Diversity and evolutionary trends in the floral characters of some taxa of Scrophulariaceae sensu lato

Magdy M. MOURAD
U. K. ABDEL-HAMEED
I. H. MARIAM
M. E. TANTAWY
Botany Department, Faculty of Science,
Ain Shams University, Cairo (Egypt)

Published on 26 June 2015

ABSTRACT
The diversity of the floral characters in 17 species of Scrophulariaceae Juss. (belonging to 12 genera) was carried out through the tracing of their states as pictured by the organ vascularization. According to the statement of evolution (floral criteria) the character states were given evolutionary grades and the latter were “clipped” to their corresponding taxa. Trends of evolution in the floral characters were found to be gamosepaly, sympetaly, bilateral symmetry, reduction trends in the number of stamens as well as their vascularization and the occasional presence of a placental vascular cord as a fusion product of the carpellary ventral traces. None of the taxa under investigation could be considered as advanced over the other since all retained mosaic evolution expressed by variation in the vascular pattern in sepals, petals, stamens and carpels. In addition the obtained data confirmed that the line of evolution inside tribe Antirrhineae is from Antirrhinum majus L. (representing less advanced case) to Kickxia aegyptiaca (L.) Nábělek (the most advanced studied species). Russelia equisetiformis Schlecht. & Cham. occupied the lowest position vs Scrophularia xantloglossa Boiss. (tribe Cheloneae). The ventral cord and lateral carpellary bundles pattern supported the taxonomic location of Paulownia tomentosa (Thunb.) and Torenia fournieri Linden ex E. Fourn. under family Scrophulariaceae.

KEY WORDS
Scrophulariaceae, evolution, floral morphology, floral anatomy.
INTRODUCTION

The family Scrophulariaceae Juss. contains about 270 genera and 5100 species (Mabberley 1997), which show a great morphological diversity in life forms. The traditional Scrophulariaceae had been divided into several monophyletic families: Scrophulariaceae, Plantaginaceae, Linderniaceae, Paulowniaceae, Schlegeliaceae, Phrymaceae, Calceolariaceae and Orobancheaceae (APG III 2009; Olmstead et al. 1995, 2001; Albach et al. 2005; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Schäferhoff et al. 2010).

Literature exemplified by those of Stebbins (1974; 1977), Cronquist (1988) and Stace (2011) direct the attention towards the study of the character states for a conceivable perception of the evolutionary trends. Among the floral characters of the Scrophulariaceae sympetaly, bilateral symmetry, stamen number and number in taxa having only three traces. Such traces may be in the form of vascular complex representing the evolutionary climax, resulting from the fusion of the traces carpellaires ventrales. Aucun des taxons étudiés ne peut être regardé comme particulièrement avancé sur un autre, car tous montrent une évolution en mosaïque, bien illustrée par la variation de l’architecture vasculaire des sépales, pétales étafines et carpelles. Les résultats obtenus confirment en outre qu’à l’intérieur de la tribu des Antirrhineae une direction évolutive ascendante peut être tracée depuis Anthericum majus L. to Kickxia aegyptiaca (L.) Nábělek. Dans la tribu des Cheloneae, Russelia equisetiformis Schlecht. & Cham. apparait moins avancée que Scrophularia xanthoglossa Boiss. La combinaison faisceau placentaire axial/faisceaux carpellaires latéraux confirme la position taxonomique de Paulownia tomentosa (Thunb.) Steud. et Toernia fournieri Linden ex E. Fourn. dans la famille des Scrophulariaceae.

MATERIAL AND METHODS

Flower buds of 17 taxa of Scrophulariaceae representing wild and horticultural species (nine and eight species respectively) were collected. The collecting data are shown in Table 1. The wild species were identified by the aid of Täckholm (1974) and Stebbins (1974). Evolutionary, there are diverse trends in the stamens, the change in number both increases and decreases and the sterilization through suppression of the differentiation of the archesporial tissue or their conversion to staminodes (Bessey 1915 and Stebbins 1974).

In concept adopted by Bessey (1915), Takhtajan (1969), Hutchinson (1973), Lawrence (1969), Stebbins (1974) and Stace (1984), the fusion of the carpellaries ventral bundles is an advance over their distinction. The presence of a compitum is more advanced than its absence. The floral nectaries are regarded phylogenetically more advanced than the extra floral nectaries (Frey-Wyssling 1933). To cite but a few we can refer to the work of Schäferhoff et al. (2010) on cladistic analysis of Lamiales.

