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

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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 xanthoglossa* 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.

RÉSUMÉ

Diversité et tendances évolutives des caractères floraux de quelques taxons de Scrophulariaceae sensu lato. La diversité florale de 17 espèces de Scrophulariaceae Juss. (appartenant à 12 genres) a été analysée à travers les états de caractères définis par la vascularisation des organes. Dans une perspective évolutive, des degrés d'avancement ont été attribués à ces états de caractères et rattachés aux taxons correspondants. Les tendances évolutives de la fleur sont la gamosépalie, la sympétalie, la symétrie bilatérale, la réduction du nombre d'étamines et de leur vascularisation, ainsi que la formation d'un faisceau placentaire axial, résultant de la fusion des 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 étamines et carpelles. Les réultats obtenus confirment en outre qu'à l'intérieur de la tribu des Antirrhineae une direction évolutive ascendante peut être tracée depuis *Antirrhinum majus* L. to *Kickxia aegyptiaca* (L.) Nábělek. Dans la tribu des Cheloneae, *Russelia equisetiformis* Schlecht. & Cham. apparaît moins avancée que *Scrophularia xanthoglossa* Boiss. La combinaison faisceau placentaire axial/faisceaux carpellaires latéraux confirme la position taxonomique de *Paulownia tomentosa* (Thunb.) Steud. et *Torenia fournieri* Linden ex E. Fourn. dans la famille des Scrophulariaceae.

MOTS CLÉS
Scrophulariaceae, évolution, morphologie florale, anatomie florale.

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 Orobanchaceae (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 as well as fertility in addition to the aspect of ovarian vascular supply proved in many places to be not only diagnostic for species delimitation but also useful in the evolutionary evaluation of this family relative to Sympetalae associates.

Different approaches for the understanding of character patterns are continuously tried. Studies on floral anatomy, especially those on the vascularization patterns and its disposal have been strongly recommended since 1951 when Puri's review clearly demonstrated cases about many morphological problems that were solved following this approach.

The evolutionary line is from five sepals to four and the fusion of sepals forming synsepalous calyx has occurred repeatedly in many evolutionary lines, and it is usually intercalary rather than congenital. The sepal supply may be numerous (the primitive case), an evolutionary climax is reached by a progressive decrease in the number in taxa having only three traces. Such traces may be derived from the same source (Warner 1933; Lindsey 1938; Rao 1949) which was considered as the primitive case than from different sources (Joshi 1942) these different sources may be in the form of vascular complex representing the evolutionary climax. An acceptable concept is that the evolutionary shift is from radial to bilateral symmetry. Meanwhile, the zygomorphic corolla has long been considered an adaptive mechanism for entomophily (Delevoryas 1962; Hufford 1992) and this entomophily becomes more secured by the presence of a nectary disc for the visiting vectors (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 carpellary 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.

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 Boulos (2002) while the horticultural ones by Bailey (1949) and Bailey & Bailey (1976). The wild species were further matched against dried specimens in the Herbarium at Ain Shams University, Faculty of science (CAIA), Cairo University, Faculty of science (CAI), Flora and Phytotaxonomy Research Department (CAIM) and Orman Botanical Garden (Geiza). Voucher specimens of the studied taxa were kept in CAIA.

The mature flower buds of the taxa under the investigation were fixed and preserved in formalin-aceto-alcohol (F.A.A.),

