

ANATOMICAL OBSERVATIONS ON A DESERT GROUP OF *SAVIA* SPECIES

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ABSTRACT. The N African/SW Asiatic species-group centred on *Salvia aegyptiaca* L. (Labiateae) was investigated anatomically; eight of the eleven \pm desert species were studied. Characters of petiole, stem and leaf anatomy, stomata and indumentum proved to be very uniform in all the species and emphasised that this is a well-knit alliance of closely related species. On the basis of the slight anatomical differences and the available morphological characters, an informal grouping of the species is proposed.

INTRODUCTION

The species-group centred on *Salvia aegyptiaca* L. (sect. *Eremosphace* Bge.; sect. *Notiosphace* Benth. p.p.) contains 11 currently recognised species growing in the desert regions of N Africa, Arabia and SW Asia; they are generally useful marker species for the Saharo-Sindian phytogeographical region. By far the most widespread species is *S. aegyptiaca* with a continuous west to east range of over 5000 miles, from the Cape Verde Islands to the deserts of Sind. Most of the others are relatively local in their distribution and only three extend somewhat outwith the range of *S. aegyptiaca* (Hedge 1974, fig. 9). The greatest concentration of species is in Iran where 7 occur.

The species-group is characterised as follows. Low-growing (usually under 20 cm), much branched shrubs with thick woody rootstocks, and small simple usually revolute leaves. Calyces somewhat enlarging in fruit with a slightly reflexed upper lip. Flowers small, usually less than 10 mm, white to pink; corolla upper lip \pm straight, tube annulate. Staminal connectives c. 1-2 mm; lower thecae fertile. Nutlets black, trigonous, mucilaginous on wetting.

On the combination of these characters this species-group is clearly isolated from all other groups of Old World (and New World) *Salvia*. Briquet (1895) placed the species in his subgenus *Viasala* sect. *Eremosphace* Bge.; the only other member of the subgenus being the monotypic sect. *Neosphace* Briq. with *S. nilotica* Vahl, clearly quite unrelated to the species under discussion here, being allied to several species from the eastern Cape region of S Africa. Although Briquet's infra-generic classification is quite out-dated, nothing more recent on a world basis exists and until a new classification is available, recognition of informal natural species-groups—such as that of *S. aegyptiaca* is often the best way to indicate relationships or disjunctions. In a previous paper dealing with the African species of the genus (Hedge, 1974) the question of the distinctness of the species-groups amongst the African species was discussed and it was shown that several of them were very distinctly separated from all other species-groups. The *S. aegyptiaca* species-group certainly comes within this category and there is, apparently, no other with which it can be compared or contrasted. On present evidence it gives every impression of having developed autochthonously within the Saharo-Sindian region.

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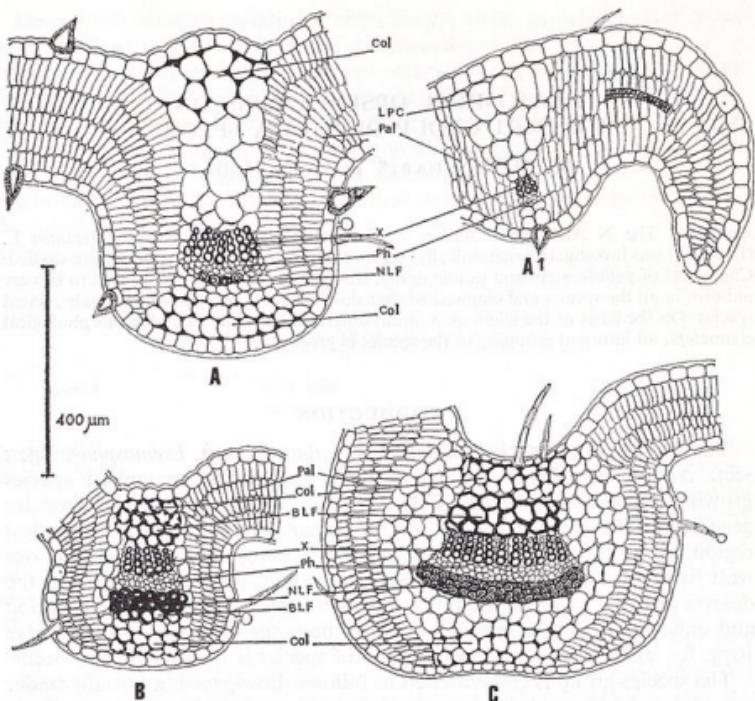