The objective of the present work is the study of the floral anatomical characters of taxa under investigation; then matching the obtained results against the classical evolutionary statements accepted by several phylogenists.
embedded in paraffin wax, then sectioned at 10-15 μm according to Johansen (1940). Sections were stained in Crystal violet-Erythrosine combination. Microphotographs of specific structures were redrawn and presented in cumulative plates. Table 2 shows the microfloral characters and its grades. Table 3 show species and its corresponding grades they acquired and the sum of the evolutionary grades. The schematic placement showing the evolutionary trends of the studied taxa are shown in Table 4. Note: The lateral carpellary bundles (L.Cs) = Septal bundles.

RESULTS

RECEPTACLE CONDITION
The receptacle vascular supply shows continuous siphonostelic structure in all examined taxa (Fig. 1A).

CALYX CONDITIONS
The sepal median bundle diverged from sepal median-staminal complex as in Scrophularia xanthoglossa Boiss. (Fig. 1B, C) or from the central stele as in Patulonia tomentosa (Thunb.) (Fig. 1D, E), from petal-sepal marginal complex (Kickxia aegyptiaca) (Fig. 1F, G) or from both petal-sepal marginal complexes and sepal median bundle, and the petal trace derived from petal-sepal marginal complex (Torenia fournieri Linden ex E. Fourn.). I, J, petal supplied by a single trace, derived from the central stele, then branched into several accessory bundles in the corolla tube (Patulonia tomentosa), K, L, petal trace derived from both petal-sepal marginal complex and central stele (Veronica anagallis-aquatica L.). Abbreviations: P.B., petal bundle; P.M.B., petal median bundle; P.Sma.C., petal sepal marginal complex; P.T., petal trace; S.Ma.B., sepal marginal bundle; S.Ma.T., sepal marginal trace; S.M.B., sepal median bundle; Siph., siphonostele; Sm.St.C., sepal median staminal complex; St.T., staminal trace. Scale bars: 0.5 mm.

CORolla CONDITIONS
Each petal has a single trace derived from the central stele in different ways: from the central stele, then branched into several
accessory bundles in the corolla tube as in *Paulownia tomentosa* (Fig. 1I, J), or from petal-sepal marginal complex as in 15 taxa (Fig. 1H) or from both petal-sepal marginal complex & central stele as in *Veronica anagallis-aquatica* L. (Fig. 1K, L).

**ANDROECIUM CONDITIONS**

Five staminal traces splitted directly from the central stele and through their routes to the expressing morphological organs behave as follows:

**Five fertile stamens**

As in *Verbascum letourneuxii* Asch. & Schweinf., *V. sinatricum* Benth. and *V. sinuatum* L. (Fig. 2A), the posterior one is suppressed in corolla tube as in *Antirrhinum majus* (Fig. 2B) or represented in the staminode as in *Russelia equisetiformis* (Fig. 2C).

**Posterior trace (Staminode)**

Diverged from staminal dorsal carpellary complex, the two postero-lateral traces came from staminal ventral carpellary complexes and the two antero-lateral traces came from staminal lateral carpellary complexes as in *Anarrhinum pubescens* and *Kickxia aegyptiaca* (Fig. 2D-F).

**Posterior stamen and two postero-lateral traces**

Came from central stele and the two antero-lateral traces came from staminal lateral carpellary complexes as in *Linaria maroccana* Hook.f. (Fig. 2G).
Five traces
Diverged from sepal median staminal complexes, the posterior one suppressed in the corolla tube while the other four enter the four fertile stamens as in *Scrophularia xanthoglossa* (Fig. 2H).

Four traces split directly from the central stele as in *Digitalis purpurea* L., *D. lanata* Ehrh., *Psilostrophe lanata* and *Sutera cordata* (Fig. 2I, J), from the central stele & staminal lateral carpellary complex as in *Torenia fournieri* Linden ex E. Fourn. (Fig. 2K).

Two traces split directly from the central stele as in *Veronica anagallis-aquatica*, *V. anagalloides* Guss. and *V. catenata* Pellegr. (Fig. 2L).