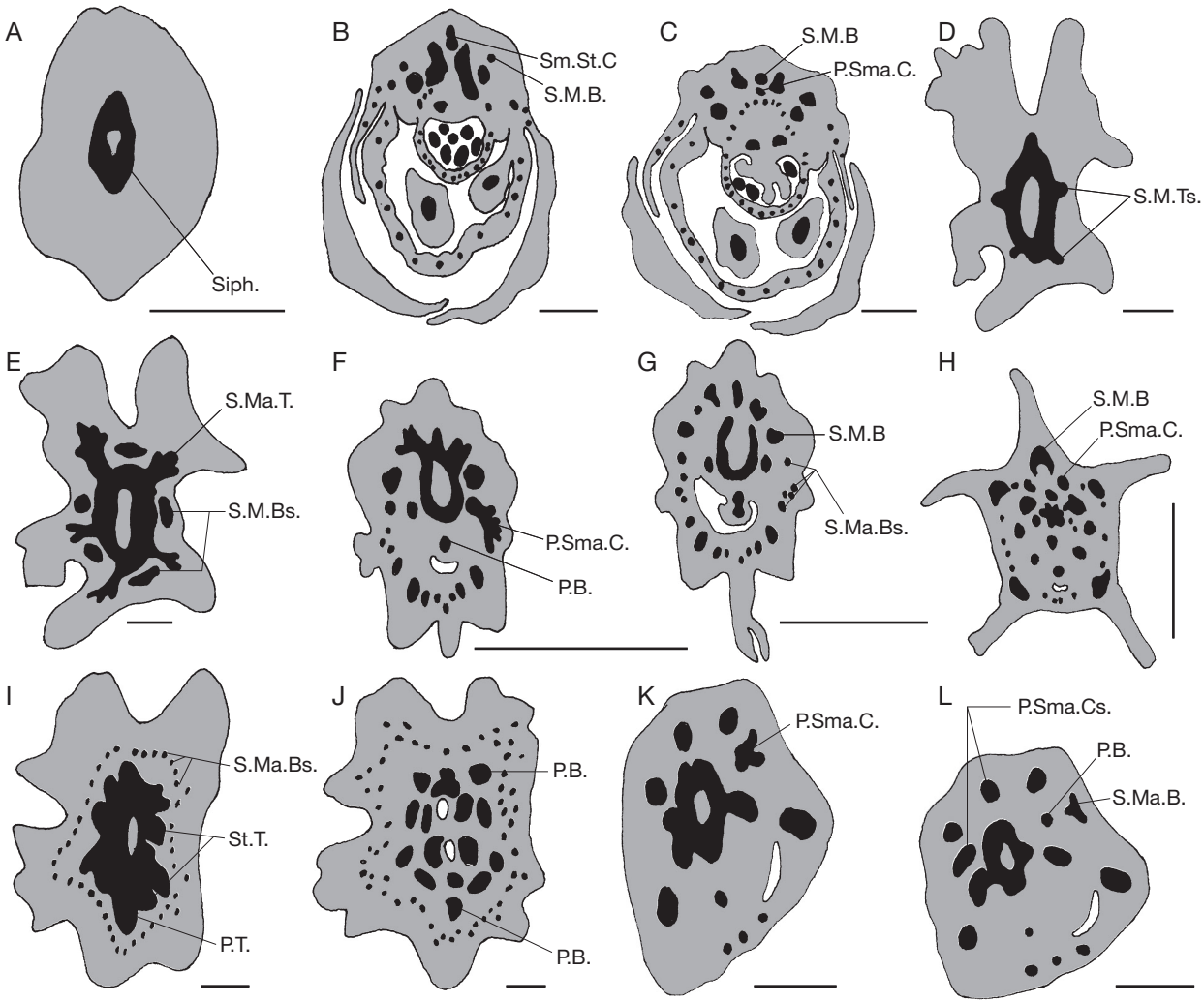

Fig. 1. — Receptacle, calyx and corolla conditions: **A**, receptacle vascular supply shows continuous siphonostelic structure (*Anarrhinum pubescens* Fresen. Hort. ex Loudon); **B**, **C**, sepal median bundle diverged from sepal median-staminal complex (*Scrophularia xanthoglossa* Boiss.); **D**, **E**, sepal marginal bundles came from the central stele (*Paulownia tomentosa* (Thunb.)); **F**, **G**, sepal marginal bundles came from petal-sepal marginal complex (*Kickxia aegyptiaca*); **H**, sepal marginal bundles came 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 (*Paulownia 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.

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 the remaining studied taxa (16 taxa). The sepal marginal bundles came either directly from the central stele as in *Paulownia tomentosa* (Thunb.) (Fig. 1D, E), from petal-sepal marginal complex as in *Anarrhinum pubescens* Fresen. Hort. ex Loudon, *Antirrhinum majus* L., *Kickxia aegyptiaca* (L.) Nábělek, *Russelia equisetiformis* Schlecht. & Cham. and *Scrophularia xanthoglossa* (Fig. 1F, G) or from both petal-sepal marginal complexes and sepal median bundle in the remaining 11 studied taxa (Fig. 1H).