FIG. 1. Transverse sections of part of lamina through midrib. A-A¹, *S. aegyptiaca*: A, transverse section through the midrib; A¹, transverse section through a smaller bundle near the margin. B, *S. trichocalycina*. C, *S. santolinifolia*. BLF, broad-lumened fibres; Col, collenchyma; LPC, large parenchyma cells; NLF, narrow-lumened fibres; Pal, palisade; Ph, phloem; X, xylem.

As part of general studies in Old World *Salvias* and prior to a formal taxonomic revision, this species-group seemed well-suited to anatomical studies both from the point of view of assessing species relationships and also from that of investigating the internal structure of plants adapted to extremely xeromorphic conditions.

The geographical ranges of the species examined are:

- S. aegyptiaca* L. Cape Verde and Canary Islands, N Africa, Sudan, Ethiopia eastwards to Pakistan and India.
- S. deserti* DCne. Sinai, Israel, Transjordan, Arabia.
- S. eremophila* Boiss. C & S Iran.
- S. lacei* Mukerjee. Pakistan (near Quetta). Only known from type.
- S. macilenta* Boiss. Arabia (Oman), S Iran, SW Afghanistan.
- S. santolinifolia* Boiss. S Iran, Pakistan (Makran, Baluchistan etc. to Quetta), SE Afghanistan, India (Punjab, Kutch).
- S. tebesana* Bge. SW Iran.
- S. trichocalycina* Benth. SE Afghanistan, adjacent Pakistan.

