

RESEARCH ARTICLE

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FLORAL MORPHOLOGY OF SOME TAXA OF CRASSULACEAE

ABSTRACT:

The floral anatomical characters in 22 species of Crassulaceae (including nine genera) were investigated. We noticed the presence of vascular complexes in all the studied taxa. These complexes represent fused vascular traces of two entities either radially of the same whorl (as the fused ventral carpellary traces complex) or neighboring tangentially of two or more successive whorls (as the petal median-antepetalous stamen, petal median-dorsal carpellary-nectary scale vascular complex). These fused vascular complexes are considered as advanced case. Except in five taxa, the sepal is three-traced; one median and two marginal in the remaining taxa. The marginal bundles show a great diversification in their origin. The petal is one-traced, originates independently in few cases or conjoint with the antepetalous stamen bundles in many cases. The stamen is one-traced, two whorls of bundles; the antepetalous whorl (usually originates with the petal bundle) and the inner antesepalous whorl (the bundles of which originate either from the central stele or conjoint with the lateral carpellary and nectary scale traces in a complex). The carpel is five-traced in all the studied taxa; one dorsal, two ventral and two laterals. Such a case is referred to as a primitive case. The nectary scales supplied each by a number of traces. Such traces usually originate with the dorsal carpellary-petal median-antepetalous stamen traces in a complex. The nectary scales are referred to as of foliar nature. Based on both the source and number of whorls of vascular traces, the studied taxa could be grouped under four groups and nine subgroups. Such grouping proved to be more distinctive. A core position was suggested for the genus *Kalanchoe*, and the two studied *Sedum* are more advanced species.

KEY WORDS:

Crassulaceae, Floral vascularization, *Kalanchoe*, Nectary scales, Vascular complexes.

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INTRODUCTION:

Crassulaceae is a cosmopolitan family, mainly in warm regions but its chief development in South Africa, including about 25 genera and 900 species (Heywood, 1978; Cronquist, 1981).

Generally, the anatomical structure of the flower in angiosperms provided many useful characters which may be used in taxonomic and phylogenetic studies, where the internal characters of the flowers may be more useful in certain cases than the external because of the frequent persistence of the vascular supply of the lost organs after all external evidences have disappeared (Van Tieghem, 1871; Subramanyam, 1960; Rosa and Scatena, 2007; Bachelier and Endress, 2009; Nuraliev *et al.*, 2011; Novikoff and Kazemirska, 2012). The distribution of floral nectaries in the Magnoliatae is studied by Dahlgren (1975 & 1980) who distinguished two types of floral nectaries; nectariacaduca and nectariapersistentia. On the basis of their nature and their localization, nectariapersistentia are typical of the Rosidae. Nikolić *et al.* (2015) studied the morphological characters of nectary scales

among 14 populations of *Jovibarba heuffelii* complex (Crassulaceae).

Considering the floral anatomy of Crassulaceae, the floral vasculature and development have been described generally by Wassmer (1955), Jensen (1966), and Quimby (1971). For specific taxa; *Sedum* (Henslow, 1891; Eames, 1931; Puri, 1951; Thart, 1985), *Kalanchoe* (Tillson, 1940), *Sedum* and *Crassula* (Eckert, 1966), *Diamorpha* and *Sedum* (Sherwin and Wilbur, 1971), *Hylotelephium* (Hart, 1985), and *Crassula pageae* (Jäger-Zürn, 1989). Quimby's investigation (1939) was the most earlier and comprehensive, including most genera of the family. He found that the floral anatomy of the species of Crassulaceae considered in his study could be placed in "four rather distinct vascular group" that formed a series from the most primitive vascular pattern (Group I) to the most advanced (Group IV). Flowers of Group I have six whorls of traces involved in vascularization; those of Group II have five whorls: those in Group III have four whorls, and those of Group IV have three whorls.

The early most comprehensive treatment of Crassulaceae based on floral morphology was that of Berger (1930), who classified the family into six subfamilies. These subfamilies have been grouped into two lineages by Hart and Eggli (1995); a *Crassula* lineage (including Cotylenoideae, Crassuloideae and Kalanchoideae) and a *Sedum* lineage (including Echeveroideae, Sedoideae and Sempervivoideae).

on the basis of embryology, Mauritson (1933) considered the Crassuloideae to stand Table 1. Collection Data

apart from the Cotylenoideae, Echeveroideae, Sedoideae, and Sempervivoideae. He considered the Kalanchoideae to be a third taxon that was phylogenetically somewhat intermediate between the other two (Crassuloideae and Cotylenoideae)

Using phylogenetic analysis of cpDNA restriction site data, Van Ham and Hart (1998) recognized two subfamilies viz. Crassuloideae and Sedoideae. Hart (1995), Mort *et al.* (2001), and Mayuzumi and Ohba (2004) recognized seven major clades belonging to three subfamilies as suggested earlier by Thorne (1983 & 1992) and led to Thiede and Eggli classification (2007)

The aim of this work is to show whether or not the classification based on morphological characters can be supported by data of detailed anatomical features of the flowers, the bearing of the floral morphology in the present family on some evolutionary considerations, and the determination of the nature of the nectary scales associated with floral organs.

MATERIAL AND METHODS:

In the present study 22 taxa were collected from different localities representing 21 ornamental species and one wild species (*Umbilicus horizontalis*). The ornamental and wild species and their localities in Egypt were presented in table 1. The identification of the ornamental species takes place by the aid of Bailey (1949), and Bailey and Bailey (1976). *Umbilicus horizontalis* was identified according to Täckholm (1974) and Boulos (1999).