Corolla conditions

Each petal has a single trace derived from the central stele in different ways: from the central stele, then branched into several

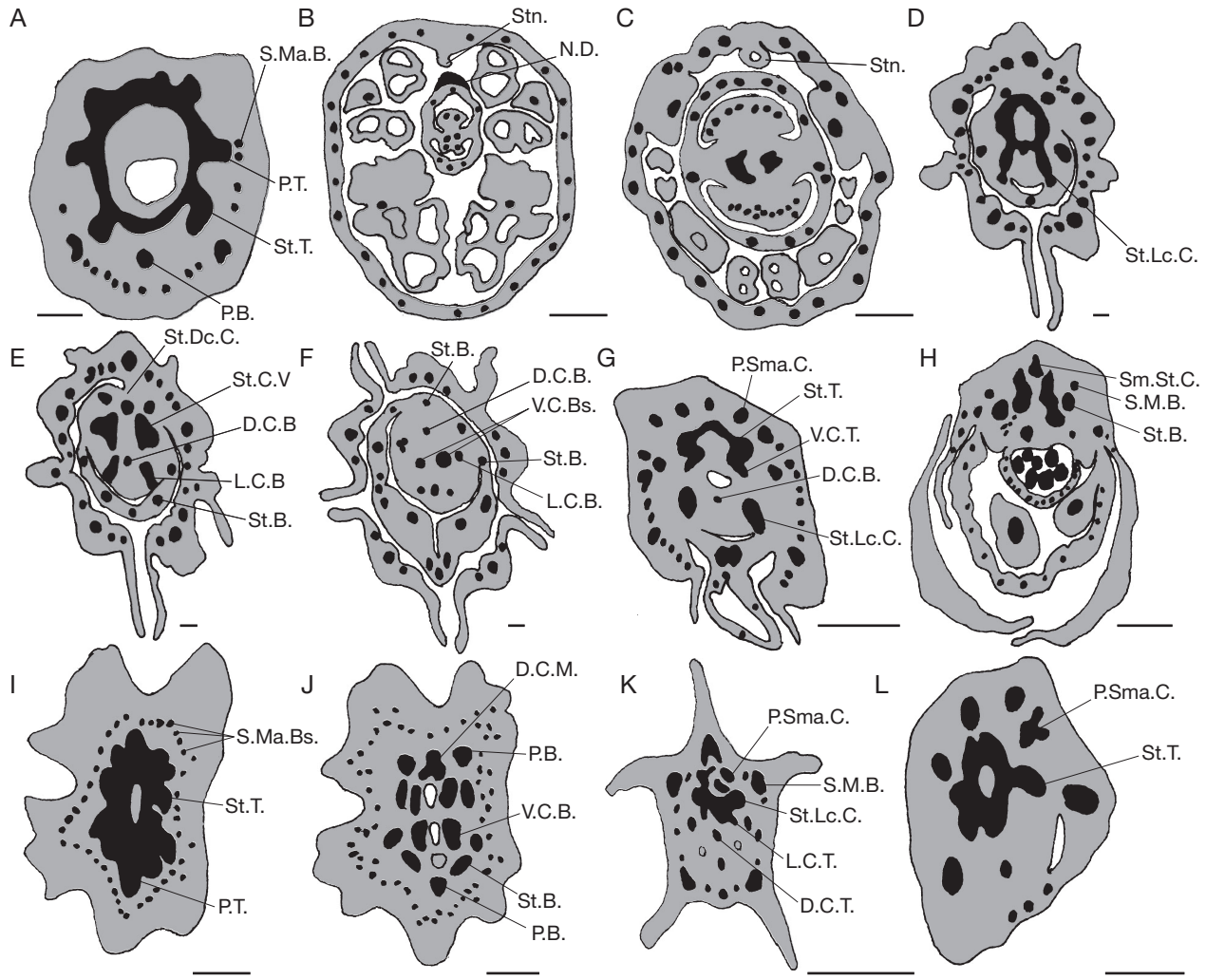

Fig. 2. — Androecium conditions: **A**, five staminal traces splitted from the central stele supplying five fertile stamens (*Verbascum letourneuxii* Asch. & Schweinf.); **B**, posterior staminal trace suppressed in corolla tube (*Antirrhinum majus* L.); **C**, posterior staminal trace represented by staminode (*Russelia equisetiformis* Schlecht. & Cham.); **D**-**F**, five staminal traces diverged from both staminal dorsal carpellary complex and staminal lateral carpellary complex, and staminal ventral carpellary complex (*Kickxia aegyptiaca* (L.) Nábělek); **G**, five staminal traces diverging from staminal lateral carpellary complex and central stele (*Linaria maroccana* Hook.f.); **H**, five stamina traces diverged from sepal median staminal complexes, the posterior one suppressed in the corolla tube while the other four enter the four fertile stamens (*Scrophularia xanthoglossa* Boiss.); **I**, **J**, four staminal traces splitted from the central stele (*Paulownia tomentosa* (Thunb.)); **K**, four staminal traces splitted from the central stele and staminal lateral carpellary complex (*Torenia fournieri* Linden ex E. Fourn.); **L**, two staminal traces diverged from the central stele (*Veronica anagallis-aquatica* L.). Abbreviations: **D.C.B.**, dorsal carpellary bundle; **D.C.T.**, dorsal carpellary trace; **L.C.B.**, lateral carpellary bundle; **L.C.T.**, lateral carpellary trace; **N.D.**, nectariferous disc; **P.B.**, petal bundle; **P.Sma.C.**, petal sepal marginal complex; **P.T.**, petal trace; **S.Ma.B.**, sepal marginal bundle; **S.M.B.**, sepal median bundle; **St.B.**, staminal bundle; **St.C.Vs.**, staminal carpellary vascular supply; **St.Dc.C.**, staminal dorsal carpellary complex; **St.Lc.C.**, staminal lateral carpellary complex; **St.T.**, staminal trace; **Stn**, staminode; **V.C.B.**, ventral carpellary bundle; **V.C.T.**, ventral carpellary trace. Scale bars: 0.5 mm.

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. sinaiticum* 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).

