 c-e) Once all the sepal traces become differentiated the sepals are separated as a tube from the receptacular tissue (Fig. 1 e-g.). Further amplification of the sepal supply takes place in the calyx tube through the branching of the sepal median bundles (Figs.1 g & h). After the divergence of the peripheral traces to the sepals the remaining receptacular vascular tissue undergoes dissection to give five petal-stamen complexes lying on the same radii of the sepal laterals (Fig. 2 c-e). Each complex divides to give an outer trace to a petal and an inner one to the antepetalous stamen (Fig.2 e & f.). On the same radii of the sepal medians five traces to the antesepalous stamens are cut from the dissected siphonostele (Fig 4 a-d). At the final differentiation of the ten staminal traces all the staminal filaments are cut from the receptacular tissue to form a closed tube (Fig .2 g-j). The remains of the dissected vascular stock form the ovary supply and assumes a crescent mass (Fig. 2 e) which later differentiates into one carpellary dorsal and two carpellary ventral traces (Fig. 2 e-h). The ventral bundle forms the supply to two ovules, while the dorsal bundle branches in the carpellary wall (Fig. 2. i-j). At a higher level the dorsal as well as the ventral traces form the stylar supply (Fig. 2 m). The style is hollow.

Dolichos lablab **(Fig. 3**)- The receptacular supply is a continuous siphonostele (Fig. 3 a). Ten vascualr arms protrude assuming 10 urn-shaped vascular complexes (Fig. 3 b & c). Five of these represent the sepal-antesepalous stamen-nectary disc complexes, alternating with five petal-antepetalous stamen-nectary disc complexes (Fig.3 c & d). At a higher level each of the former five complexes gives three sepal traces to each sepal; one median and two laterals and the residue forms the antesepalous stamen-disc complex (Fig.3 e). At the same level each of the five petal-antepetalous stamen-disc complex gives a petal trace (Fig. 3 e & f) while the residue forms the antepetalous stamen-disc complex (Fig. 3 g-i). At the level where the keel petals (carina) and the wing petals (alae) become distinct the vexillary staminal filament appears as distinct entity leaving a fenestra on both sides and the remaining nine filaments are fused to form the tube (Fig.3 i&j). At the same level, the nectary disc appears like a continuous tissue and extends to a short distance containing ten bundles (Fig.3 g-i). The gynoecium is supplied with three traces; one median and two ventrals (Fig.3 g). In the carpellary wall, the dorsal bundle branches and the two ventral bundles become fused toward the top of the ovary (Fig.3 m&n). The style is hollow and supplied by one dorsal and two fused ventral bundles (Fig.3 n).

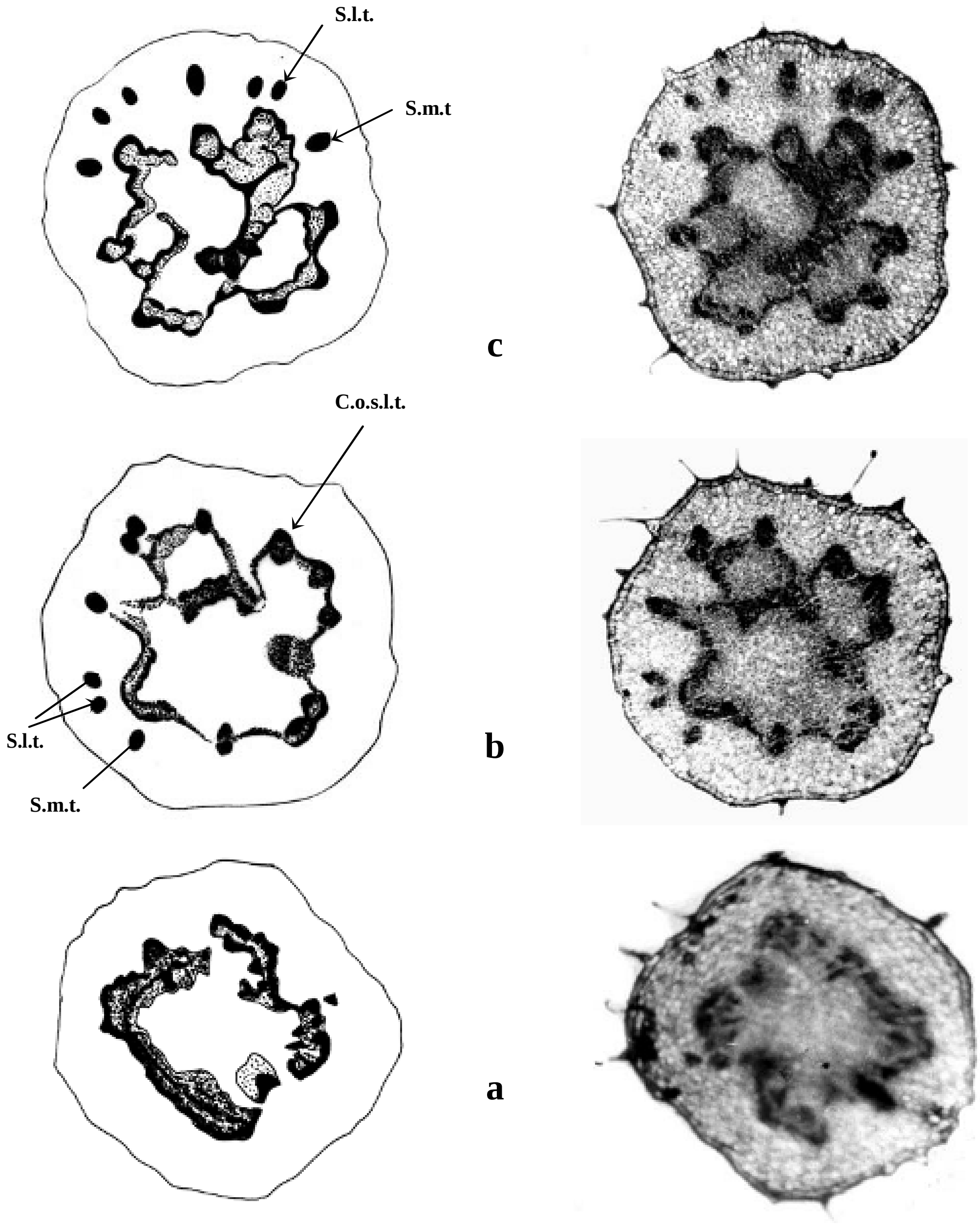


Fig. 2. Floral vascularization of *Ononis vaginalis*; (x 25). Co.s.l.t.. Conjoint sepal lateral trace, S.l.t.. Sepal lateral trace, S.m.t.. sepal mediam trace.