**GYNOECIUM CONDITIONS**

**Dorsal carpellary bundles**
Two dorsal bundles arose directly from the central stele in 13 taxa (Fig. 3C). In *Anarrhinum pubescens*, *Antirrhinum majus*, *Kickxia aegyptiaca* and *Linaria maroccana* the anterior dorsal bundle arose directly from the stele while the posterior dorsal carpellary bundle arose from the staminal dorsal carpellary complex (Fig. 3A).

**Lateral carpellary bundles (Septal bundles)**
Originated directly from the central stele in seven studied taxa, (two for each carpel as in *Digitalis purpurea* and *D. lanata*, several as in *Russelia equisetiformis*, *Scrophularia xantho-
A – Wild Taxa

<table>
<thead>
<tr>
<th>Character</th>
<th>Character state (grade)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sepal number (A)</td>
<td>Five sepals (1) Four sepals (2)</td>
</tr>
<tr>
<td>Sepal union (B)</td>
<td>Free (1) United (2)</td>
</tr>
<tr>
<td>Sepal median trace source (C)</td>
<td>Central stele (1) Sepal median-staminal complex (2)</td>
</tr>
<tr>
<td>Sepal marginal trace source (D)</td>
<td>Central stele (1) Petal sepal marginal complex (2) Petal sepal marginal complex + sepal median bundle (3)</td>
</tr>
<tr>
<td>Sepal supply (E)</td>
<td>Numerous (1) One sepal four-traced + other sepals three-traced (2) Three traced (3)</td>
</tr>
<tr>
<td>Petal number (F)</td>
<td>Five petals (1) Four petals (2)</td>
</tr>
<tr>
<td>Corolla cohesions (G)</td>
<td>Corolla tube (1) Bilipped corolla tube (four &amp; one) (2) Bilipped corolla tube (two &amp; three)</td>
</tr>
<tr>
<td>Petal trace source (H)</td>
<td>Central stele (1) Stele + Petal sepal marginal complex (2) Petal sepal marginal complex (3)</td>
</tr>
<tr>
<td>Anther lobes (I)</td>
<td>All ditheccous (1) Two monothecous &amp; two diheccous (2) All monothecous (3)</td>
</tr>
<tr>
<td>Stamens (J)</td>
<td>Five fertile stamen (1) Four fertile + one staminode (2) Four fertile + one suppressed bundle (3) Four fertile (4) Two fertile (5)</td>
</tr>
<tr>
<td>Staminal trace number (K)</td>
<td>Five (1) Four (2) Two (3)</td>
</tr>
<tr>
<td>Staminal trace source (L)</td>
<td>From central stele (1) From central stele + one complex (2) All from one complex (3) From central stele + two complexes (4) From three complexes (5)</td>
</tr>
<tr>
<td>Dorsal carpellary bundle source (M)</td>
<td>Central stele (1) Central stele + staminal lateral carpellary bundle (2)</td>
</tr>
<tr>
<td>Lateral carpellary bundle number (N)</td>
<td>Numerous (1) Four (2) Two (3)</td>
</tr>
<tr>
<td>Lateral carpellary bundle source (O)</td>
<td>Dorsal carpellary mass (1) Central stele + dorsal carpellary mass (2) Central stele (3)</td>
</tr>
<tr>
<td>Ventral carpellary bundle number (P)</td>
<td>Central stele + staminal lateral carpellary complex (4) Staminial carpellary vascular supply + staminal lateral carpellary complex (5)</td>
</tr>
<tr>
<td>Ventral carpellary bundle behaviour (Q)</td>
<td>Four (1) Two (2) Ventral cord (3)</td>
</tr>
<tr>
<td>Disc (R)</td>
<td>Separated (1) Remain as it is (2) Fused (3)</td>
</tr>
<tr>
<td>Compitum (S)</td>
<td>Present with vasculature (1) Present without vasculature (2) Absent (3)</td>
</tr>
</tbody>
</table>