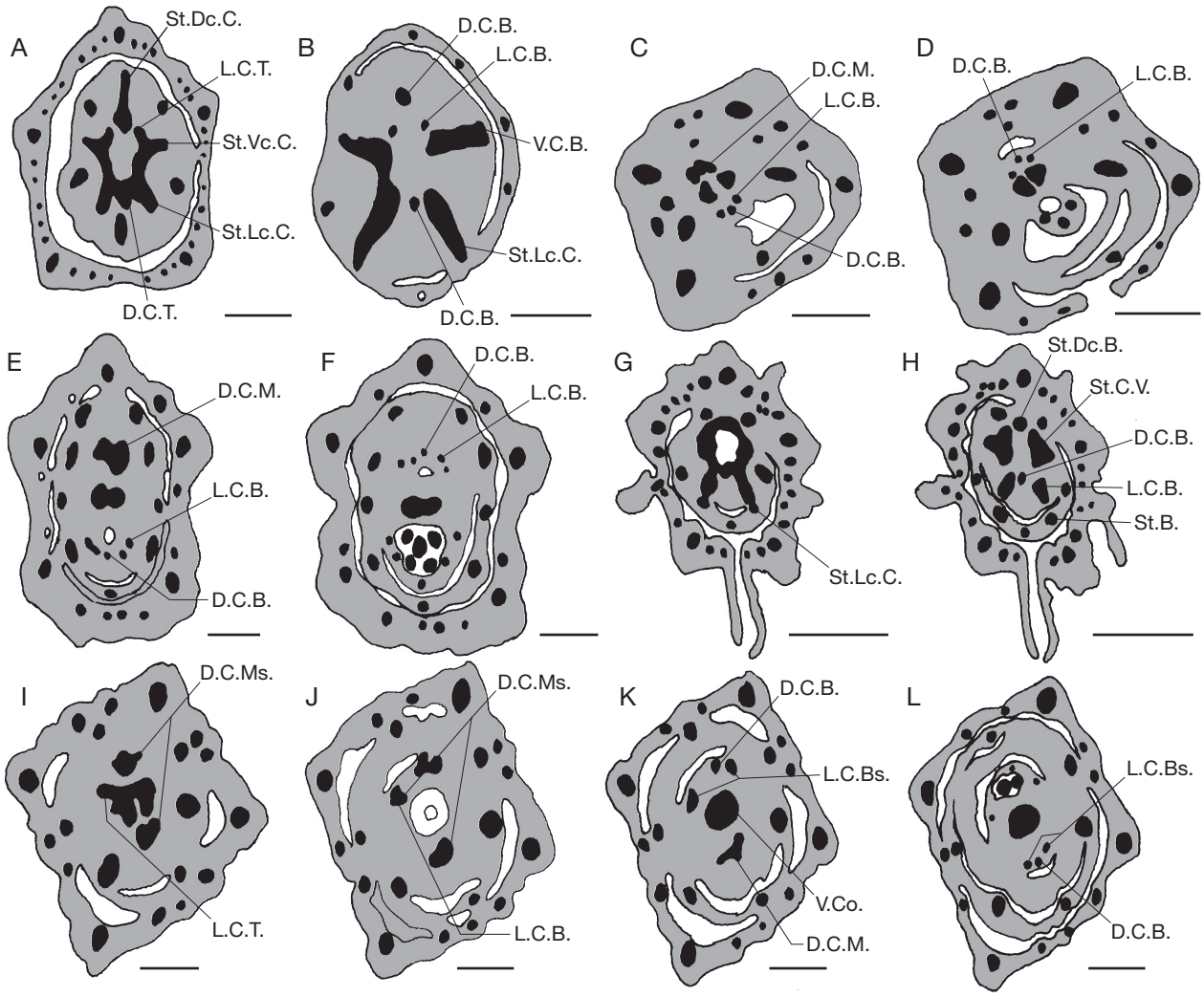

Fig. 3. — Gynoecium conditions: **A**, the anterior dorsal carpellary bundle arose from the stele, while the posterior dorsal carpellary bundle arose from the staminal dorsal carpellary complex (*Anarrhinum pubescens* Fresen. Hort. ex Loudon); **B**, the lateral carpellary bundles originated from the central stele and staminal lateral carpellary complex (*Anarrhinum pubescens*) (two per each carpel); **C**, **D**, the lateral carpellary bundles originated from the ramification of the dorsal carpellary mass (two per each carpel) (*Veronica anagalloides* Guss.); **E**, **F**, the lateral carpellary bundles originated from the ramification of the dorsal carpellary mass (four per each one) (*Sutera cordata* Kuntze); **G**, **H**, each carpel has two lateral carpellary bundles, one from staminal carpellary complex and one from staminal lateral carpellary mass (*Kickxia aegyptiaca* (L.) Nábělek); **I**-**L**, each carpel has two carpellary bundles, one originated from dorsal carpellary mass, and one from both the central stele and dorsal carpellary mass (*Veronica anagallis-aquatica* L.). Abbreviations: **D.C.B.**, dorsal carpellary bundle; **D.C.M.**, dorsal carpellary mass; **D.C.T.**, dorsal carpellary trace; **L.C.B.**, lateral carpellary bundle; **L.C.T.**, lateral carpellary trace; **St.B.**, staminal bundle; **St.C.Vs.**, staminal carpellary vascular supply; **St.Dc.C.**, staminal dorsal carpellary complex; **St.Lc.C.**, staminal lateral carpellary complex; **St.Vc.C.**, staminal ventral carpellary complex; **V.C.B.**, central carpellary bundle; **V.Co.**, ventral cord. Scale bars: 0.5 mm.

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., *Paulownia tomentosa* and *Sutera cordata* Kuntze (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* Pennell (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-*