No.	Taxa	Source
1	<i>Adromischus cooperi</i> A. Berger	Cactus International Farm, Kaliobeia.
2	<i>Aeonium decorum</i> (Webb) Bolle	~
3	<i>Cotyledon orbiculata</i> L.	~
4	<i>Crassulacapitelle</i> Thunb.	Bot. Garden, Faculty of Agriculture, Kafr El-Sheikh Univ.
5	<i>C. springtime</i> Hort. (Hybrid)	Cactus International Farm, Kaliobeia.
6	<i>Echeveriasetosa</i> Rose & Purpus	~
7	<i>Graptopetalum paraguayense</i> (N.E.Br.) E. Walther	~
8	<i>Kalanchoe beharensis</i> Drake	Orman Bot. Garden, Giza.
9	<i>K. blossfeldiana</i> Poelln.	Bot. Garden, Faculty of Science, Ain Shams Univ.
10	<i>K. daigermontiana</i> Raym. Hamet & H. Perrier	Orman Botanical Garden, Giza.
11	<i>K. fedtschenkoi</i> Raym. Hamet & H. Perrier	Bot. Garden, Faculty of Science, Ain Shams Univ.
12	<i>K. kwensis</i> Hort. (Hybrid)	Orman Bot. Garden, Giza.
13	<i>K. laciniata</i> (L.) Dc.	Cactus International Farm, Kaliobeia.
14	<i>K. longiflora</i> Schltr. ex J. M. Wood	Orman Bot. Garden, Giza.
15	<i>K. marmorata</i> Baker	Cactus International Farm, Kaliobeia.
16	<i>K. orgyalis</i> Baker	~
17	<i>K. rosei</i> Raym. Hamet & H. Perrier	Orman Bot. Garden, Giza.
18	<i>K. sexangularis</i> N.E.Br.	~
19	<i>K. thyrsiflora</i> Harv.	~
20	<i>Sedum album</i> L.	Cactus International Farm, Kaliobeia.
21	<i>S. nussbaumeriana</i> Bitter	~
22	<i>Umbilicus horizontalis</i> (Guss.) DC.	Burg El-Arab, Mediterranean Coastal Region (Brimley cave).

The mature flower buds of the studied species were fixed and preserved in (F.A.A.), embedded in paraffin wax, then serially sectioned at 10-15 μ according to the conventional method (Johansen, 1940). Sections stained in crystal violet-erythrosine combination. The photos were captured with Canon power shot A 720 IS digital camera (40 x).

The abbreviation "Comp." is used when the vascular supply for more than one organ (sepal, petal, stamen, nectary scale and ovary) are derived together. The legends used throughout for the floral vascularization as in the following:

Comp. I: petal median-antepetalous stamen complex.

Comp. II: Antesepalous stamen-lateral carpellary complex.

Comp. III: dorsal carpellary-nectary scale complex.

Comp. IV: Sepal marginal-petal median-antepetalous stamen complex.

Comp. V: Nectary scale-antesepalous stamen-lateral carpellary complex.

Comp. VI: Petal median-dorsal carpellary-nectary scale complex.

Comp. VII: Sepal marginal-petal median-antepetalous stamen-dorsal carpellary-nectary scale complex.

Comp. VIII: Petal median-antepetalous stamen-dorsal carpellary-nectary scale complex.

Table 2. Floral Vasculature in the Sepal and Petals of the Studied Taxa of Crassulaceae

Taxa No.	Character Taxa	Receptacle Vasculature	Sepal Vasculature		Petal Vasculature			
			S.M.B.	S.Ma.Bs.	P.M.B.	P.Acc.Bs.		
			Branching	Presence	Source	Branching	Source	
1	<i>Adromischuscooperi</i>	Cont.s.s.	-	+	S.	Comp.I	+	P.M.B.
2	<i>Aeonium decorum</i>	Cont.s.s.	-	+	Comp.IV	Comp.IV	+	P.M.B.
3	<i>Cotyledon orbiculata</i>	Cont.s.s.	-	-	-	Comp.I	+	P.M.B.
4	<i>Crassulacapitella</i>	Diss.S.S.	-	-	-	S.	+	P.M.B.
5	<i>C.springtime</i>	Cont.s.s.	-	-	-	Comp.VI	-	-
6	<i>Echeveriasetosa</i>	Cont.s.s.	-	+	Comp.IV	Comp.IV	+	P.M.B.
7	<i>Graptopetalum paraguayense</i>	Cont.s.s.	+	+	Comp.VII	Comp.VII	+	P.M.B.
8	<i>Kalanchoe beharensis</i>	Cont.s.s.	+	+	S.	Comp.I	+	P.M.B.
9	<i>K. blossfeldiana</i>	Cont.s.s.	-	-	-	Comp.VIII	+	P.M.B.
10	<i>K. daigremontiana</i>	Cont.s.s.	+	+	S.	Comp.I	+	P.M.B.
11	<i>K. fedtschenkoi</i>	Cont.s.s.	+	+	S.M.B.	Comp.I	+	P.M.B.
12	<i>K. kwensis</i>	Cont.s.s.	-	+	Comp.VII	Comp.VII	+	PM.B.
13	<i>K. laciniata</i>	Cont.s.s.	+	+	S.M.B.	Comp.VIII	-	Comp.I
14	<i>K. longiflora</i>	Cont.s.s.	-	+	Comp.IV	Comp.IV	-	Comp.I
15	<i>K. marmorata</i>	Cont.s.s.	-	+	S.	Comp.I	-	Comp.I
16	<i>K.orgyalis</i>	Cont.s.s.	-	+	S.	Comp.I	-	-
17	<i>K. rosei</i>	Cont.s.s.	+	+	S.MB.	Comp.I	+	P.M.B.
18	<i>K. sexangularis</i>	Cont.s.s.	+	+	S.M.B.	Comp.VIII	-	Comp.I
19	<i>K. thyrsoiflora</i>	Cont.s.s.	+	+	S.	Comp.I	+	P.M.B.
20	<i>Sedum album</i>	Diss.S.S.	-	+	Comp.VII	Comp.VII	+	P.M.B.
21	<i>S. nussbaumeriana</i>	Diss.S.S.	+	+	Comp.VII	Comp.VII	+	P.M.B.
22	<i>Umbilicus horizontalis</i> var. <i>horizontalis</i>	Cont.s.s.	-	-	-	Comp.I	-	-

(+): present, (-): absent, Cont.S.S.: Continuous siphonostele, Diss.S.S.: Dissected siphonostele, P. Acc.Bs.: Petal accessory bundles, P.M.B.: Petal median bundle, S.: Stele, S.M.B.: Sepal median bundle, S.Ma.Bs.: Sepal marginal bundles.