B – Horticultural Taxa

<table>
<thead>
<tr>
<th>Character</th>
<th>Character state (grade)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sepal number (A)</td>
<td>Five sepals (1) Four sepals (2)</td>
</tr>
<tr>
<td>Sepal union (B)</td>
<td>Free (1) United (2)</td>
</tr>
<tr>
<td>Sepal median trace source (C)</td>
<td>Central stele (1) Sepal median-staminal complex (2)</td>
</tr>
<tr>
<td>Sepal marginal trace source (D)</td>
<td>Central stele (1) Petal sepal marginal complex (2) Petal sepal marginal complex + sepal median bundle (3)</td>
</tr>
<tr>
<td>Sepal supply (E)</td>
<td>Numerous (1) One sepal four-traced + other sepals three-traced (2) Three traced (3)</td>
</tr>
<tr>
<td>Petal number (F)</td>
<td>Five petals (1) Four petals (2)</td>
</tr>
<tr>
<td>Corolla cohesions (G)</td>
<td>Corolla tube (1) Bilipped corolla tube (four &amp; one) (2) Bilipped corolla tube (two &amp; three)</td>
</tr>
<tr>
<td>Petal trace source (H)</td>
<td>Central stele (1) Stele + Petal sepal marginal complex (2) Petal sepal marginal complex (3)</td>
</tr>
<tr>
<td>Anther lobes (I)</td>
<td>All ditheccous (1) Two monothecous &amp; two diheccous (2) All monothecous (3)</td>
</tr>
<tr>
<td>Stamens (J)</td>
<td>Five fertile stamen (1) Four fertile + one staminode (2) Four fertile + one suppressed bundle (3) Four fertile (4) Two fertile (5)</td>
</tr>
<tr>
<td>Staminal trace number (K)</td>
<td>Five (1) Four (2) Two (3)</td>
</tr>
<tr>
<td>Staminal trace source (L)</td>
<td>From central stele (1) From central stele + one complex (2) All from one complex (3) From central stele + two complexes (4) From three complexes (5)</td>
</tr>
<tr>
<td>Dorsal carpellary bundle source (M)</td>
<td>Central stele (1) Central stele + staminal lateral carpellary bundle (2)</td>
</tr>
<tr>
<td>Lateral carpellary bundle number (N)</td>
<td>Numerous (1) Four (2) Two (3)</td>
</tr>
<tr>
<td>Lateral carpellary bundle source (O)</td>
<td>Dorsal carpellary mass (1) Central stele + dorsal carpellary mass (2) Central stele (3)</td>
</tr>
<tr>
<td>Ventral carpellary bundle number (P)</td>
<td>Central stele + staminal lateral carpellary complex (4) Staminial carpellary vascular supply + staminal lateral carpellary complex (5)</td>
</tr>
<tr>
<td>Ventral carpellary bundle behaviour (Q)</td>
<td>Four (1) Two (2) Ventral cord (3)</td>
</tr>
<tr>
<td>Disc (R)</td>
<td>Separated (1) Remain as it is (2) Fused (3)</td>
</tr>
<tr>
<td>Compitum (S)</td>
<td>Present with vasculature (1) Present without vasculature (2) Absent (3)</td>
</tr>
</tbody>
</table>

Table 2. — Microfloral characters, their states and grades of taxa under investigation.
VENTRAL CARPELLARY BUNDLES
As ventral cord in six studied taxa (fusion of four ventral carpellary bundles) throughout. In *Sutera cordata* the ventral cord at slightly higher level separated into two distinct masses (each one is fusion of two ventrals, Fig. 4A, B). In the form of two distinct masses one for each carpel in nine taxa (Fig. 4C). In *Verbascum* spp. and *Anarrhinum pubescens* the two masses fused above in the form of ventral cord (Fig. 4D, E). The four ventral bundles at the beginning fused into two masses at a higher level as in *Paulownia tomentosa* (Fig. 4E, G). In all the studied taxa the ventral carpellary bundles originated from the central stele except in *Kikiaea aegyptica* from staminal carpellary vascular supply (Fig. 4H-J). However the ventral bundles after feeding the ovules fade out at the top of the ovary.

NECTARIFEROUS DISC CONDITIONS
Non-vascularized disc in 12 out of 15 studied taxa (Fig. 4K) or vascularized in *Digitalis purpurea*, *D. lanata* (vascularity originated from the dorsal and lateral carpellary bundles, Fig. 4L) and *Russelia equisetiformis* (from the remnants of petal and staminal supply, Fig. 4C). Out of all studied taxa, ten taxa possess a compitum.