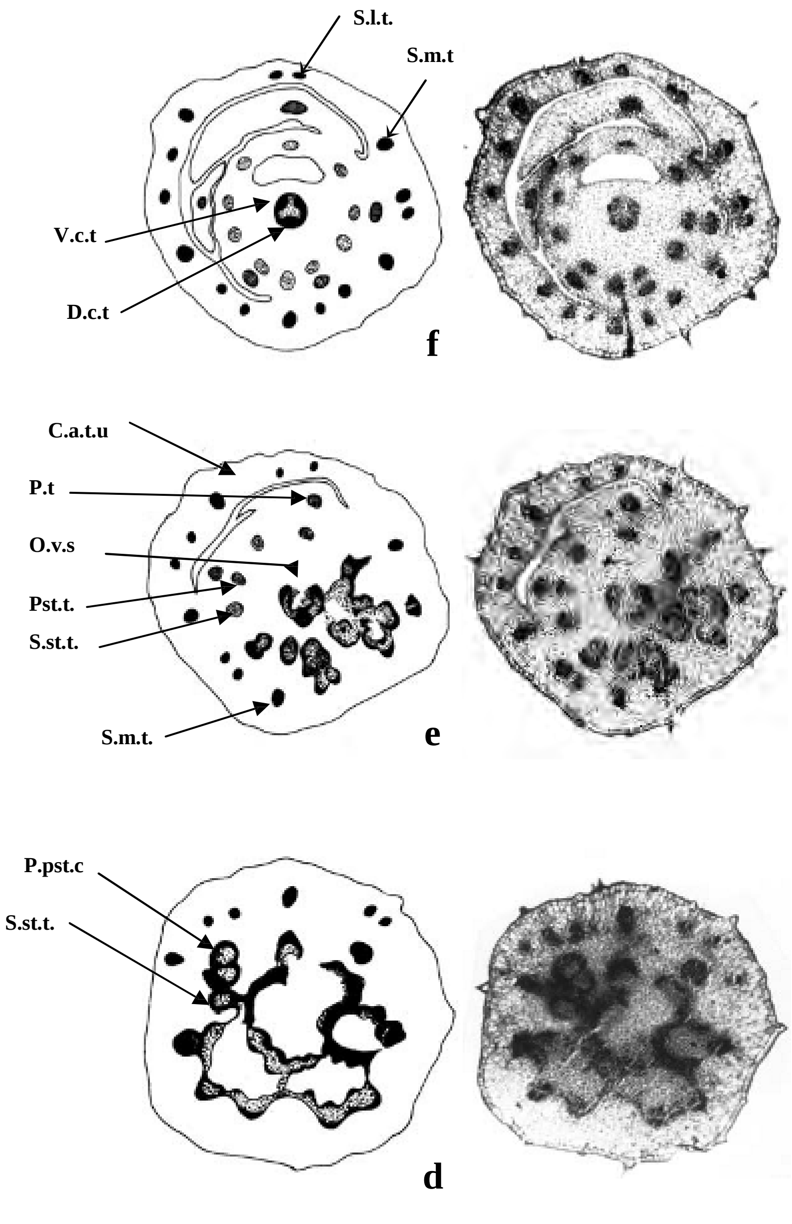


Fig. 2 (Cont.). Floral vascularization of *Ononis vaginalis*; (x 25). Ca.tu. calyx tube, D.c.t. Dorsal carpel tissue P.t. peltal trace, P. pst. c. Petal – antepetalous stamen complex, Pst.t. antepetalous stamen trace, S.l.t.. Sepal lateral trace, S.m.t. sepal mediam trace, o.v.s. ovary vascular supply, Sst.t. antesepalous stamen trace, V.c.t.. Vertral carpel trace.

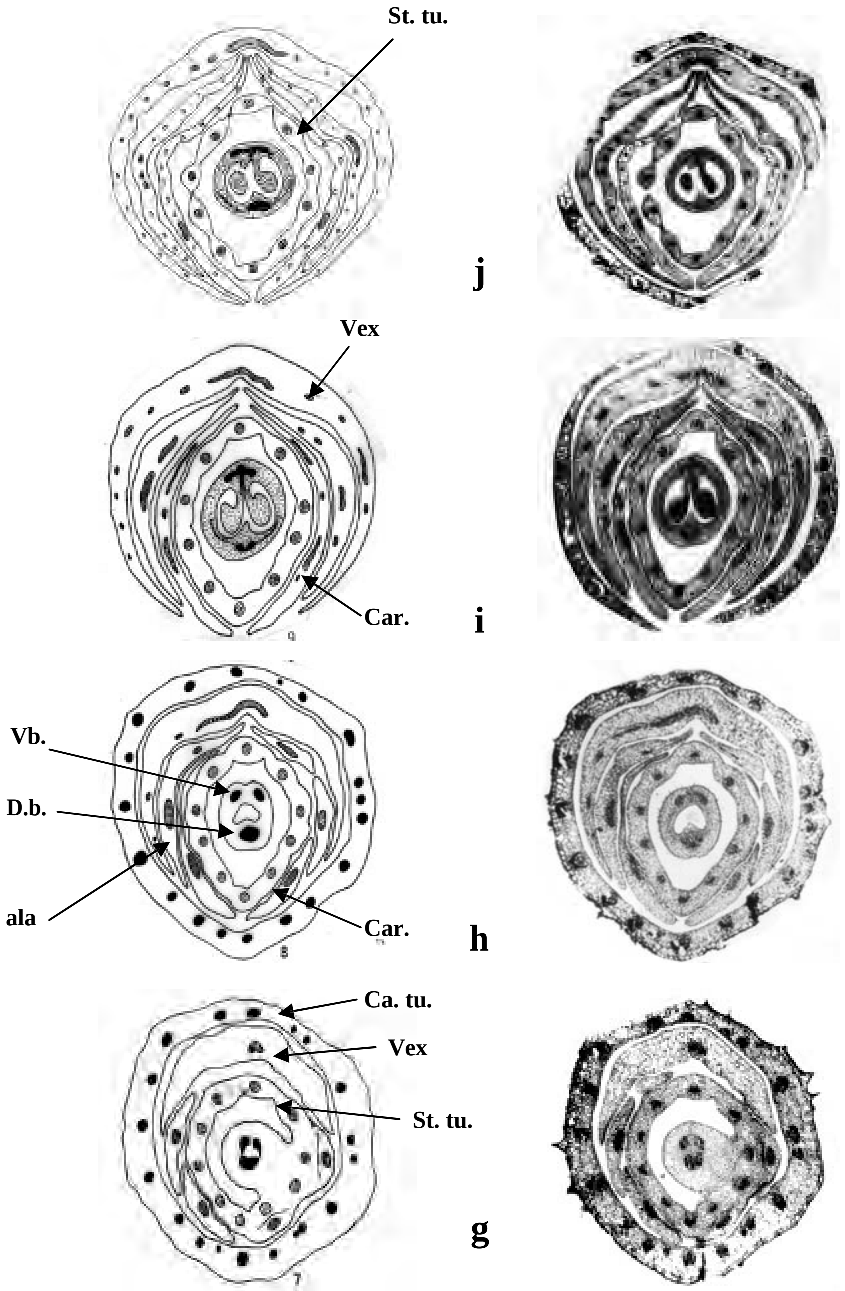


Fig. 2. (cont.). Floral vascularization of *Onionis vaginalis* (x 25). Car., Carina; Ca. tu., calyx tube; D.b., Dorsal bundle; St. tu., Stamen tube; V.b., Ventral bundle; Vex., Vexillum.