RESULTS:

The micro-floral characters of the 22 studied taxa are enumerated in tables 2 & 3 and plates 1- 5:

The flower tetramerous in all studied *Kalanchoe* species (12 spp.); pentamerous in *Adromischuscooperi*, *Cotyledon orbiculata*, the two *Crassula* species (*Crassula capitella* and *C. springtime*), *Echeveriasetosa*, *Graptopetalum paraguayense*, the two *Sedum* species (*Sedum album* and *S. nussbaumeriana*) and *Umbilicus horizontalis*; and hepta-, or octamerous in *Aeoniumdecorum*.

The stamens are as twice as the petals in all studied taxa present in two obdiplostemonouswhorls, except in the two *Crassula* species where the antepetalous stamen whorl absent (haplostemonous).

The carpels are eu-apocarpeous to semi-apocarpous (slightly connate at the base). Each carpel has a nectary scale from its back near the base (isomerous).

Pedicle condition:

Continuous siphonostele of vascular tissue in all the taxa studied.

Receptacle conditions:

Continuous siphonostele in 19 studied taxa dissected siphonostele in *Crassulacapitella* and the two *Sedum* species (Table 2).

Calyx conditions:

Except in *Cotyledon orbiculata*, the two *Crassula* species, *Kalanchoe blossfeldiana* and *Umbilicus horizontalis* where the sepal receives only one median trace (plate 1a&b), the sepal in the remaining 17 taxa receives three traces; one median and two marginals. However, in the above exceptional five taxa the one median trace undergoes no branching throughout (Table 2 and plate 1).

Considering the origin of the marginal traces, the following patterns are met with:

- 1- Directly diverge from the central stele as in *Adromischuscooperi*, *Kalanchoe beharensis*, *K. daigremontiana*, *K. marmorata*, *K. orgyalis* and *K. thyrsoiflora* (Plate 1c).
- 2- Diverge from branching of the median bundle as in *Kalanchoe fedtschenkoi*, *K. laciniata*, *K. rosei* and *K. sexangularis* (Plate 1d).
- 3- Diverge from a sepal marginal-petal median-antepetalous stamen vascular complex (Comp. IV) in *Aeonium decorum*, *Echeveriasetosa*, *Kalanchoe longiflora* (Plate 1e).
- 4- Diverge from a sepal marginal-petal median-antepetalous stamen-dorsal carpellary-nectary scale vascular complex (Comp. VII) in *Graptopetalum paraguayense*, *Kalanchoe kwensis* and the two *Sedum* species (Plate 1f).

Corolla conditions:

Generally, it is well established that the petal supplies by a single trace derived in different ways (Table 2 and Plates 2 & 3):

- 1- Independently, from the central stele, then branched into several accessory bundles in the corolla tube in *Crassulacapitella* (Plate 2a).
- 2- Derived conjoint in the petal median-antepetalous stamen vascular complex (Comp. I) in ten taxa (Plate 2b).
- 3- Derived conjoint in the sepal marginal-petal median-antepetalous stamen vascular complex (Comp. IV) in *Aeonium decorum*, *Echeveriasetosa* and *Kalanchoe longiflora* (Plate 2c).
- 4- Derived conjoint in the petal median-dorsal carpellary-nectary scale vascular complex (Comp. VI) in *Crassula springtime* (Plate 2d).
- 5- Derived conjoint in the sepal marginal-petal median-antepetalous stamen-dorsal carpellary-nectary scale vascular complex (Comp. VII) in *Graptopetalum paraguayense*, *Kalanchoe kwensis* and two *Sedum* species (Plate 2e).
- 6- Derived conjoint in the petal median-antepetalous stamen-dorsal carpellary-nectary scale vascular complex (Comp. VIII) in *Kalanchoe blossfeldiana*, *K. laciniata* and *K. sexangularis* (Plate 2f).

Except in *Crassula springtime*, *Kalanchoe orgyalis* and *Umbilicus horizontalis* where the petal has no accessory bundles (Plate 3a), the petal in the remaining taxa has such bundles (Plate 3b&c). The latter originated either from the branching of the petal median bundle in 15 taxa or from Comp. I (petal median-antepetalous stamen supply) in *K. laciniata*, *K. longiflora*, *K. marmorata* and *K. sexangularis*. The vascular ramification begins in the corolla tube in the 19 taxa and continues in the petal lobes to accompany the expansion of the corolla limbs.

Androecium conditions:

The stamens in 20 of the studied taxa appeared obdiplostemonous since the bundles of the outer whorl (antepetalous stamen whorl) arise fused with the petal median bundle (Table 3 and Plates 2 & 3).

The Antepetalous Stamen Vasculature:

Either derived conjoint with the petal supply; Comp. I (Plate 2b) or conjoint with more than one organ whorl; Comp. IV (Plate 2c), Comp. VII (Plate 2e), or Comp. VIII (Plate 2f).

The Antesepalous Stamen Vasculature:

1- Directly from the central stele in the two *Crassula* species, *Kalanchoe daigremontiana*, *K. fedtschenkoi*, *K. marmorata* and *K. thyrsoiflora* (Plate 3d).

2- Derived conjoint in the nectary scale-antesepalous stamen-lateral carpellary vascular complex (Comp. V) in *Aeonium decorum* (Plate 3e).

3- Derived conjoint in the antesepalous stamen-lateral carpellary vascular complex (Comp. II) in the remaining 15 taxa (Plate 3f).

Nectary Scales conditions:

The scales shape: ovate in *Kalanchoe daigremontiana*, *K. fedtschenkoi* and *K. rosei*, linear in seven taxa, Quadrate in 12 taxa. The apices of nectary scales in the studied taxa show great variation (Table 3 and Plate 5).