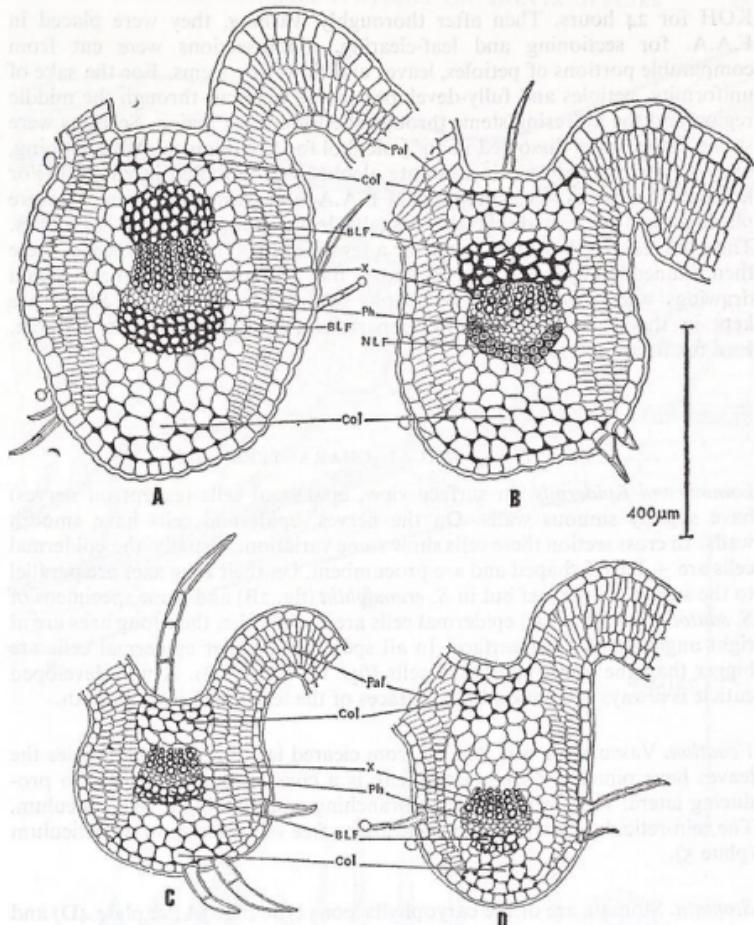


FIG. 2. Transverse sections of part of lamina through the midrib. A, *S. santolinifolia*; B, *S. eremophila*; C, *S. deserti*; D, *S. macilenta*.
 BLF, broad-lumened fibres; Col, collenchyma; NLF, narrow-lumened fibres; Pal, palisade; Ph, phloem; X, xylem.

The following three species were not examined: *S. chudaei* Battand. & Trab., endemic to the Ahaggar and Tibesti mountains of the southern Sahara; *S. gabrielii* Rech. fil., S Iranian, apparently known only from the type; *S. bazmanica* Rech. fil., S Iranian, apparently known only from the type.

MATERIALS AND METHODS

In the present study only herbarium material (at E) was used; it is listed in Appendix 1. Specimens for examination were placed in 1% solution of

KOH for 24 hours. Then after thoroughly washing, they were placed in F.A.A. for sectioning and leaf-clearing. Hand-sections were cut from comparable portions of petioles, leaves and flowering stems. For the sake of uniformity, petioles and fully-developed leaves were cut through the middle region and the flowering stems through the lowermost region. Sections were stained in safranin dissolved in 70% alcohol for five minutes. After staining, sections were dehydrated in absolute alcohol and mounted in euparal. For leaf-clearing, leaves were taken out of F.A.A. and washed with water before placing them in Eau de Javelle; usually leaves will clear after 24 hours. These leaves were boiled in water for a few minutes. The cleared leaves were then stained, dehydrated and mounted like leaf sections. Camera lucida drawings were made and photographs taken from the slides. Slides are kept in the herbarium, Biology Department, Pahlavi University, Shiraz, Iran for future reference.

ANATOMICAL CHARACTERS

Lamina and Epidermis. In surface view, epidermal cells (except on nerves) have slightly sinuous walls. On the nerves, epidermal cells have smooth walls. In cross section these cells show some variation. Usually, the epidermal cells are \pm barrel-shaped and are procumbent, i.e. their long axes are parallel to the surface of the leaf but in *S. eremophila* (fig. 2B) and some specimens of *S. santolinifolia* (fig. 2A) epidermal cells are upright, i.e. their long axes are at right angles to the leaf surface. In all species the upper epidermal cells are bigger than the lower epidermal cells (fig. 1A-C, 2C-D). A well-developed cuticle is always present on both surfaces of the leaf which is \pm smooth.

Venation. Vasculature was studied from cleared leaves. In all the species the leaves have pinnate vasculature. There is a conspicuous single midrib producing lateral veins with the veins branching and forming a vein-reticulum. The vein-reticulum is closed, i.e. there are no free vein endings in the reticulum (plate 5).

Stomata. Stomata are of the caryophyllaceous type (fig. 3A; & plate 4D) and are present on both surfaces of the leaf. On the lower surface the stomata are confined to stomatal grooves. These stomatal grooves have no regular pattern and are present between the ridges produced by raised nerves of the vein-reticulum (fig. 3A; plate 4B, 5 A,B). The raised nerves bordering the stomatal grooves are provided with trichomes which protect the stomata lying deep in the stomatal grooves.

In species with distinctly lobed margins, further protection for the stomata is afforded by these overlapping lobes. The number of stomata per unit area is always higher on the lower surface than on the upper surface. In material of *S. aegyptiaca* from Iran, Afghanistan and Pakistan it was estimated that the number of stomata is about 600 per mm^2 on the lower surface and about 350 stomata per mm^2 on the upper surface. The number of stomata per unit area is lower in specimens examined from the western end of the species range.