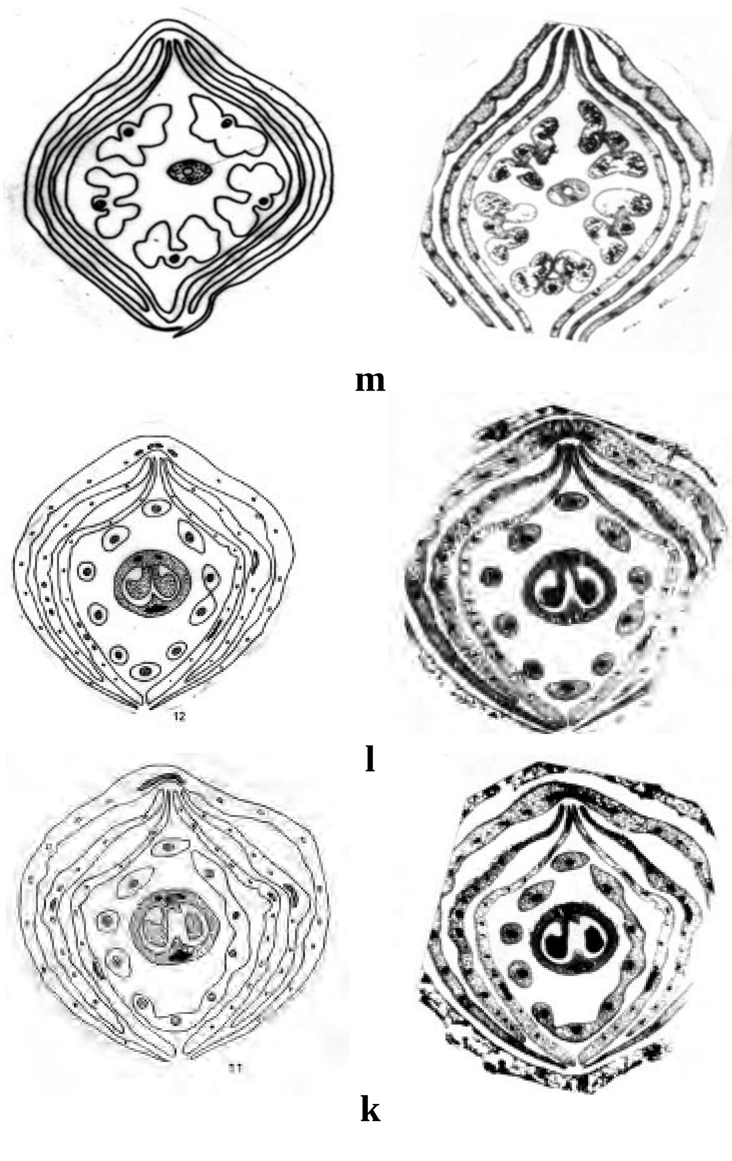


Fig. 2. (cont.). Floral vascularization of *Onionis vaginalis* (x 25).

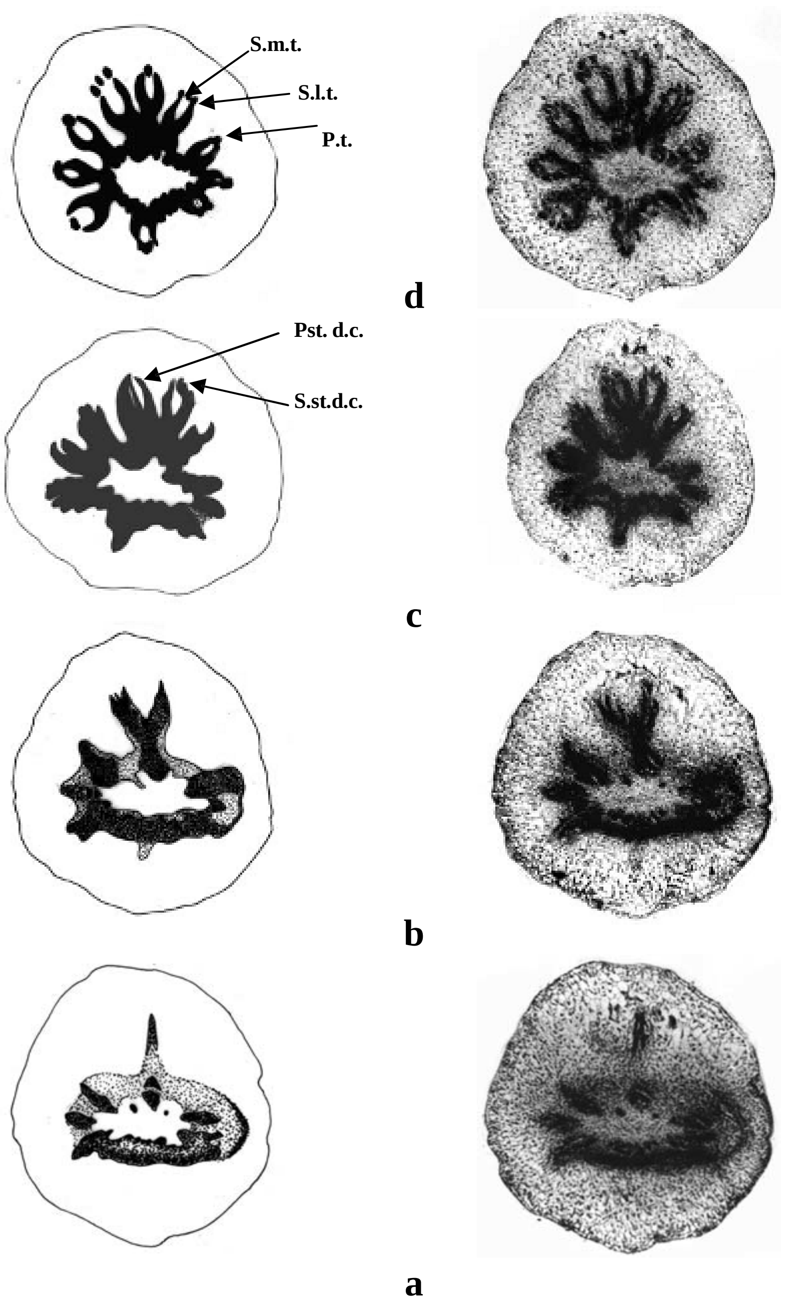


Fig. 3. Floral vascularization of *Dolichos lablab* (x 25). P.st.d.c., petal – stamen- disc complex ; P.t., petal trace; S.l.t., sepal lateral trace; S.m.t, sepal median trace; S.st.d.c., Sepal – stamen – dise comlex.