In all the studied taxa, the nectary scale vascularized by a number of bundles that are detached as in the following ways (Table 3 and Plate 4):

1- From the dorsal carpellary-nectary scale vascular complex (Comp. III) in 13 studied taxa (Plate 4a).

2- Partially from the nectary scale-antesepalous stamen-lateral carpellary vascular complex (Comp. V) and Comp. III in *Aeonium decorum* (Plate 4b).

3- From the petal median-dorsal carpellary-nectary scale vascular complex (Comp. VI) in *Crassula springtime*.

4- From the sepal marginal-petal median-antepetalous stamen-dorsal carpellary-nectary scale vascular complex (Comp. VII) in *Graptopetalum paraguayense*, *Kalanchoe kwensis* and the two *Sedum* species (Plate 4e).

5- From petal median-antepetalous stamen-dorsal carpellary-nectary scale vascular complex (Comp. VIII) in *Kalanchoe blossfeldiana*, *K. laciniata* and *K. sexangularis* (Plate 4f).

Carpel conditions:

Origin and behavior of the carpellary bundles summarized as follows: (Table 3 and Plate 4):

1- The dorsal carpellary bundles arise conjoint with the nectary scale bundles in different vascular complexes (Comp. III, Comp. VI, Comp. VII and Comp. VIII).

2- The lateral carpellary bundles either originated directly from the central stele in six taxa (Plate 4c) or conjoint with the antesealous stamen bundles in different vascular complexes (Comp. II; Plate 4f and

Comp. V; Plate 4e) in the remaining 16 studied taxa.

In all the studied taxa, both the dorsal and the two lateral bundles after supplying the carpel run through the style and fade out at the stigmatic level.

3- The ventral carpellary bundles originated fused as one bundle from the receptacular stele in all studied taxa. The fused ventral bundles, each split radially into two, enter two adjacent carpels to feed the ovules and fade out at the ovary top (Plate 4 d & e).

Table 3. Floral Vasculature in the Stamens, Carpels and Nectary Scales and Nectary Scales Morphology of the Studied Taxa of Crassulaceae

Taxa No.	Character Taxa	Stamen Vasculature			Carpel and Nectary Scale Vasculature			Morphology of nectary scales	
		As.St.B.	Ap.St.B.	Division of P.-St. complex	D.C.B.	L.C.Bs.	N.Sc.Bs.	Shape	Apex
		Source	Source		Source	Source	Source		
1	<i>Adromischuscooperi</i>	Comp.II	Comp.I	Base of C.T.	Comp.III	Comp.II	Comp.III	Quadrate	Emarginate
2	<i>Aeonium decorum</i>	Comp.V	Comp.IV	Base of C.T.	Comp.III	Comp.V	Comp.V + Comp.III	Quadrate	Bitten
3	<i>Cotyledon orbiculata</i>	Comp.II	Comp.I	Base of C.T.	Comp.III	Comp.II	Comp.III	Quadrate	Truncate
4	<i>Crassulacapitella</i>	S.	-	--	Comp.III	S.	Comp.III	Quadrate	Emarginate
5	<i>C.springtime</i>	S.	-	--	Comp.VI	S.	Comp.VI	Quadrate	Emarginate
6	<i>Echeveriasetosa</i>	Comp.II	Comp.IV	Above middle of C.T.	Comp.III	Comp.II	Comp.III	Quadrate	Truncate
7	<i>Graptopetalum paraguayense</i>	Comp.II	Comp.VII	Above middle of C.T.	Comp.VII	Comp.II	Comp.VII	Quadrate	Truncate
8	<i>Kalanchoe beharensis</i>	Comp.II	Comp.I	Above middle of C.T.	Comp.III	Comp.II	Comp.III	Quadrate	Truncate
9	<i>K. blossfeldiana</i>	Comp.II	Comp.VIII	Above middle of C.T.	Comp.VIII	Comp.II	Comp.VIII	Linear	Retuse
10	<i>K. daigremontiana</i>	S.	Comp.I	Base of C.T.	Comp.III	S.	Comp.III	Ovate	Blunt
11	<i>K. fedtschenkoi</i>	S.	Comp.I	Base of C.T.	Comp.III	S.	Comp.III	Ovate	Blunt
12	<i>K. kwensis</i>	Comp.II	Comp.VII	Above middle of C.T.	Comp.VII	Comp.II	Comp.VII	Linear	Acute
13	<i>K. laciniata</i>	Comp.II	Comp.VIII	Above middle of C.T.	Comp.VIII	Comp.II	Comp.VIII	Linear	Emarginate
14	<i>K. longiflora</i>	Comp.II	Comp.IV	Above middle of C.T.	Comp.III	Comp.II	Comp.III	Linear	Emarginate
15	<i>K. marmorata</i>	S.	Comp.I	Above middle of C.T.	Comp.III	S.	Comp.III	Linear	Acute
16	<i>K.orgyalis</i>	Comp.II	Comp.I	Above middle of C.T.	Comp.III	Comp.II	Comp.III	Quadrate	Emarginate
17	<i>K. rosei</i>	Comp.II	Comp.I	Base of C.T.	Comp.III	Comp.II	Comp.III	Ovate	Blunt
18	<i>K. sexangularis</i>	Comp.II	Comp.VIII	Above middle of C.T.	Comp.VIII	Comp.II	Comp.VIII	Linear	Blunt
19	<i>K. thyrsiflora</i>	S.	Comp.I	Above middle of C.T.	Comp.III	S.	Comp.III	Quadrate	Bitten
20	<i>Sedum album</i>	Comp.II	Comp.VII	Above middle of C.T.	Comp.VII	Comp.II	Comp.VII	Quadrate	Bitten
21	<i>S. nussbaumeriana</i>	Comp.II	Comp.VII	Above middle of C.T.	Comp.VII	Comp.II	Comp.VII	Quadrate	Truncate
22	<i>Umbilicushorizontalis</i> var. <i>horizontalis</i>	Comp.II	Comp.I	Above middle of C.	Comp.III	Comp.II	Comp.III	Linear	Blunt

(+): present, (-): absent, Ap.St.B.: Antepetalous stamen bundle, As.St.B.: Antesealous stamen bundle, C.T.: Corolla tube, D.C.B.: Dorsal carpellary bundle, L.C.Bs.: Lateral carpellary bundles, N.Sc.Bs.: Nectary scale bundles, S.: Stele.