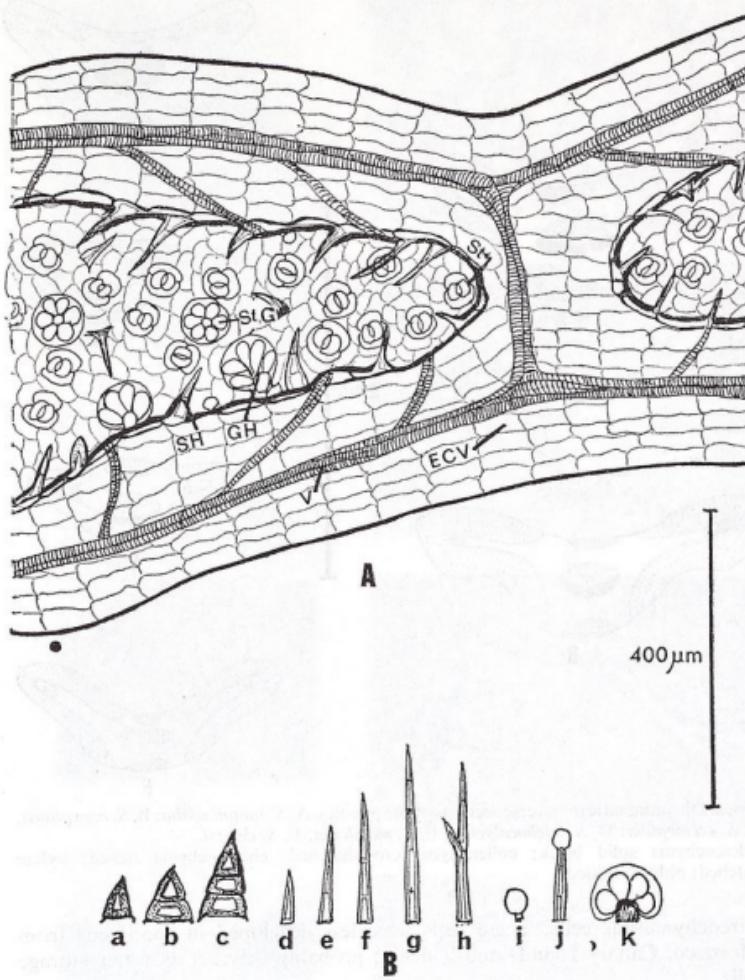


FIG. 3. A, cleared leaf showing parts of stomatal grooves of *S. aegyptiaca*. ECV, epidermal cells over the veins; GH, glandular hairs; SH, simple hairs; St, stomata; St G, stalked gland; V, vein.
B, a-k, types of trichomes.

Mesophyll. Leaves are always isobilateral and mesophyll is entirely composed of palisade cells (fig. 1A-C, 2A-D). The lower palisade layers are continuous with the chlorenchymatous cells in the flank of the midrib. The presence of only palisade in the lamina and chlorenchyma in the flanks of midrib are certainly xeromorphic features. In *S. aegyptiaca* (fig. 1A¹; plate 4E), over the smaller bundles in the lamina are always groups of large thin-walled