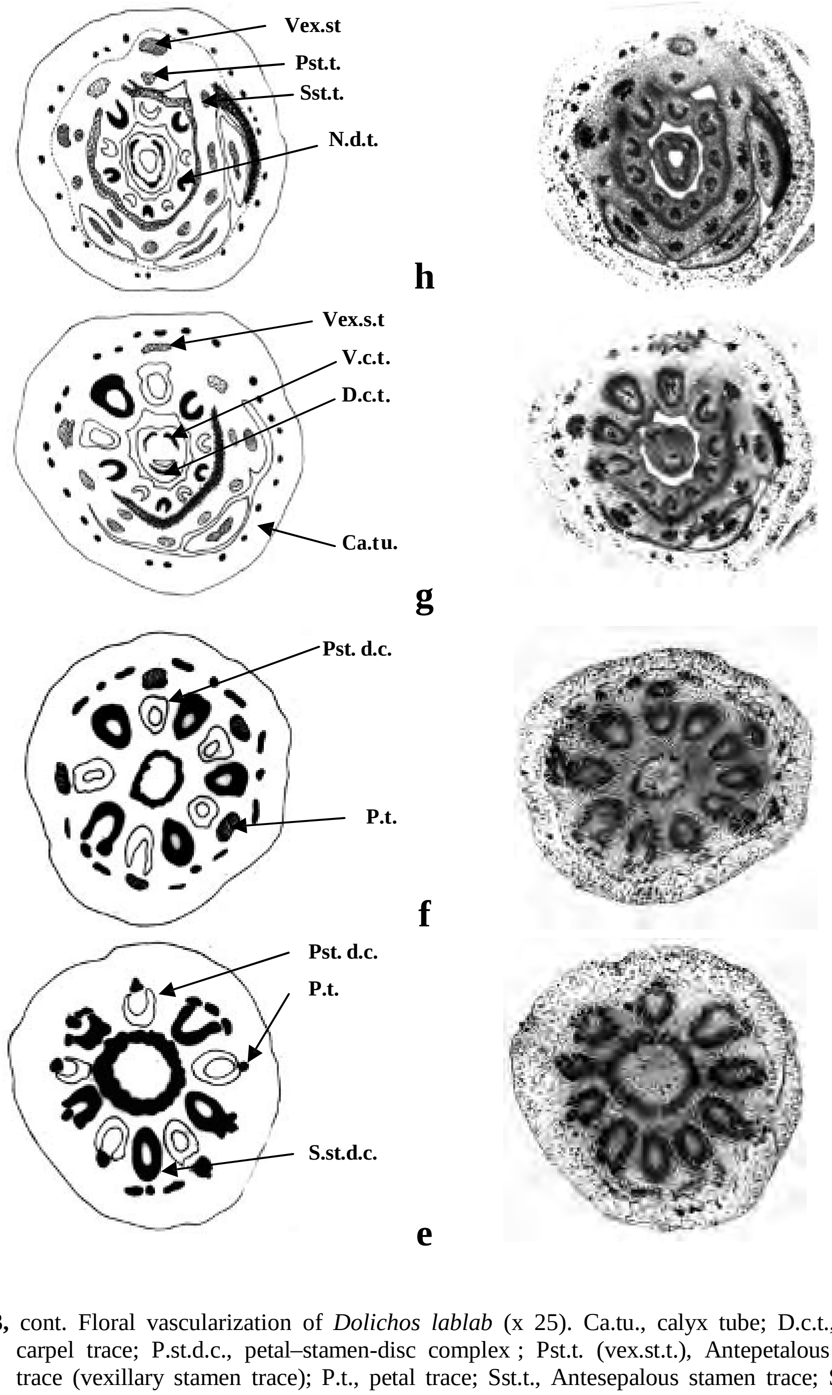
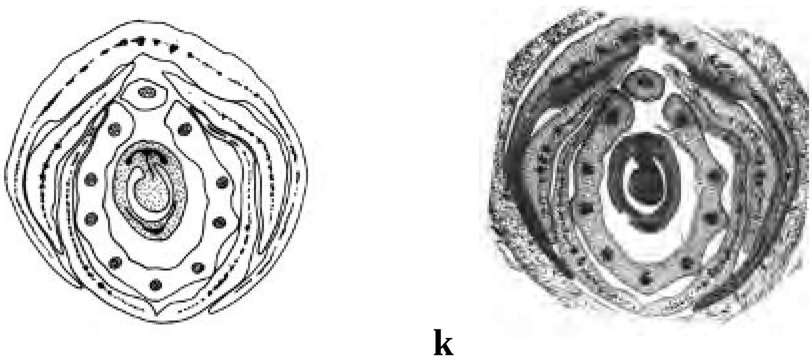
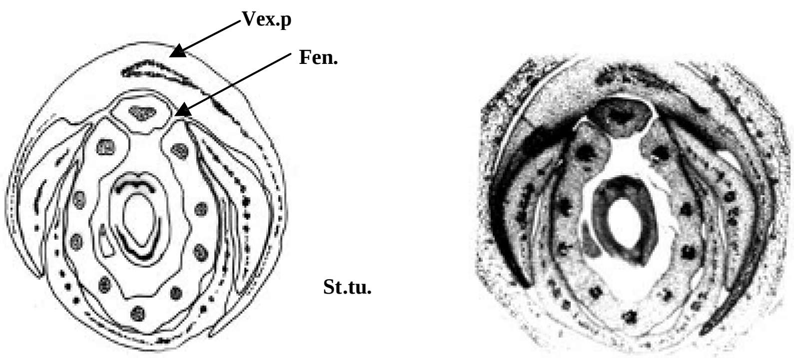


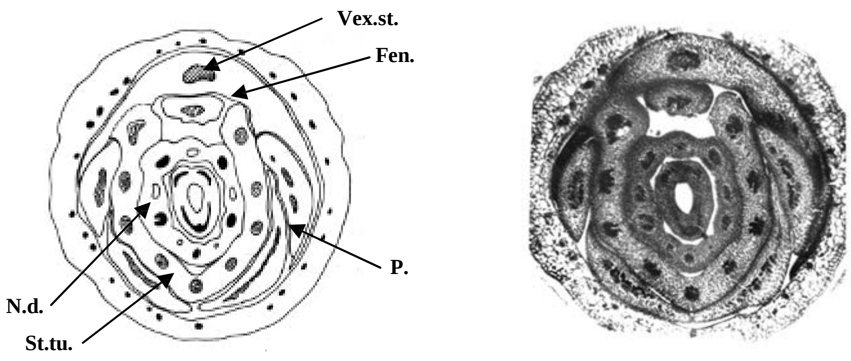
Fig. 3, cont. Floral vascularization of *Dolichos lablab* (x 25). Ca.tu., calyx tube; D.c.t., Dorsal carpel trace; P.st.d.c., petal–stamen-disc complex ; Pst.t. (vex.st.t.), Antepetalous stamen trace (vexillary stamen trace); P.t., petal trace; Sst.t., Antesepalous stamen trace; S.st.d.c., Sepal – stamen – disc complex, V.c.t., vertral carpel trace; Vex. st, Vexillary stamen.



k

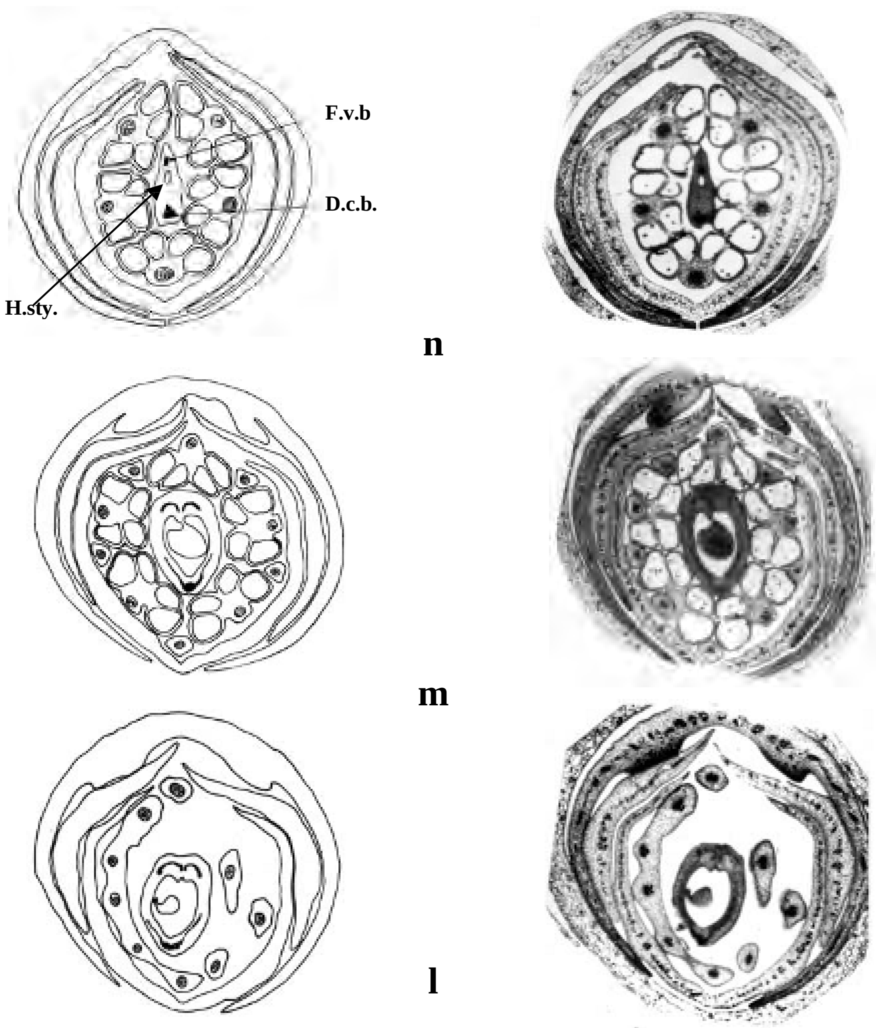


j



i

Figs. 3, cont. Floral vascularization of *Dolichos lablab* (x 25). Fen., Fenestra; N.d, Nictary disc; p.petal St. tu., Staminal tube, Vex. p., Vexillary petal; Vex. st., Vexillary stamen.