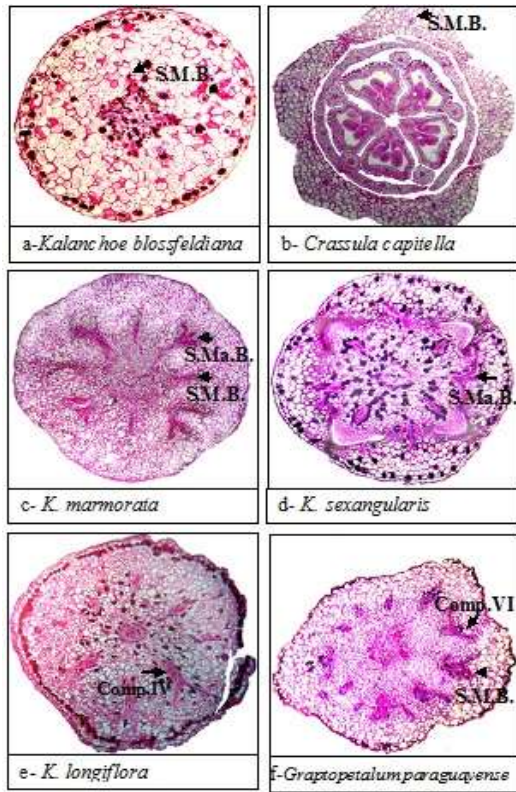


Plate 1. Sepal Vasculature (× 40)
 Photos (a & b): Sepal Median Bundle; Photos (c - f): Source of Sepal Marginal Bundles; S.M.B.: Sepal median bundles; S. Ma.B.: Sepal marginal bundle

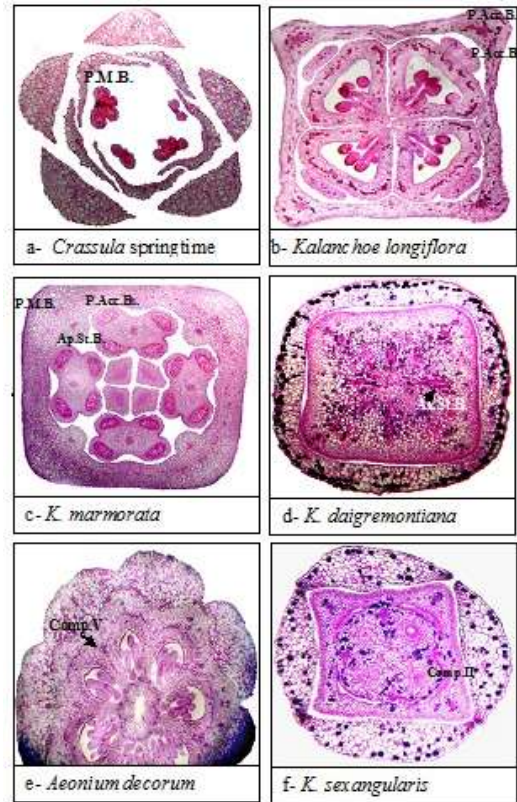


Plate 3. Petals and Antepetalous Stamen Vasculature (× 40). As.St.B: Antepetalous stamen bundle; P.Acc.Bs.: Petal accessory bundles bundle; P.M.B.: Petal median bundle.

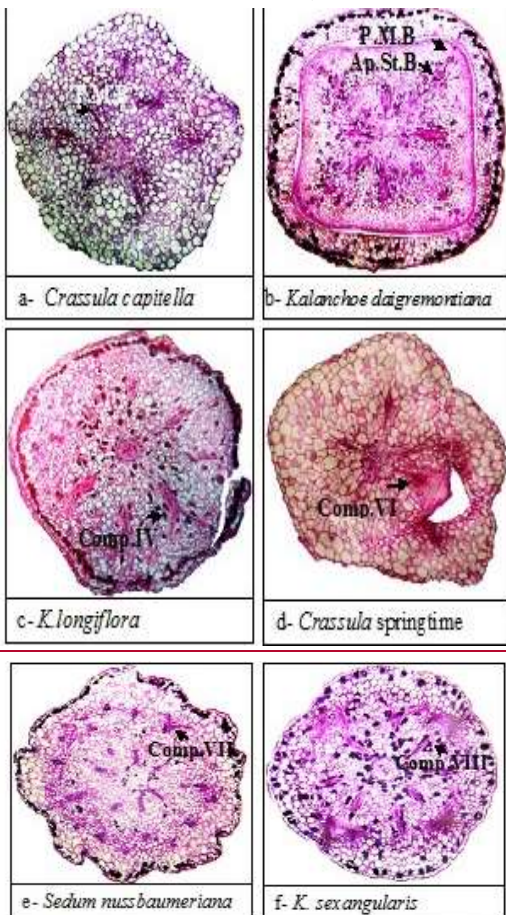


Plate 2. Photos (a – f): Source of petal bundles × 40. Ap.St.B. (Tr.) Antepetalous stamen bundle; P.M.B.: Petal median bundle.