Table 1. — Collection Data. Abbreviations: **A**, Alexandria-Marsa Matroh road, Egypt; **B**, Around water irrigation canal, Kafr El-Sheikh, Egypt; **C**, Botanical Garden, Faculty of Science, Ain Shams University, Abbassia, Cairo, Egypt; **D**, Burg El-Arab and Mariut Regions, Alexandria, Egypt; **E**, El-Zohria Botanical Garden, Doki, Egypt; **F**, Mashtal Faculty of Pharmacy, Cairo University, Saft Al-Laban, Cairo, Egypt; **G**, Orman Botanical Garden, Giza, Egypt; **H**, Wadi El-Arbeen, Saint Katherine, Egypt; **I**, Wadi Talaa, Saint Katherine, Egypt; **J**, Rashid, Al-Bossaili region, Alexandria, Egypt.

A – Wild Taxa	**Original description**	**Locality**
Anarrhinum pubescens Fresen. Hort. Ex Loudon	*Hortus Britannicus* [Loudon] 250 (1830) (IK)	H
Kickxia aegyptiaca (L.) Nábělek	*Spisy vydavane přirodovadeckou fakultou Masarykovy university* 70: 31 (1926) (IK)	D
Scrophularia xanthoglossa Boiss.	*Diagnoses Plantarum Orientalium ser.* 1, 12: 38. (1853) (IK)	I
Verbascum letourneuxii Asch. & Schweinf.	*in* Aschers. & Schwein., Ill. *Flora of Egypt* (*Mémoires de l'Institut d'Égypte*) 2: 114, 189 (1887) (IK)	A
V. sinaiticum Benth.	*Prodromus Systematis Naturalis Regni Vegetabilis* [A. P. de Candolle] 10: 236 (1846) [8 Apr 1846] (IK)	H
V. sinuatum L.	*Species Plantarum* 1: 178 (1753) [1 May 1753] (IK)	H
Veronica anagallis-aquatica L.	*Species Plantarum* 1: 12 (1753) (IK)	J
V. anagalloides Guss.	*Pl. Rar.* 5. t. 3. (IK)	B
V. catenata Pennell	Rhodora 1921, xxiii. 37 (IK)	B
B – Horticultural Taxa		**Source**
Antirrhinum majus L.	*Species Plantarum* 2: 617 (1753) [1 May 1753] (IK)	C
Digitalis purpurea L.	*Species Plantarum* 2: 621 (1753) [1 May 1753] (IK)	G
D. lanata Ehrh.	*Beiträge zur Naturkunde* [Ehrhart] vii. 152. (IK)	F
Linaria maroccana Hook.f.	*Botanical Magazine* 98: t. 5983 (1872) (IK)	E
Paulownia tomentosa (Thunb.) Steud.	*Nomenclator Botanicus* [Steudel], ed. 2. ii. 278 (1841) (IK)	G
Russelia equisetiformis Schlecht. & Cham.	*Linnaea* 6: 377 (1831) (IK)	C
Sutera cordata Kuntze	*Revisio Generum Plantarum* 2: 467 (1891) [5 Nov 1891] (IK)	G
Torenia fournieri Linden ex E. Fourn.	Ill. *Horticultural abstracts* xxiii. 129. t. 249 (1876) (IK)	G