Figs. 3, cont. Floral vascularization of *Dolichos lablab* (x 25). D.c.b., dorsal carpel bundles; Fen., Fenestra; F.v.b., Fused ventral bundles, H.sty., Hollow style;

***Crotalaria aegyptiaca* (Fig.4)**
Case A , a flower with 10 united stamens

The receptacle is supplied by a continuous siphonostele (Fig.4a) which differentiates into 10 vascular protrusions (Fig.4 b&c). Each of the latter divides to give two masses lying on the same radius (Fig.4 c-g) ; and at a higher level the receptacle contains 20 vascular traces in two whorls: outer and inner (Fig. 4g). Five of the outer whorl form the sepal median traces (Fig.4i). The other five, still of the outer whorl, form the sepal lateral-petal complexes (Fig.4 i-j). The inner 10 traces represent the vascular supply to the ten stamens. All these traces are included in a hypanthial tissue (Fig.4 g-k). At a more higher level, the hypanthial tissue becomes broken into its components: the calyx tube being separated first, followed by a tissue formed of petals and stamens (Fig.4 l) . Finally the staminal tube becomes separated as fused 10 filaments (Fig.4n&o) and remains opened adaxially (Fig.4pi). The ovary is supplied by three traces; one dorsal and two ventrals (Fig. 4h); the latter remain distinct in the style (Figs.4q&r) and the stylar canal is provided by filamentous hairs at its top (Fig. 4t).

Case B , a flower with 10 distinct stamens

Floral vascularization is of the same plan as A except that the stamens arise distinct at the early beginning of their separation from the hypanthial tissue (Fig. 4p.ii).

Discussion

The receptacle vasculature in the three investigated species is more or less a continuous siphonostele. However, Gupta (1980), observed 10 vascular traces in the receptacle of other species of *Ononis*, namely *O. repens* and *O. spinosa*.

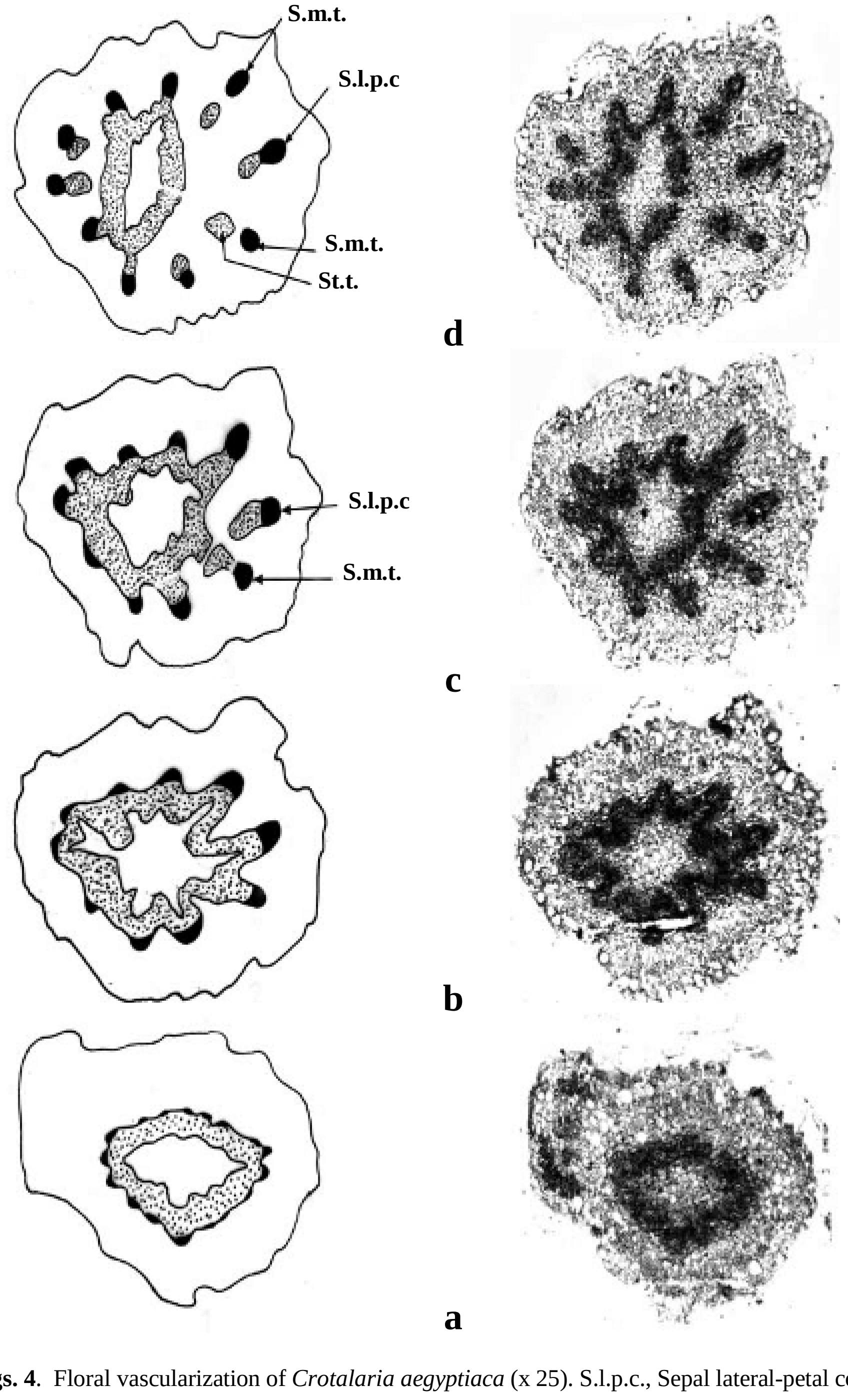
As regards the perianth and the stamen supply, Moore as early as 1936 referred to two types of vasculature in the papilionaceous Leguminosae. The Dihiate type of vasculature is with two cycles of traces supplying the perianth and the stamens. This type was further sub-divided into the *Baptisia* sub-type in which the calyx lateral traces are fused with the petal traces; and the *Lathyrus* sub-type in which the calyx laterals branch from the medians and fuse behind the petal traces. In the Unihiate type of vasculature, the perianth, stamens and the disc are supplied by one cycle of strands.

In the present work, the vasculature in *Ononis vaginalis* belongs to the Dihiate type, particularly the sub-type Baptisia , where two cycles of traces are recorded. The outer cycle is formed of ten traces; five of which are the sepal medians and the other five are the five laterals. The inner cycle is as well formed of ten strands; five of them are petal-stamen complexes and the other five are the stamen traces. Although our observations agree with those of Moore (1936 a) as regards the type, yet it was observed that the petal traces were not conjoint with the sepal laterals as he claimed. Murty and Gupta (1975) claimed that *Ononis repens* and *O. spinosa* belong to the same Dihiate type.