DISCUSSION
Calyx vasculature patterns of *Paulownia tomentosa* is considered a valuable diagnostic character that helps in getting separated from the related studied taxa. This is supported by the concept of Pennell (1935), Nakai (1949), Takhtajan (1980), Olmstead et al. (2001), APG III (2009), and Schäferhoff et al. (2010).

The androecium vasculature (number and behavior) shared in the separation of studied *Digitalis* species from *Veronica* spp. in two distinct tribes viz. Digitalaceae & Veronicaeae respectively and this agrees with Bellini (1907), Rouy (1909), Pennell (1921), Melchior (1964), Thieret (1967) and Oxelman et al. 2005. *Torenia fournieri* separated away from the studied taxa based on data obtained from androecium vasculature as reached by Rahmanzadeh et al. 2005 and APG III 2009, Schäferhoff et al. 2010, separated it according to chloroplast sequences.

Data of lateral carpellary bundles (septal bundles) confirmed that *Paulownia tomentosa* is more related to Scrophulariaceae than Bignoniaceae and this agrees with the concepts of: Piechura (1980), Armstrong (1985), Guèdès (1974), Olmstead & Reeves (1995) and Spangler & Olmstead (1999). The presence of a ventral cord is considered a valuable taxonomic character confirming that *Torenia fournieri* is more related to Scrophulariaceae than Linderniaceae as reached by Bentham (1846), Wettstein (1891), Fischer (1992; 2004), Albach et al. (2005a) and Oxelman et al. (2005), and disagree with the work of Schäferhoff et al. (2010). *Paulownia tomentosa* goes away from the related studied taxa on the basis of ventral cord and this conclusion is supported by Pennell (1935), Nakai (1949), Takhtajan (1980), Olmstead et al. (2001), APG III (2009), Schäferhoff et al. 2010.

The vascularized or non-vascularized disc and compitum are considered as characters of taxonomic value sharing in separation of studied *Digitalis* from *Veronica* species in Digitalaceae and Veronicaeae respectively as reached by Bellini (1907), Rouy (1909), Pennell (1921), Melchior (1964), Thieret (1967) and Oxelman et al. (2005). As regards its nature, the nectary disc in the present work can be referred as of foliar nature in *Digitalis purpurea*, *D. lanata* and *Russelia equisetiformis* and of receptacular nature in the rest of the studied taxa.

EVOLUTIONARY EVALUATION
Surveying all the recorded characters, the vasculature cases met with show marked plasticity thus leading to different evolutionary levels in the studied taxa. A character state as an evolutionary evidence is governed by the statement of evolution set forth by a number of taxonomists, headed by Bessey (1915), and of all the statements those about the flower are of our present concern.
The application of the statement to the character states leads to the postulation of some evolutionary grades which can be arranged in an ascending order and can further be “clipped” to the taxa. However, it is quite clear that any taxon do not get all the higher nor the lower grades of the character. In other words any taxon presents a mosaic of less and more advanced characters and the judgment that a particular taxon is the most primitive or the most advanced will certainly be a bias.

Convinced by the above generally applicable concept and in view of the present data the most important trends in the evolution of the floral characters in Scrophulariaceae are subsequently presented.

**At tribe level**

**In tribe Antirrhinaceae**

The line of evolution is from the less advanced *Antirrhinum majus* to the more advanced *Kickxia aegyptiaca*. The latter exhibits a considerable number of advanced characters *viz*. sepal marginal, petal, staminal and carpel supply evolved from vascular complexes, bilipped corolla tube (2,3), four fertile stamens and one staminode, two ventral carpellary bundles, absence ofnectary disc and presence of comitum.

*Antirrhinum majus* exhibits some of less advanced characters *viz*. distinct five sepals with sepal median bundles arose from central stele, sepal bundles numerous, five petals, ditheccous anthers, five staminal traces, the latter with dorsal carpellary bundles coming from central stele while the lateral carpellary bundles from dorsal carpellary mass. *Anarrhinum pubescens* and *Linaria maroccana* are the intermediate ssp. of this tribe exhibiting amalgamation between advanced and less advanced characters.