Table 2. — Microfloral characters, their states and grades of taxa under investigation.

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

glossa, Verbascum letourneuxii, V. sinaiticum and *V. sinuatum*). From the central stele & staminal lateral carpellary complex as in *Anarrhinum pubescens, Linaria maroccana* & *Torenia fournieri* (two per each carpel, Fig. 3B) or from the ramification of the dorsal carpellary mass (two per each carpel, Fig. 3C, D) as in *Antirrhinum majus, Paulownia tomentosa*, *Veronica anagalloides* and *V. catenata* or four per each carpel (Fig. 3E, F) as in *Sutera cordata*). In *Kickxia aegyptiaca* each carpel has two lateral carpellary bundles one from staminal carpellary complex and one from staminal lateral carpellary mass (Fig. 3G, H). In *Veronica anagallis-aquatica* each carpel has two bundles; one originated from dorsal carpellary mass, and one from both the central stele & dorsal carpellary mass (Fig. 3I-L). In all the studied taxa, the dorsal and lateral carpellary bundles extend to feed the style and fade out beneath the stigmatic level.

Table 3. — Grades of the floral morphological characters and the sum of the evolutionary grades of taxa under investigation.

		Character																			
no.	**Taxa**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**	**Sum**
1	*Anarrhinum pubescens* Fresen. Hort. Ex Loudon	1	1	1	2	1	1	3	3	1	2	1	5	2	3	4	2	3	2	1	39
2	*Antirrhinum majus* L.	1	1	1	2	1	1	3	3	1	3	1	2	2	3	1	2	2	2	2	34
3	*Digitalis purpurea* L.	1	1	1	3	1	1	1	3	1	4	2	1	1	3	3	3	2	1	2	35
4	*D. lanata* Ehrh.	1	1	1	3	1	1	2	3	1	4	2	1	1	3	3	3	2	1	2	36
5	*Kickxia aegyptiaca* (L.) Nábělek	1	1	1	2	1	1	3	3	1	2	1	5	2	3	5	2	2	3	2	41
6	*Linaria maroccana* Hook.f.	1	1	1	3	1	1	3	3	1	2	1	4	2	3	4	2	2	2	2	39
7	*Paulownia tomentosa* (Thunb.)	1	2	1	1	1	1	1	1	1	4	2	1	1	3	1	1	3	2	1	29
8	*Russelia equisetiformis* Schlecht. & Cham.	1	1	1	2	1	1	1	3	1	2	1	1	1	1	3	2	2	1	1	27
9	*Scrophularia xanthoglossa* Boiss.	1	1	2	2	1	1	3	3	3	3	1	3	1	1	3	2	2	2	2	37
10	*Sutera cordata* Kuntze	1	1	1	3	3	1	1	3	2	4	2	1	1	2	1	3	1	2	2	35
11	*Torenia fournieri* Linden ex E. Fourn.	1	2	1	3	1	1	3	3	1	4	2	2	1	3	4	3	2	2	1	40
12	*Verbascum letourneuxii* Asch. & Schweinf.	1	1	1	3	1	1	1	3	1	1	1	1	1	1	3	2	3	3	2	31
13	*V. sinaiticum* Benth.	1	1	1	3	1	1	1	3	1	1	1	1	1	1	3	2	3	2	2	30
14	*V. sinuatum* L.	1	1	1	3	1	1	1	3	1	1	1	1	1	1	3	2	3	2	2	30
15	*Veronica anagallis-aquatica* L.	2	1	1	3	2	2	1	2	1	5	3	1	1	3	2	3	2	2	1	38
16	*V. anagalloides* Guss.	2	1	1	3	2	2	1	3	1	5	3	1	1	3	1	2	3	2	1	38
17	*V. catenata* Pennell	2	1	1	3	2	2	1	3	1	5	3	1	1	3	1	3	2	2	1	38