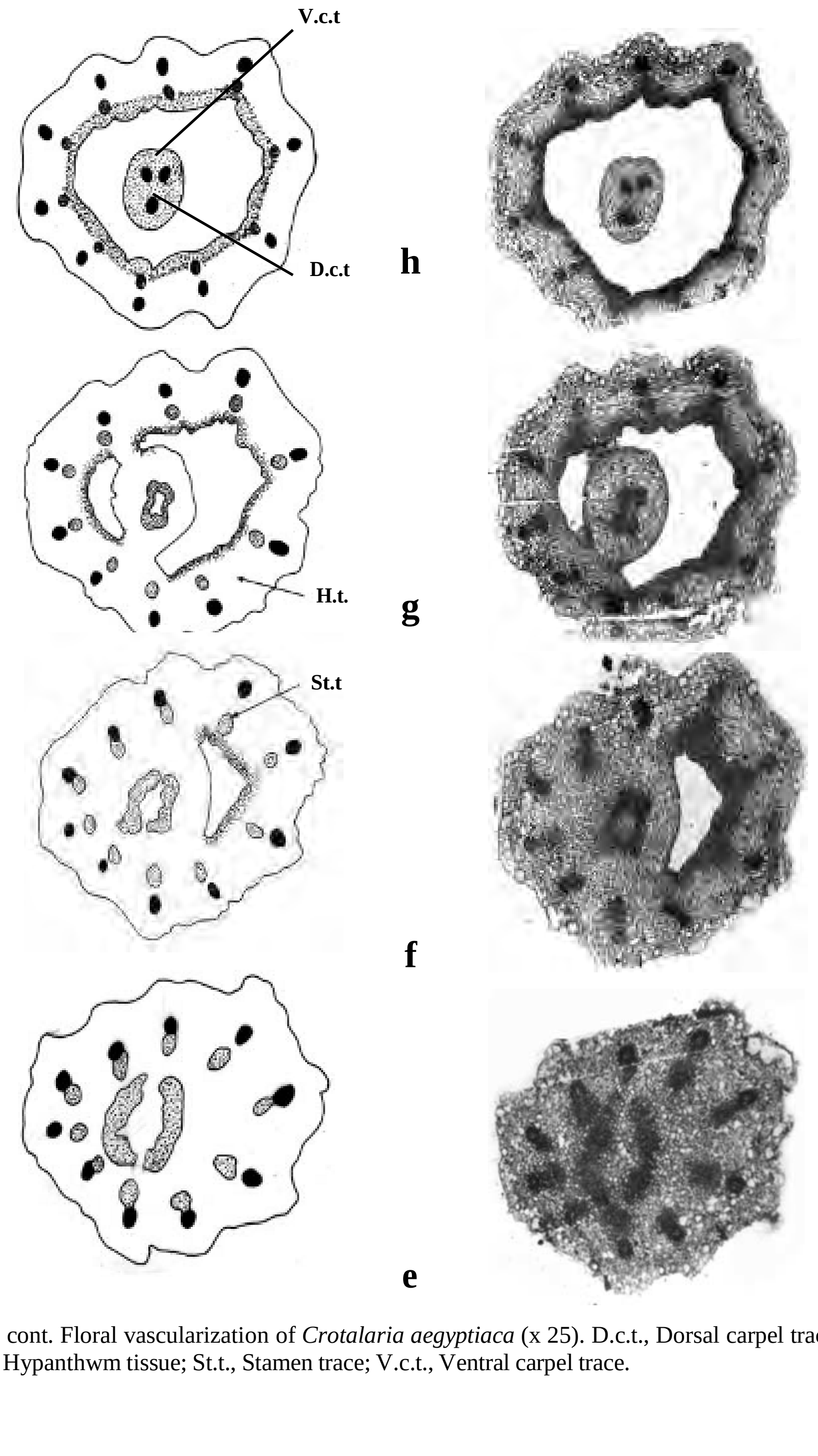
In *Dolichos lablab,* one cycle of 10 strands is observed. Five strands represent the vascular complexes to the sepal (both median & laterals) - antesepalous stamen-disc, and the other five represent five petal-antepetalous stamen-disc complexes.

In *Crotalaria aegyptiaca,* the ground plan of vascularization is the same as that of *Dolichos lablab* except for the fusion of the sepal laterals with the petal traces (not so in *Dolichos lablab*). Moreover, the stamen supply comes from one source viz. the original receptacular supply through a tangential division which tackes place in the whole set of strands; in addition to the lacking of the intrastaminal nectary disc.

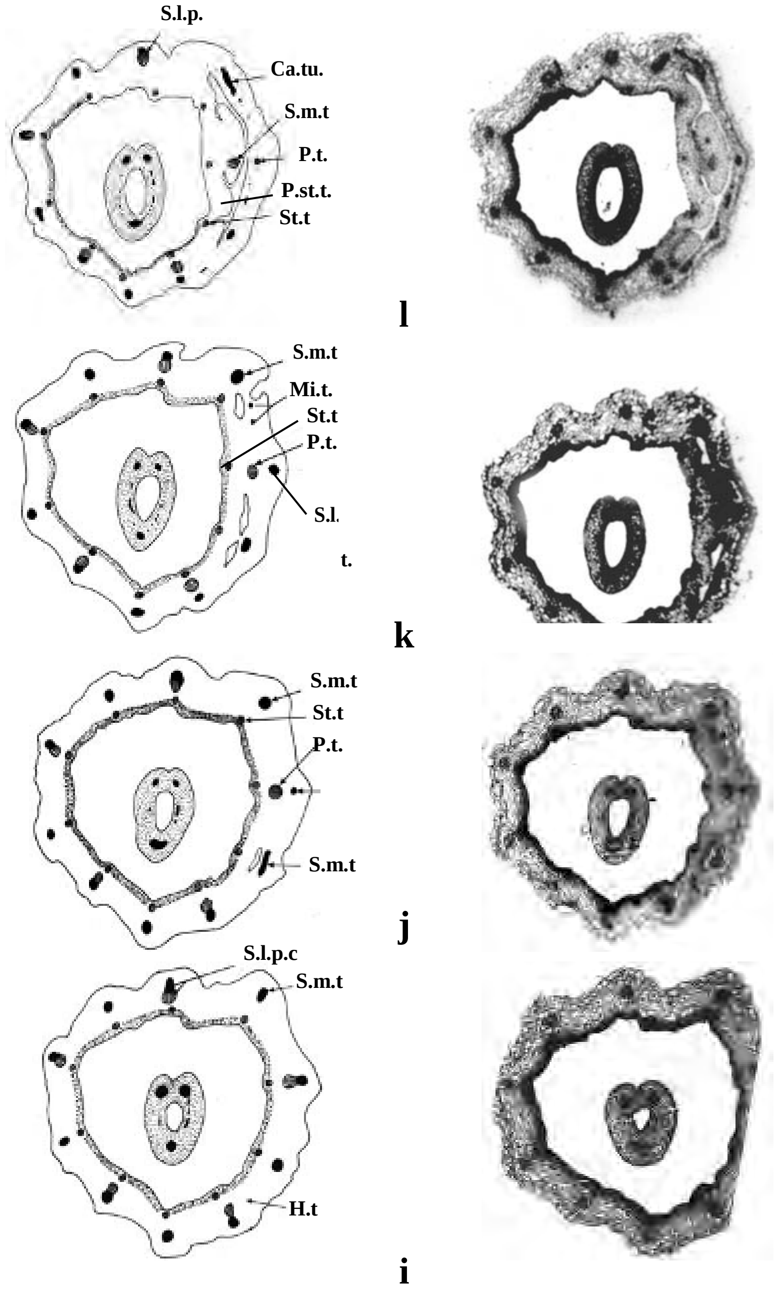
As regards the stamen adelphy, the anatomical investgation shows that the staminal traces are distinct from their early differentiation and remain as such throughout. Morphologically, the staminal filaments behave differently in the three species studied. In *Ononis vaginalis* the stamens are monadelphous with the filaments united to from a closed tube. In this species the intrastaminal nectary disc is lacking. In this respect our observation is in accord with Westerkamp & Weber (1999) who suggested that in taxa which are nectar-sterile, a fusion of all the 10 staminal filaments into a complete tube is observed.