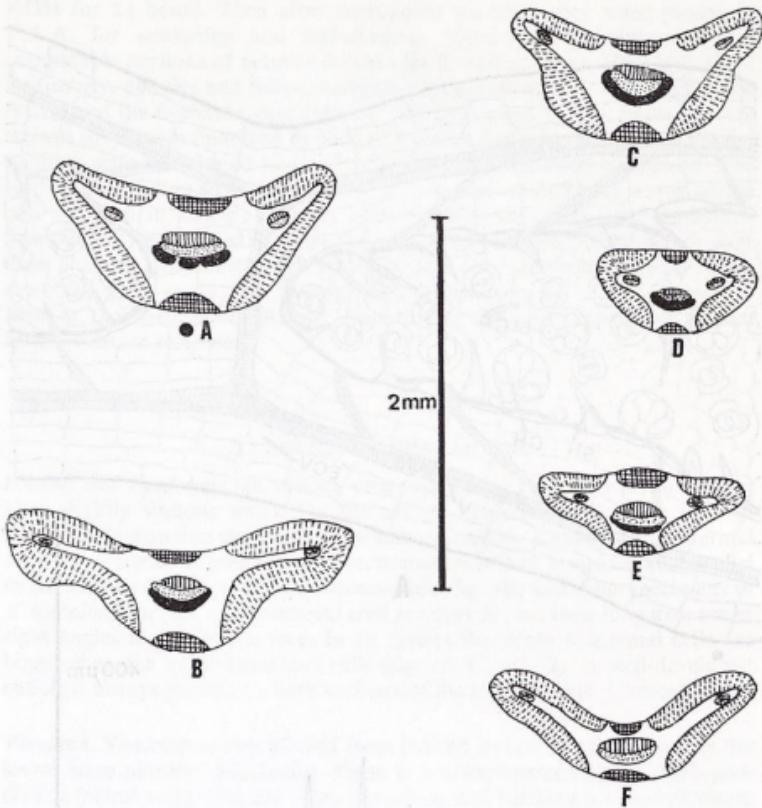
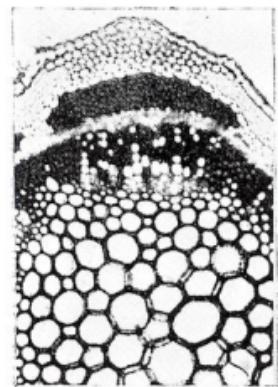


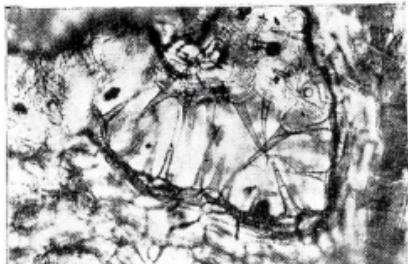
FIG. 4. Diagrammatic transverse sections of the petioles. A, *S. santolinifolia*; B, *S. aegyptiaca*; C, *S. eremophila*; D, *S. trichocalycina*; E, *S. macilenta*; F, *S. deserti*. Sclerenchyma solid black; collenchyma cross-hatched; chlorenchyma ticked; xylem hatched; phloem dotted.

parenchymatous cells. These cells were less developed in specimens from Morocco, Canary Islands and Tunisia; probably they act as water storage cells.

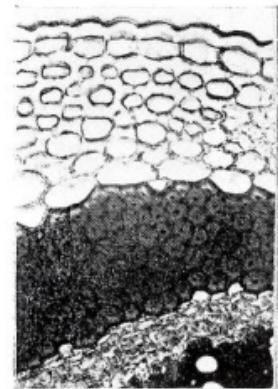
Midrib. There is a single vascular bundle in the midrib. On the abaxial side of the phloem there are always fibres, which may be few in number or in groups. In *S. aegyptiaca* (fig. 1A) and *S. eremophila* (fig. 2B) these fibres are narrow-lumened. In *S. deserti* (fig. 2C), *S. macilenta* (fig. 2D) and *S. lacei*, they are broad-lumened. In *S. trichocalycina* (fig. 1B) and *S. tebesana*, both narrow-lumened and broad-lumened fibres are found on the abaxial side of the phloem. In *S. santolinifolia* in some specimens these abaxial fibres are narrow-lumened (fig. 1C) and in the other specimens are broad-lumened (fig. 2A). On the upper side of xylem, broad-lumened fibres were only noticed in *S. trichocalycina* (fig. 1B), *S. santolinifolia* (fig. 1C, 2A) and *S. eremophila* (fig.