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. 4F, G). In all the studied taxa the ventral carpellary bundles originated from the central stele except in *Kickxia aegyptiaca* 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* (vasculature 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.* Digitaleae & Veroniceae 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 Digitaleae and Veroniceae 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.

Table 4. — Schematic placement showing the evolutionary trends of the studied taxa (*K. aegyptiaca* (L.) Nábělek, *T. fournieri* Linden ex E. Fourn., *L. maroccana* Hook.f., *A. pubescens* Fresen. Hort. ex Loudon, *V. anagallis-aquatica* L., *V. anagalloides* Guss., *V. catenata* Pennell, *S. xanthoglossa* Boiss., *D. lanata* Ehrh., *S. cordata* Kuntze, *D. purpurea* L., *A. majus* L., *V. letourneuxii* Asch. & Schweinf., *V. sinaiticum* Benth., *V. sinuatum* L., *P. tomentosa* (Thunb.) Steud. and *R. equisetiformis* Schlecht. & Cham.) of Scrophulariaceae Juss., according to Bentham & Hooker's system (1873).

	Subtribe					**Vandellieae**	**Veroniceae**	**Eudigitaleae**
	Tribe	**Verbasceae**	**Antirrhineae**	**Cheloneae**	**Manuleae**	**Gratioleae**	**Digitaleae**	
	Series (subfamily)	**Pseudo-solaneae**	**Antirrhinoideae**				**Rhinanthoideae**	
Evolutionary Trends	12		*K. aegyptiaca*					
	11					*T. fournieri*		
	10		*L. maroccana* *A. pubescens*					
	9						*V. anagallis-aquatica* *V. anagalloides* *V. catenata*	
	8			*S. xanthoglossa*				
	7							*D. lanata*
	6				*S. cordata*			*D. purpurea*
	5		*A. majus*					
	4	*V. letourneuxii*						
	3	*V. sinaiticum* *V. sinuatum*						
	2			*P. tomentosa*				
	1			*R. equisetiformis*				

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 Antirrhineae

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 of nectary disc and presence of compitum.

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, dithecous anthers, five staminal traces, the latter with dorsal carpellary bundles coming from central stele while the lateral carpellary bundles from dorsal carpellary mass. *Anarrhinum pubescence* and *Linaria maroccana* are the intermediate spp. 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, dithecous 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 *Russelia* 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, dithecous 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