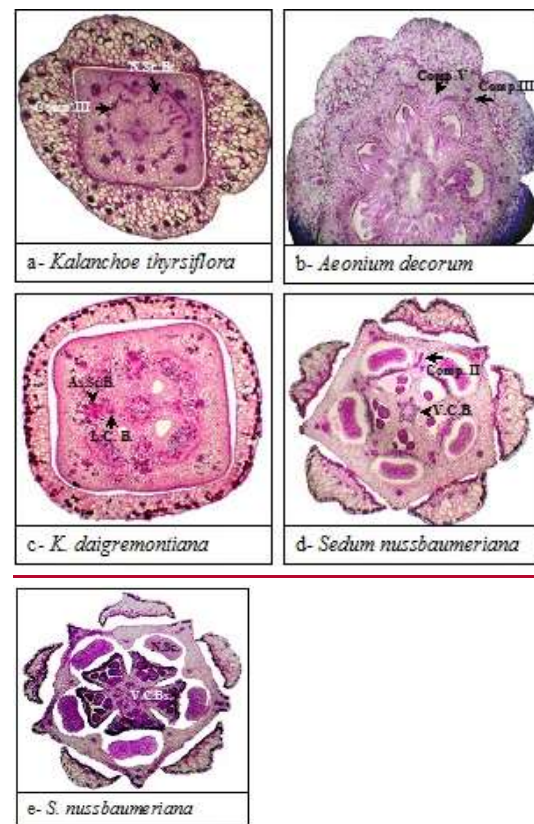


Plate 4. Nectary Scale and Carpel Vasculature (× 40). As.St.B.: Antepetalous stamen bundle; L.C.B.: Lateral capillary bundle; N.Sc.Bs.: Nectary scale bundles; V.C.B.: Ventral capillary bundle.

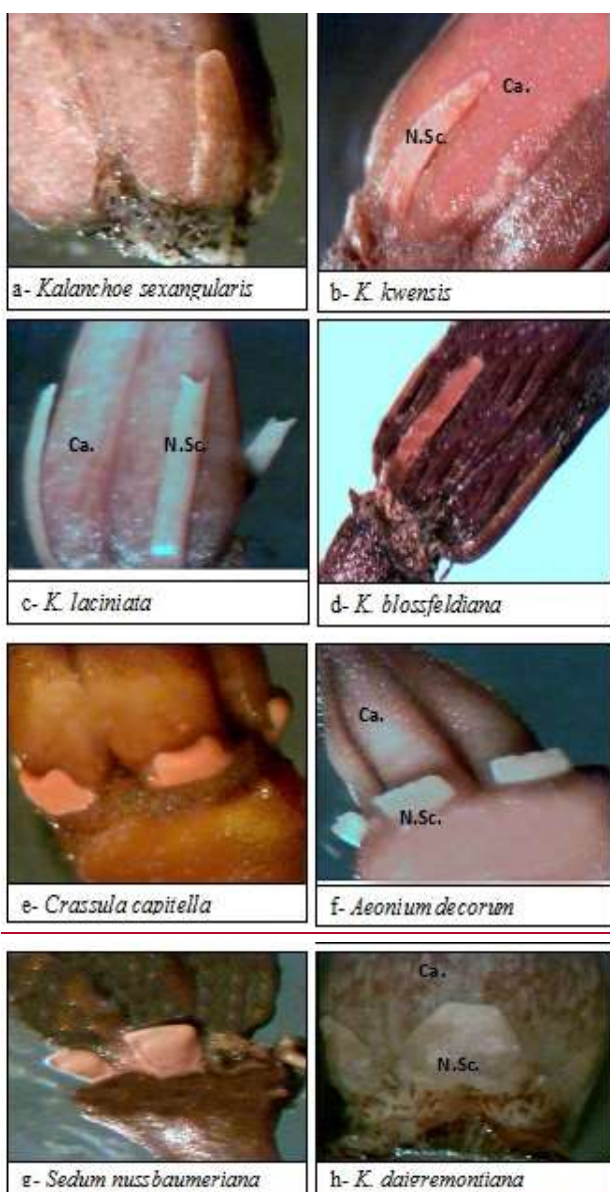


Plate 5. Nectary Scales and Carpels (x 40)
Ca: Carpel; N.Sc.: Nectary Scale

DISCUSSION:

Generally, the sepal is a three-traced organ. Such trace may be derived from the same source (Rao, 1949) or from different sources (Joshi, 1942; Al-Nowaihi and Khalifa, 1973). Except in five taxa, the sepal is three-traced; one median and two marginals in the remaining taxa. The marginal bundles show a great diversification in their origin. The sepals of *Cotyledon orbiculata*, the two *Crassula* species, *Kalanchoe blossfeldiana* and *Umbilicus horizontalis* receives only one median trace, which is a fairly unusual trait but is nevertheless reported in at least six genera (Puri, 1951), as well as *Sedumaizoon* (Subramanyam, 1955). Puri postulated that the lack of lateral bundles correlated with the poor development of mesophyll, since mesophyll can form procambium only when it at least two or more cell layers thick. In contrast, the sepals of the above five taxa are

small where in the remaining 17 taxa are broader and thicker. The origin of the marginal traces in the studied taxa, agree with Tillson (1940) and Jensen (1966).

The stamens in 20 of the studied taxa appeared obdiplostemonous since the bundles of the outer whorl (antepetalous stamen whorl) arise fused with the petal median bundle. The obdiplostemony was suggested early by Bancroft and Diekson (1932) who claimed that the antepetalous stamen bundles arise conjoint with the petal median bundles. The absence of antepetalous stamen whorl in *Crassula* is referred to as an advanced case. Obdiplostemony seems to be inherent in the vascular patterns of any flower with two whorls of stamens in Quimby's Groups I, II, and III as evidenced by fusion of the outer stamen trace to the petal trace. The stamen is one-traced, two whorls of bundles; the antepetalous whorl (usually originates with the petal bundle) and the inner antesepalous whorl (the bundles of which originate either from the central stele or conjoint with the lateral carpellary and nectary scale traces in a complex).