**In tribe Cheloneae**

*Russelia equisetiformis* occupies the lowest position vs. *Scrophularia xanthoglossa*. The former species exhibits a considerable number of less advanced characters *viz*. five distinct sepals, sepal median bundles origin from the central stele, numerous sepal vascular bundles, five petals, ditheccous anthers, five staminal traces from the central stele, dorsal carpellary bundles arose from the central stele, lateral carpellary bundles numerous, nectariferous disc vascularized and the compitum is wanting. *Scrophularia xanthoglossa* shows several advanced characters *viz*. sepal median, sepal marginal and petal bundles protruding from vascular complexes, bilipped corolla tube (2,3), monothecous anthers, one suppressed staminal bundle, two ventral carpellary bundles, non-vascularized nectariferous disc and presence of a compitum. *Paulownia tomentosa* acquired the second level of primitiveness after the *Ruselia* among the studied taxa, owing to the subsequent characters *viz*. five sepals, sepal median, sepal marginal, petal, staminal and dorsal carpellary bundles arising from the central stele, five petals, ditheccous anthers, lateral carpellary bundles from the dorsal carpellary mass, four ventral carpellary bundles and absence of compitum.

**In tribe Gratioleae**

*Torenia fournieri* occupies a highest status through sepals united, sepal marginal, petal and lateral carpellary bundles originated from vascular complexes, corolla bilipped (2,3), four staminal traces, ventral cord and non-vascularized nectariferous disc.

**In tribe Digitaleae**

*Veronica anagallis-aquatica, V. anagalloides & V. catenata* occupied highest level of evolution due to the following advanced characters *viz*. four sepals, the sepal marginal, petal supply arising from...
vascular complexes, one sepal four-traced and the remaining ones three-traced, four petals, two staminal traces, two lateral carpellary bundles, presence of ventral cord and non-vascularized nectary disc.

**In tribe Manuleae**

*Digitalis lanata* and *Sutera cordata* occupied an intermediate level among the studied taxa exhibiting heterogeneous characters (advanced & primitive). *Digitalis lanata* exceeds *D. purpurea* owing to its bilipped corolla.

**In tribe Verbascaceae**

*Verbascum letourneuxii*, *V. sinaticum* and *V. sinuatum* occupy primitive status due to the less advanced characters size, five distinct sepals, sepal median, staminal and dorsal carpellary bundles from the central stele, five petals, dithecous anthers, five staminal traces originated from the central stele to five fertile stamens and numerous lateral carpellary bundles. Absence of nectariferous disc raises *Verbascum letourneuxii* over *V. sinaticum* and *V. sinuatum*.

**AT SUBFAMILY LEVEL**

*Antirrhineae*

Antirrhineae acquired the most advanced position in Antirrhinoideae, this is in accord with Pennell (1935) and Thieret (1976), and disagrees with Schäferhoff et al. (2010). Tribe Gratiolaeae acquired an advanced position in the present study, this agrees with Bentham & Hooker (1876) and Wettstein (1891), and disagrees with Pennell (1935) and Thieret (1976).
Psuedosolaneae

Psuedosolaneae occupied the primitive position including Verbasceae which was considered as the most primitive tribe (Wettstein 1891).

Rhinanthoideae

Rhinanthoideae is considered as intermediate subfamily in between the advanced Antirrhinoideae and the primitive Psuedosolaneae.

From the all foregoing data, the states of the most significant floral morphological attributes are dealt with and arranged in an evolutionary order. The sum of the values given to a taxon is considered as evolutionary score for that taxon. Based on these scores, the taxa under investigation showed 12 grades having corresponding score ranging from 27 to 41 (Table 4).

CONCLUSION

The obtained data confirmed that the line of evolution inside tribe Antirrhineae is from *Antirrhinum majus* (representing less advanced case) to *Kickxia aegyptiaca* (the most advanced studied species). *Russelia equisetiformis* occupied the lowest position vs *Scrophularia xanthoglossa* (tribe Cheloneae). The ventral cord and lateral carpellary bundles pattern studied species).

The ventral cord and lateral carpellary bundles pattern of Problem Genera.

REFERENCES


Puri V. 1951. — The role of floral anatomy in the solution of morphological problems. *Botanical Review* 17: 471-553


Submitted on 2nd May 2013; accepted on 17 February 2014; published on 26 June 2015.