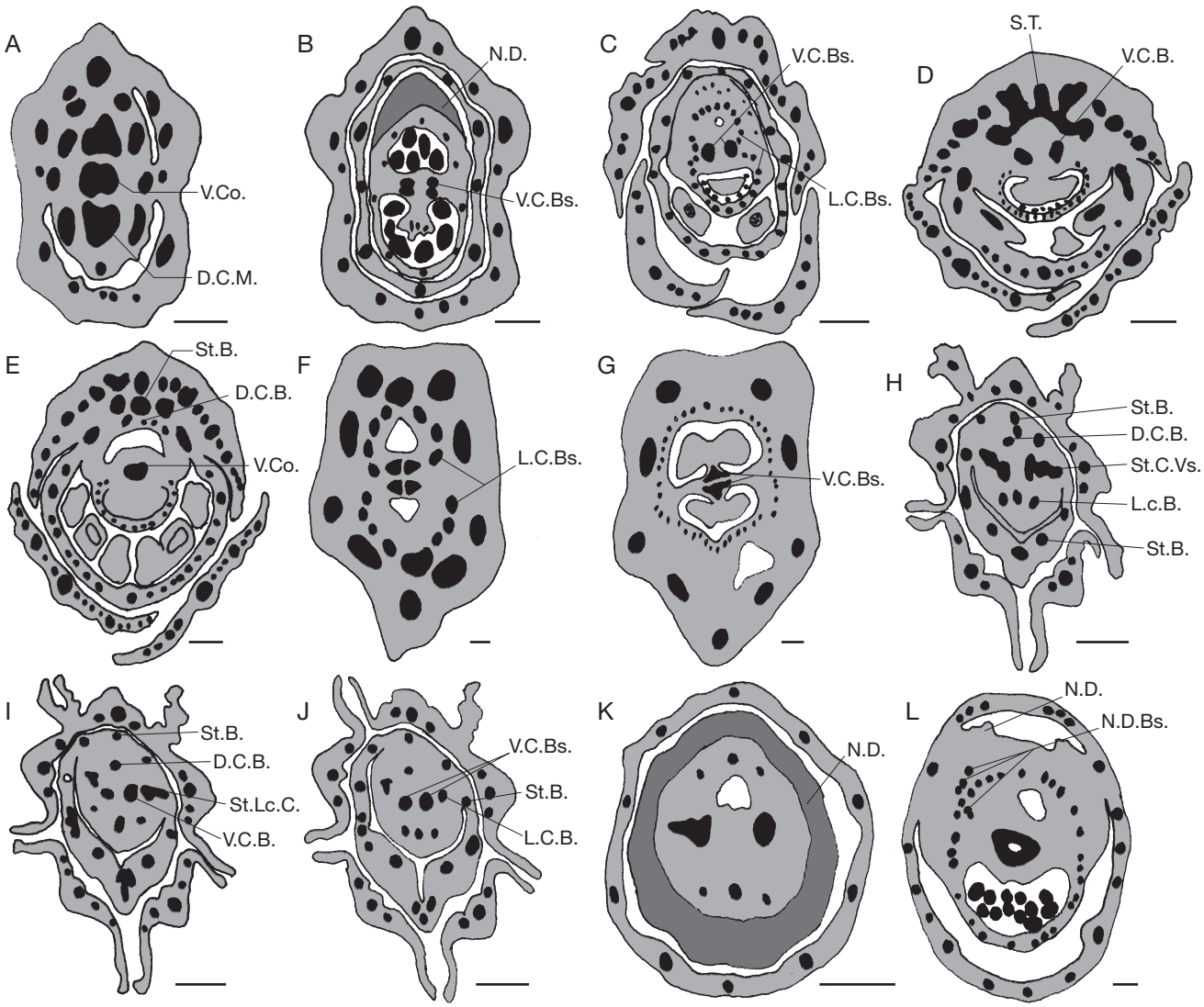

Fig. 4. — Gynoecium conditions (cont.): **A**, **B**, the ventral carpellary bundles in the form of ventral cord that separated into two distinct masses (each one arising from the fusion of two ventrals) (*Sutera cordata* Kuntze); **C**, the ventral carpellary bundies in the form of two distinct masses one for each carpel (*Russelia equisetiformis* Schlecht. & Cham.); **D**, **E**, the ventral carpellary bundles fused in the form of ventral cord above (*Verbascum letourneuxii* Asch. & Schweinf.); **F**, **G**, the ventral carpellary bundles in the form of four ventral bundles at the beginning and fused into two at a higher level (*Paulownia tomentosa* (Thunb.)); **H**-**J**, the ventral carpellary bundles originated from staminal carpellary vascular supply (*Kickxia aegyptiaca* (L.) Nábělek); **K**, the non-vascularized nectariferous disc (*Anarrhinum pubescens*); **L**, the vascularized nectariferous disc (*Digitalis purpurea* L.). Abbreviations: **D.C.B.**, dorsal carpellary bundle; **D.C.M.**, dorsal carpellary mass; **D.C.T.**, dorsal carpellary trace; **L.C.B.**, lateral carpellary bundle; **N.D.**, nectariferous disc; **N.D.Bs.**, nectariferous disc bundles; **St.B.**, staminal bundle; **St.C.Vs.**, staminal carpellary vascular supply; **St.Lc.C.**, staminal lateral carpellary complex; **V.C.B.**, ventral carpellary bundle; **V.Co.**, ventral cord. Scale bars: 0.5 mm.

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

In tribe Verbasceae

Verbascum letourneuxii, V. sinaiticum and *V. sinuatum* occupy primitive status due to the less advanced characters *viz*. 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. sinaiticum* 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 Gratioleae 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).

Pseudosolaneae
Pseudosolaneae 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 Pseudosolaneae.

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 supported the taxonomic location of *Paulownia tomentosa* and *Torenia fournieri* under family Scrophulariaceae. 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 its evolutionary score. Based on these scores, the taxa under investigation showed 12 grades having corresponding score ranging from 27 to 41. Finally it is recommended that all of these hypotheses need to be tested against more data, including both more characters and more taxa.

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