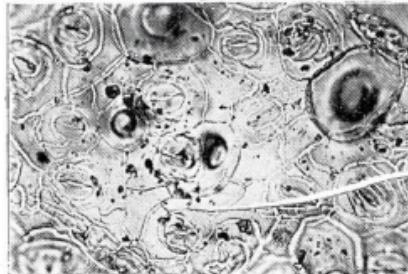
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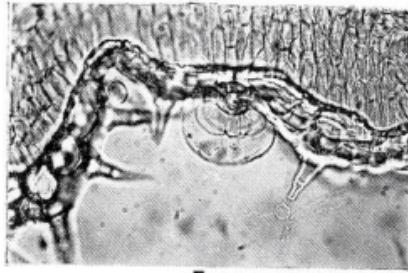
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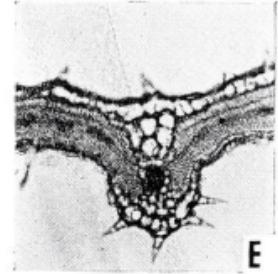
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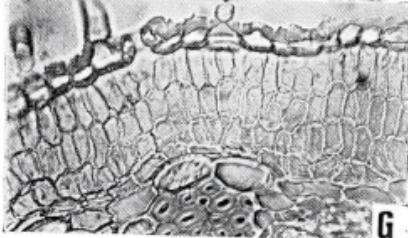
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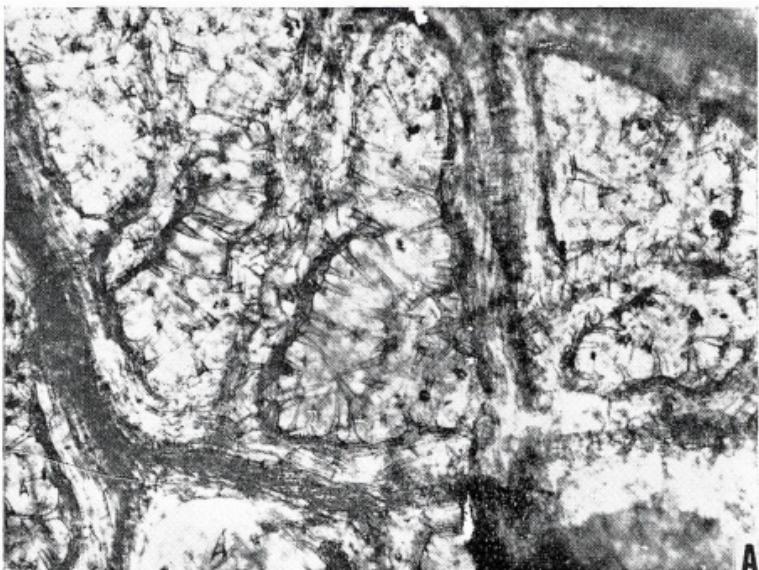


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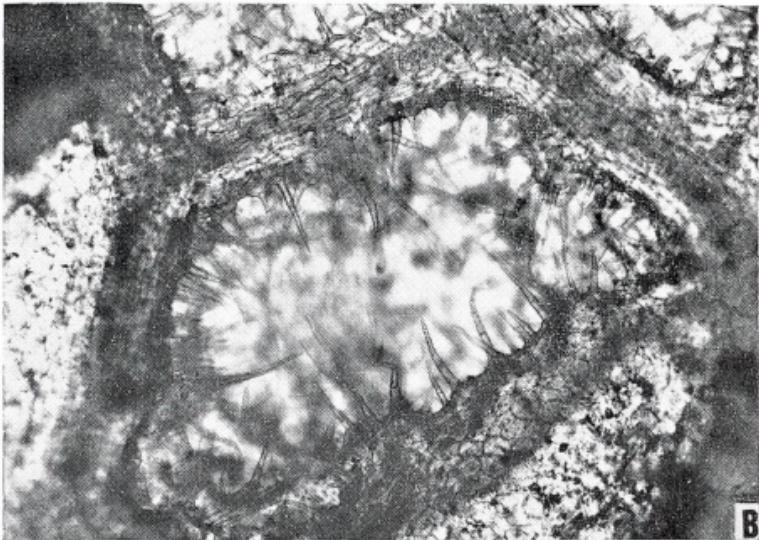