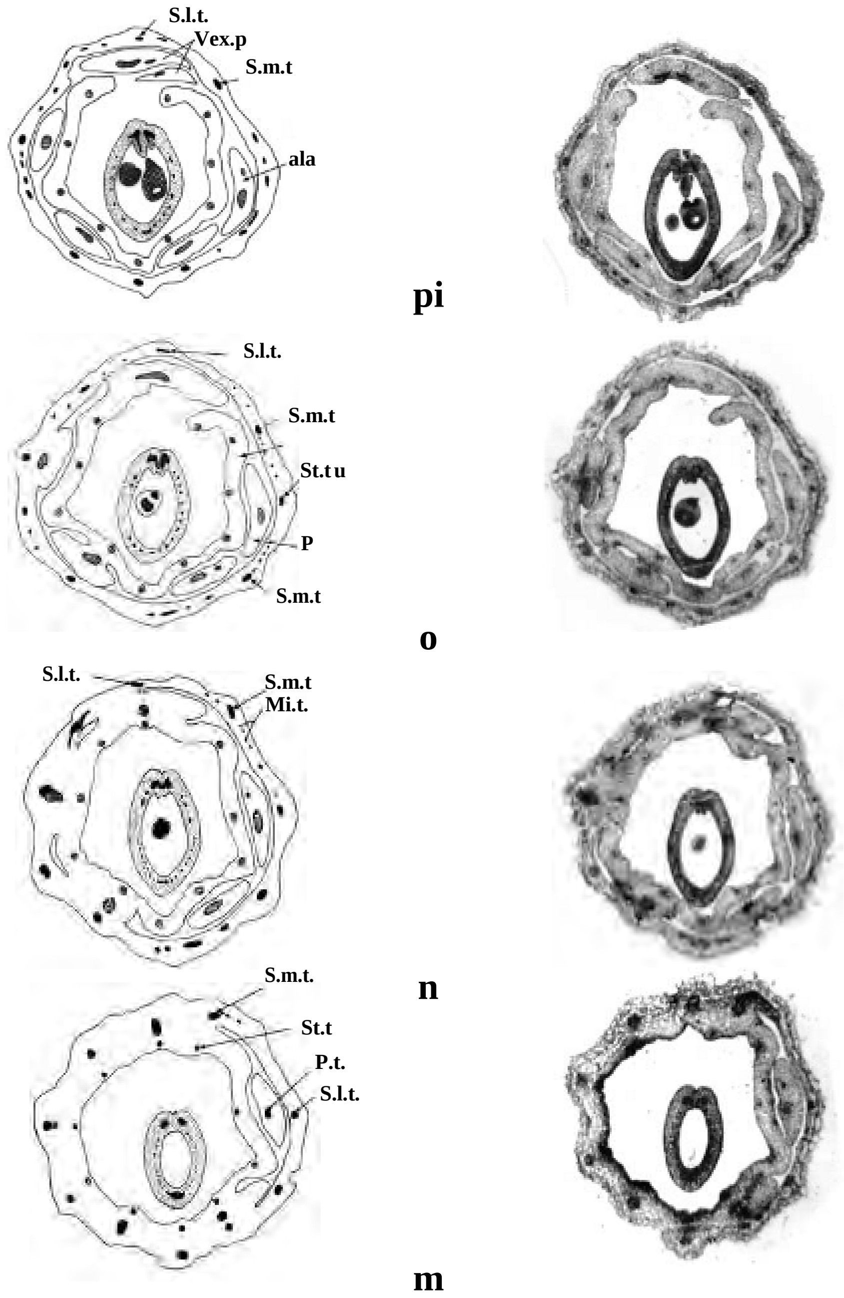
Figs. 4. Floral vascularization of *Crotalaria aegyptiaca* (x 25). S.l.p.c., Sepal lateral-petal complex; S.m.t., Sepal median trace; St.t., Stamen trace;



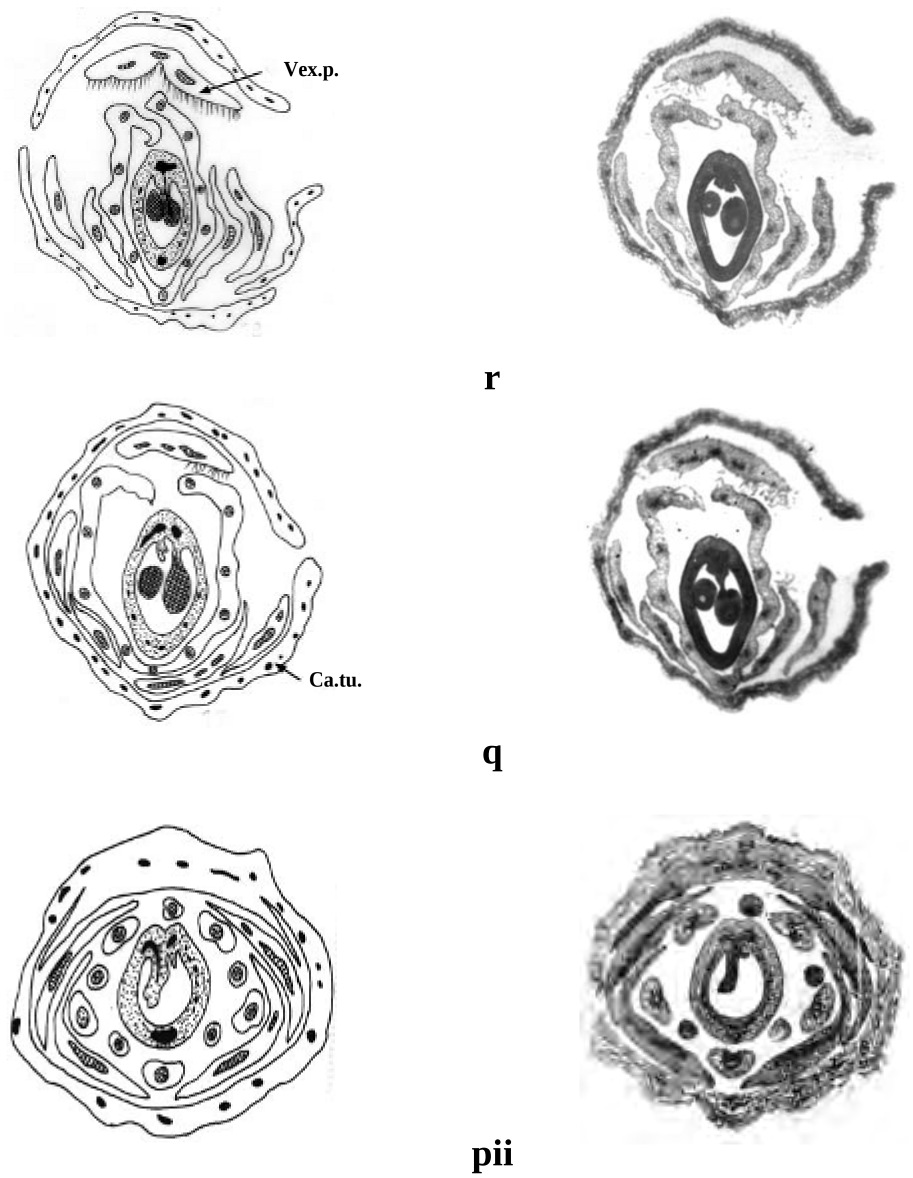
Figs. 4, cont. Floral vascularization of *Crotalaria aegyptiaca* (x 25). D.c.t., Dorsal carpel trace H.t., Hypanthwm tissue; St.t., Stamen trace; V.c.t., Ventral carpel trace.



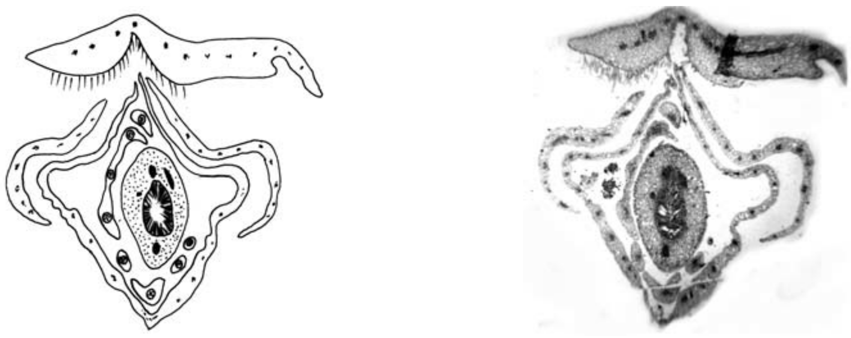
Figs. 4, cont**.** cont. Floral vascularization of *Crotalaria aegyptiaca*.(x 25). Ca.tu., Calyx tube; H.t., Hypanthium tissue (Calyx, Corolla & Androecium) ; Mi.t , Minor traces ; P.st.t, Petal-stamen tissue; P.t., Petal trace ; S.l.p..c, Sepal lateral –petal complex; S.l.t , Sepal lateral trace ; S.m.t, Sepal median trace ; St.t Stamen trace ; Vex. p., Vexillum petal.