The floral nectaries (those found on the floral organ) *sensu lato*, are regarded phylogenetically as more advanced than the extrafloral nectaries (those found on vegetative organs) as reported by Frey-Wyssling (1933). Dahlgren (1975), Cronquist (1981), and Said (1982) considered the nectary scale as a small appendage. As regards the nectary scale nature, Nair and Joseph (1957), on the anatomical bases, have interpreted it as a modified outer whorl of the carpels (some Simaroubaceae). However, Nair and Joshi (1958) considered the disc to be of receptacular nature when the disc was non-vascularized or vascularized by a large number of traces. The latter case described by Eames (1961) as "diffused pattern". With this in mind, scale in the present work, the nectary scales supplied each by a number of 3-7 traces, such traces usually originate with the dorsal carpellary-petal median-antepetalous stamen traces in a complex. The nectary can be referred to as of foliar nature. Nikolić *et al.* (2015) indicated that the characteristics of nectarines may be used as additional characters in the analysis and taxonomy of the *Jovibarba heuffelii* group. In the present work the shape and apices show great variation all over the 22 studied taxa.

Watson and Dallwitz (1992) stated that the carpels in Crassulaceae are eu-apocarpeous to semi-apocarpeous (slightly connate at the base). In this respect, Al-Nowaihi *et al.* (1998) recorded the case of partially fused carpels in Apocynaceae (i.e. fused below, distinct above). They referred to the partially fused carpels as a step of advancement over the case of completely fused carpels and as a promoter to the case

of the fully distinct carpels. The occurrence of the lateral bundles was considered as a diagnostic character and of phylogenetic significance in Malvaceae as recorded by Bates (1968) and Bates and Blanchard (1970). In all the studied taxa each two ventral carpellary bundles originated fused as one bundle from the receptacular stele. The divergence of the fused ventral carpellary bundles is in agreement with Eames and Mac Daniels (1947). The same carpel supply has been recorded by Tillson (1940), Subramanyam (1955), and Jensen (1966). The fused ventral carpellary bundles of each two adjacent carpels occur in all the studied taxa, this is a case of advancement. Hall (1954) proposed a term "heterocarpous" for this case. A general concept is that the carpel is a three-traced organ; one dorsal and two ventral traces (Eames, 1929; Fraser, 1937). However, Eames and Mac Daniels (1947) stated that the carpel has one, three, five, or several traces. The three-traced carpel is most common, the five-traced one is frequent and those with higher numbers are infrequent.

Considering the carpel in the present study (5-traced) and according to Eames (1931) such carpel is referred to as a primitive case.

Considering the floral vasculature, all the studied taxa have vascular complexes; each complex represents a vascular supply of more than one entity of more than one whorl. The case represents an advanced one. The lower number of such vascular complexes is confined to *Crassula* species; each has only one complex, whereas the remaining studied taxa each have at least two complexes. Eames and Mac Daniels (1947) recorded that the fusion takes place between bundles that are near together either tangentially (as expressed in the present study by Comp. I, Comp. IV, Comp. VII, and Comp. VIII) or radially (as the fused ventral carpellary bundles). The same author presented the Crassulaceae as an example of this behavior.

Considering the number and source of whorls of vascular traces, the studied taxa could be grouped as follows:

	(Whorl)	(Source)	(Taxa)	
Group I	1- S.M.B.	Stele		
	2- S.Ma.Bs.	Stele		
	3- P.M-Ap.St. supply	Comp. I	• <i>Kalanchoe daigermontiana</i> , <i>K. mamorata</i> , <i>K. thyrsiflora</i>	
	4- As.St.B.	Stele		
	5- L.C.B.	Stele		
	6- D.C-N.Sc. supply	Comp. III		
	7- V.C.B.	Stele		
Group II	1- S.M.B.	Stele		
	Subgroup 1	2- P.M-Ap.St. supply	Comp. I	• <i>K. fedtschenkoi</i>
		3- As.St.B.	Stele	
		4- L.C.B.	Stele	
		5- D.C-N.Sc. supply	Comp. III	
		6- V.C.B.	Stele	
Subgroup 2		1- S.M.B.	Stele	
	2- S.Ma.Bs.	Stele		
	3- P.M-Ap.St. supply	Comp. I		
	4- As.St.-L.C. supply	Comp. II		
	5- D.C-N.Sc. supply	Comp. III		
	6- V.C.B.	Stele		
Subgroup 3	1- S.M.B.	Stele	• <i>Crassulacapitelle</i>	
	2- P.M.B.	Stele		
	3- As.St.B.	Stele		
	4- L.C.B.	Stele		
	5- D.C-N.Sc. supply	Comp. III		
	6- V.C.B.	Stele		
Group III	1- S.M.B.	Stele	• <i>Aeonium decorum</i>	
	Subgroup 4	2- S.Ma.-P.M.-Ap.St.supply		Comp. IV
		3- N.Sc.-As.St.-L.C. supply		Comp. V
		4- D.C-N.Sc. supply		Comp. III
		5- V.C.B.		Stele

Subgroup 5	1-	S.M.B.	Stele		
	2-	S.Ma.-P.M.-Ap.St.supply	Comp. IV		
	3-	As.St.-L.C. supply	Comp. II	• <i>K. longiflora</i> ,	
	4-	D.C-N.Sc. supply	Comp. III	• <i>Echeveriasetosa</i>	
	5-	V.C.B.	Stele		
Subgroup 6	1-	S.M.B.	Stele		
	2-	P.m.-Ap.St. supply	Comp. I	• <i>K. rosei</i> ,	
	3-	As.St.-L.C. supply	Comp. II	• <i>Umbilicus horizontalis</i> ,	
	4-	D.C-N.Sc. supply	Comp. III	<i>Cotyledon orbiculata</i>	
	5-	V.C.B.	Stele		
Subgroup 7	1-	S.M.B.	Stele		
	2-	P.M.-D.C.-N.Sc. supply	Comp. VI		
	3-	As.St.B.	Stele	• <i>C. springtime</i>	
	4-	L.C.B.	Stele		
	5-	V.C.B.	Stele		
Group IV	1-	S.M.B.	Stele		
	Subgroup 8	2-	S.Ma.-P.M.-Ap.St.-D.C.-N.Sc.	Comp. VII	• <i>K. kwensis</i> ,
		3-	As.St.-L.C. supply	Comp. II	• <i>Graptopetalum paraguayense</i> ,
		4-	V.C.B.	Stele	* <i>Sedum album</i> , <i>S. nussbaumeriana</i>
Subgroup 9	1-	S.M.B.	Stele		
	2-	P.M.-Ap.St.-D.C.-N.Sc. supply	Comp. VIII	• <i>K. blossfeldiana</i> ,	
	3-	As.St.-L.C. supply	Comp. II	<i>K. laciniata</i> ,	
	4-	V.C.B.	Stele	<i>K. sexangularis</i>	