G

PLATE 4. *Salvia aegyptiaca*: A, cross section of a part of flowering stem ($\times 200$); B, small stomatal groove, from cleared leaf ($\times 150$); C, cross section of a part of flowering stem showing thick cuticle, collenchyma and narrow-lumened cortical fibres ($\times 800$); D, stomata at the base of stomatal groove ($\times 800$); E, cross section of a part of lamina showing all palisade tissue and a group of parenchyma cells over the smaller bundle ($\times 200$); F, cross section of a part of lamina showing lower epidermis and various types of trichomes ($\times 800$); G, cross section of a part of flowering stem showing thick cuticle and abundant chlorenchyma ($\times 800$).



A



B

PLATE 5. *Salvia aegyptiaca*: A, part of a cleared leaf showing stomatal grooves formed by the raised nerves ($\times 100$); B, single stomatal groove enlarged to show raised nerves and trichomes protecting the stomata [stomata not in focus] ($\times 200$).

2B). In all the species there is also a well-developed patch of collenchyma on the upper and lower side of the midrib. There is always a well-developed chlorenchyma tissue in the flanks of the midrib which is continuous with the palisade of the lamina (fig. 1A-C, 2A-D).

Petiole. Petioles are generally winged (fig. 4 A,B,C,E,F) but in *S. trichocalycina* (fig. 4D) and *S. tebesana* they are not winged. In all species, there is a main median vascular bundle in the petiole which is accompanied by two smaller subsidiary bundles which are usually present in the wings (fig. 4). In most of the species there is a patch of fibres on the abaxial side of the phloem of the main vascular bundles, but in *S. deserti* these fibres were not noticed. As in the midrib, there is always a patch of collenchyma on the upper and lower side of the main vascular bundle of the petiole below the epidermis. In all the species there is always a well-developed chlorenchyma in the wings and the flanks of the petioles which is also continuous over most parts of the upper side of the petioles. The presence of a number of stomata on the petiole and the extensive development of chlorenchyma tissue shows that the petiole is an efficient photosynthetic organ in these species.

Stem. The flowering stems were sectioned in the lowermost region. In cross-section the stem is usually distinctly quadrangular but in one specimen of *S. deserti* (Davis 9244) it was \pm rounded. There is always a group of collenchyma in the stem angles. Although Metcalf & Chalk (1950) reported that in some species of *Salvia*, this collenchyma later on becomes sclerified, in *S. deserti* (fig. 5C, 6B) it does not. In most specimens of *S. aegyptiaca* (figs. 5D, 6C; plate 4 A,C), the collenchyma is not sclerified, but in some a few sclerified cells were also observed in the collenchyma. In the other species, collenchyma at the angles becomes distinctly sclerified (figs. 5A,B,E,F, 6A). In all the species studied, the stem has a single layer of epidermis with a very well-developed cuticle and number of stomata. The cortex has two types of cells: the outer layer is made up of 3-4 layers of chlorenchyma (fig. 6A-C), the inner layers have small, thin-walled parenchyma without chloroplasts. Usually these parenchyma cells are quite small but in some specimens of *S. aegyptiaca* these are comparatively larger (fig. 6C). Cortical fibres which are present immediately outside the phloem show some variations in arrangement and structure. These fibres are in the form of strands scattered in the parenchyma region of the cortex. Usually there is a large strand of fibres below each angle and a number of smaller strands all around the phloem, (fig. 5,A,B,C,E,F), but in *S. aegyptiaca* (fig. 5D; plate 4A) the strands of fibres below the angles are well-developed as in the other species but other strands of fibres around the phloem are very poorly developed. In *S. deserti* (fig. 6B), the cortical fibres are \pm broad-lumened. In *S. santolinifolia* (fig. 6A), *S. eremophila*, *S. trichocalycina* and *S. tebesana*, below the sclerified collenchyma of the angles, there are well-developed strands of broad-lumened cortical fibres and below this strand is again a strand of narrow-lumened fibres. In the other species, all cortical fibres are only narrow-lumened. In all the species examined, phloem and xylem are in the form of rings. In the xylem there is always an excessive development of fibres and vessels are arranged in \pm radial rows. Pith is homogeneous and thick-walled (fig. 6A, B,C).