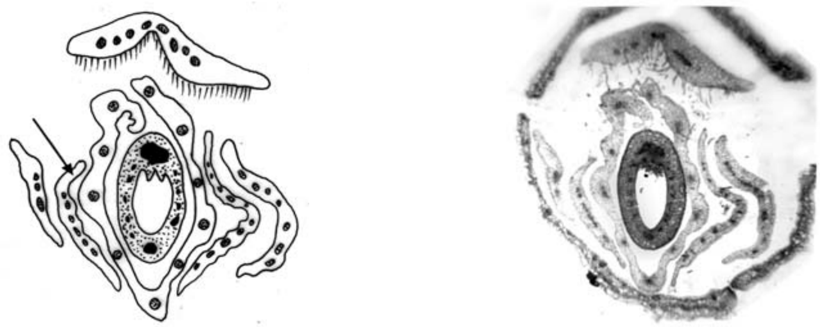
Figs. 4, cont. Floral vascularization of *Crotalaria aegyptiaca*.(x 25). Mi.t , Minor traces ; P. Petal ; P.t., Petal trace ; S.l.t , Sepal lateral trace ; S.m.t, Sepal median trace ; St.t Stamen trace ; St.tu .; Staminal tube ; Vex. p., Vexillum petal.



Figs. 4, cont. Floral vascularization of *Crotalaria aegyptiaca* **(x 25).** Ca. tu., Calyx tube; Vex.p., Vexillum petal.



t



s

Figs. 4, cont. Floral vascularization of *Crotalaria aegyptiaca* (x 25). Car., carina.

In *Crotalaria aegyptiaca*, apart from the case of the 10 distinct stamens, where the stamens are monadelphous, the staminal filaments are also united but the staminal tube is adaxially opened. Unlike *Ononis vaginalis* and *Crotalaria aegyptiaca,* the stamens in *Dolichos lablab* appear diadelphous at the base and monadelphous at the top. This monadelphy is reached at when the vexillary (adaxial) stamen differentiates as a distinct entity (diadelphy) but tends to adhere to the tube towards its top appearing as monadelphous. This mere adhesion makes it pseudomonadelphous. Where the vexillary stamen becomes separated from the tube below it leaves two fenestrae; one on each side. Here it seems logic to state that the presence of a nectary disc necessitates a nectar access (narrow orifices) to the visitor insect to ensure successful pollination and this access is the fenestrae. The same view was stated by Westerkamp & Weber (1999).Tucker (1989) concluded that the case of pseudomonadelphy is primarily diadelphous.

From the phylogenetic view point Tucker (1989) and Rodriguez – Riaňo *et al* (1999) suggested that the ten distinct stamens can behave to give either monadelphy or diadelphy; and the diadelphy in its turn can give rise to pseudomonadelphy.

As regards the nectary disc, Puri (1951) and Eames (1961) claimed that the floral nectaries in general have diverse morphological nature. Moore (1936 a), considered them to be of staminal nature in the papilionaceous Leguminosae. In the present work, the disc in *Dolichos lablab* receives its supply from the stamen traces and thus can be considered to be of foliar nature (staminal nature).

As regards the vascular supply of the gynoecium, the monocarpellate ovary in the three species is supplied by three traces; one dorsal and two ventrals and this represents the basic number of traces. In *Dolichos lablab,* the two ventral bundles fuse before passing into the style and the latter becomes supplied by two bundles only. In *Ononis vaginalis* and *Crotalaria aegyptiaca* the style is supplied by three bundles.

References

Carlquist, S. 1970. Towards acceptable evolutionary interpretations of floral anatomy. *Phytomorphology* 19: 339-362.

Eames, A. J. 1961. *Morphology of the Angiosperms*. The Mc Grow-Hill Inc. New York.

Gupta, M. 1980. Anatomy of the flower of *Ononis repens* and *O. spinosa. J. Ind. Bot. Soc.* 59: 366-369.

Henslow, G 1891. On the vascular systems of floral organs and their importance in the interpretation of the morphology of the flower. *Bot. J. Linn. Soc*. 28:151-197.

Johansen, D.A. 1940. *Plant Microtechnique*. New York Book Company.

Ladd, PG. 1994. Pollen presenters in the flowering plants form and function. *Bot. J. Linn. Soc.* 115:145-195.

Moore, J.A. 1936 a. The vascular anatomy of the flower in the papilionaceous Leguminosae I. *Am. J. Bot.* 23:279-290.

…………… 1936 b. The vascular anatomy of the flower in the papilionaceous Leguminosae II. *Am. J. Bot.* 23:349-355.

Murty, Y.S. and M., Gupta. 1975. Morphological studies in some species of *Ononis*. All India symp. On Form, Structure and Function in Plants (Abstr.): 31-32.

Polhill, R.M. 1976. Genisteae (Adans.) Benth. and related tribes (Leguminosae) *Bot. Syst.* 1:143-368.

Puri, V. 1951. The role of floral anatomy in the solution of morphological problems. *Bot. Rev*. 17: 471-553.

Rodriguez-Riaňo, T. Ortega - Olivencia, A. and Devesa, J.A. 1999. Types of androecium in the Fabaceae of SW Europe. *Ann. Bot*. 83: 109-116.

Sattler, R. 1972. Centrifugal primordial inception in floral development. *Adv. Pl. Morph*. 1972: 170-178.

Schrire, B.D. 1989. A multidescplinary approach to pollination biology in the Leguminosae In : Stirton, CH., Zarucchi, JL. eds. *Advances in Legume biology. Monographs in Systematic Botany from the Missouri Botanical Garden* 29:183-242.

Schutte, A.L. 1998. A re-evaluation of the generic status of *Amphithalea* and *Coelidium* (Fabaceae). *Taxon*. 47:55-65.

Sporne, K.R. 1958. Some aspects of floral vascular systems. *Proc. Linn. Soc. London* 169 :75-84.

Tucker, S.C. 1972. The role of ontogenetic evidence in floral morphology. *Adv. Pl. Morph.* 1972: 359-369.

……………..1987. floral initiation and development in legumes. In:Stirton CH,ed. *Advances in legume systematics*. *Royal Botanic Gardens, Kew* 3: 183-239.

……………..1989.Evolutionary implication of floral ontogeny in legumes. In : Stirton CH, Zarucchi JL. eds. *Advances in legume biology*. *Monographs in Systematic Botany from the Missouri Botanical Gardens* 29:59-75.

Westerkamp, C.1993.The Co-operation between the asymmetric flower of *Lathyrus latifolius* (Fabaceae – Vicieae) and its visitors. *Phyton* (Horn, Austria) 33: 121-137.

……………..1996. Pollen in bee-flower relations. Some considerations on mellittophily. *Botanica Acta* 109: 325-332.

……………..1997 a. Keel blossoms : bee flowers with adaptations against bees. *Flora* 142: 125-132.

…………… 1997 b. Flowers and bees are competitors – not parteners. Toward a new understanding of complexity in specialized bee flowers. *Acta Horticulturae* 437: 71-74. *(Proc. 7th International Symposium on Pollination, ed. KW. Richards).*

……………..&Weber, A. 1999. Keel floweres of the Polygalaceae and Fabaceae: A functional comparison. *Bot. J. Linn. Soc.* 129 :207-221.