The above groupings clarify that:

- 1- Group I: with seven whorls of traces, it includes three species of *Kalanchoe*.
- 2- Group II: with six whorls of traces. The diversity in the source of the majority of such whorls leads the group to diverge into three subgroups (subgroups 1-3).
- 3- Group III: with five whorls of traces. The source diversification leads the group to diverge into four subgroups (subgroups 4-7).
- 4- Group IV: with four whorls of traces. The source diversification leads the group to diverge into two subgroups (subgroups 8 and 9).

Irrespective to the source (origin) of the vascular traces, Quimby (1939) has placed the Crassulaceae into four groups; group I (with six whorls of traces), group II (with five), group III (with four), group IV (with three whorls of traces).

As traced out in the present study, when the source of vascular traces is considered in addition to the number of traces, more distinction will be achieved as follows:

Genus *Kalanchoe* (represented by 12 species) has distributed all over the main four groups

Consequently, the genus *Kalanchoe* could be suggested as a core genus. *Aeonium decorum* occupies subgroup 4 for its own (group III). The two species of *Crassula* separated into different groups and into two different subgroups. In *C. capitella* the vascular traces

represented by six whorls (including only one vascular complex, viz. dorsal carpellary-nectary scale complex; Comp. III) and in *C. springtime* there is five whorls (including only one complex, viz. petal median-dorsal carpellary-nectary scale complex; Comp. VI). The two species of *sedum* established in the same subgroup within group IV, including two complexes.

An evaluation of the micro-morphological characters in the light of evolutionary dicta by various phylogenists (Bessey, 1915; Hutchinson, 1948; Stebbins, 1974) could be presented in ascending order as primitive VS advanced: octamerous flowers VS hepta- VS penta- VS tetramerous; two whorls of stamens VS one whorl of stamens; distinct vascular traces VS fused vascular traces (complexes).

In the present study, it is noticed the presence of vascular complexes in all the studied taxa. Any of these complexes represents fused vascular traces of two entities either neighbouring radially of the same whorl (as the fused ventral carpellary traces) or neighbouring tangentially of two or more successive whorls (as the petal median-antepetalous stamen, petal median- dorsal carpellary-nectary scale vascular complex). These fused vascular complexes are considered as advanced case. Based on both the source and number of whorls of vascular traces, the studied taxa could be grouped under four groups and nine subgroups. Such grouping proved to be more distinctive. A core position was suggested for the genus *Kalanchoe* and the two studied *Sedum* are more advanced.

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أما الحزمة الوسطى فقد تظل بلا تفرع حتى نهاية جسم السبلة. المدد الوعائي للبتلة: حزمة واحدة تنشأ من النسيج الوعائي المركزي كما في حالات قليلة أو تنشأ مشتركة Conjoint مع حزمة السداة المقابلة لها في مركب Complex وقد تفرع حزمة البتلة إلى حزم جانبية أو تظل بلا تفرع حتى نهاية جسم البتلة. كما أن المدد الوعائي للسداة: حزمة لكل سداة، محيطين من الحزم، المحيط الخارجي مقابل للبتلات وينشأ غالباً مشتركاً مع حزمة البتلة- وقد يغيب المحيط المقابل للبتلات كما في جنس *Crassula* فقط أما المحيط المقابل للبتلات فينشأ من النسيج الوعائي المركزي أو مشتركاً Conjoint مع الحزم الجانبية للكرابل وحزم الحراشيف الرحيقية في نوع *Aeoniumdecorum* فقط المدد الوعائي للكرابلة: خمس حزم: واحدة ظهرية، اثنتان بطنيتان واثنتان جانبيتان تقع كل منهما بين الحزمة الظهرية والحزمة البطنية في الجهة القريبة منها. وتعد الكرابلة خماسية الحزم حالة بدائية. الحراشيف الرحيقية: تتغذى كل حرسفة بعدد من الحزم الوعائية يتراوح من 3-7 حزم تخرج هذه الإمدادات غالباً مشتركة مع الحزم الظهرية للكرابل وإمداد السداة المقابلة للبتلة.

تم دراسة الصفات التشريحية لأزهار أثنين وعشرين وحدة تصنيفية من الفصيلة الكراسيولية بهدف البحث عن علاقات الترابط بين تلك الوحدات وإمكانية استغلال النتائج في الفصل بين الأنواع. بناء على عدد محيطات الإمدادات الوعائية المتتالية ونشأتها أمكن توزيع الأنواع محل الدراسة (22 نوعاً) على عدد أربع مجموعات رئيسية (Groups) وعدد تسع تحت مجموعات (Subgroups) وأمکن من ذلك التوزيع توضيح الروابط بين الأنواع. توضح الدراسة وجود مركبات Complexes عديدة تمثل إمدادات وعائية ملتحمة لأعضاء متجاورة إما قطريا Radial لتتقسم وتعطى حزمتين متجاورتين كما في حزمتي الكرابلة البطنييتين Ventral bundles أو متجاورة مماسياً Tangential لتتقسم وتعطى إمدادات لأعضاء من محيطات متتالية كما في باقي المركبات Complexes والموجودة في باقي الأنواع تقريباً. وبعد التحام الإمدادات الوعائية لأكثر من عضو في نفس المحيط أو من المحيطات المتتالية صفة متقدمة. أيضاً المدد الوعائي للسبلة: فيما عدا خمس أنواع، فإن السبلة تتغذى بثلاث حزم: واحدة وسطى (Median) واثنتان جانبيتان (Marginals) وقد سجل تاباناً في نشأة الحزم الجانبية للبتلات.