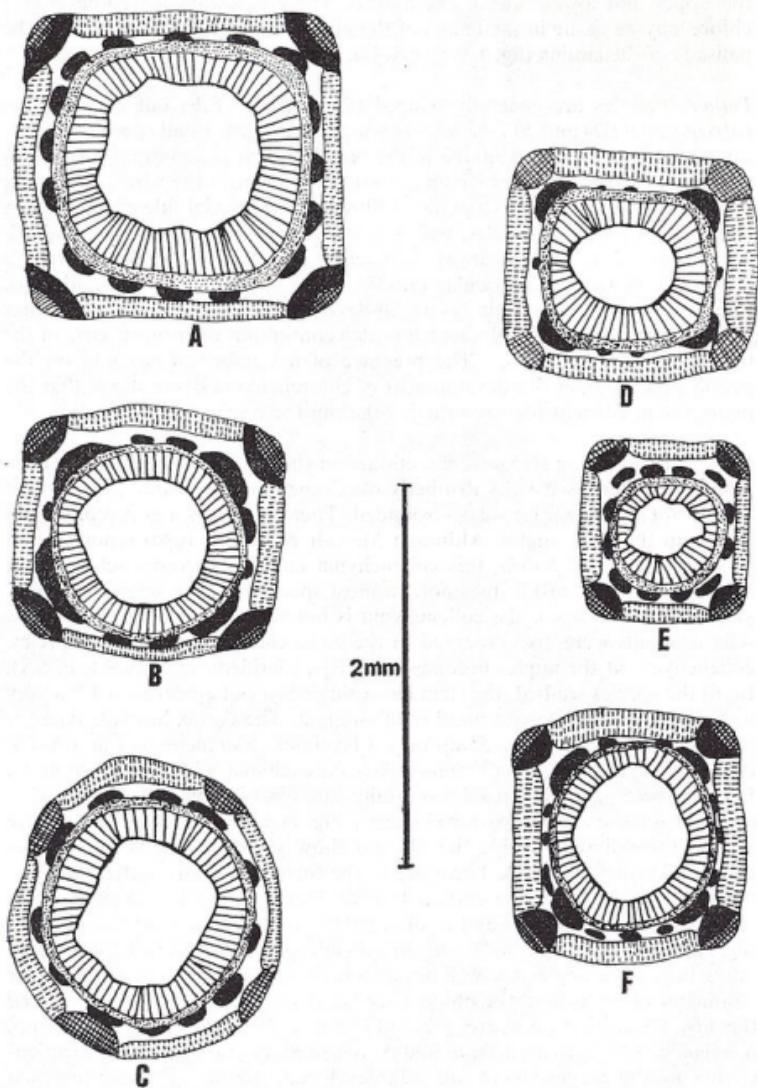


FIG. 5. Diagrammatic transverse sections of stems. A, *S. macilenta*; B, *S. santolinifolia*; C, *S. deserti*; D, *S. aegyptiaca*; E, *S. trichocalycina*; F, *S. eremophila*. Sclerenchyma solid black; collenchyma cross-hatched; chlorenchyma ticked; xylem hatched; phloem dotted.

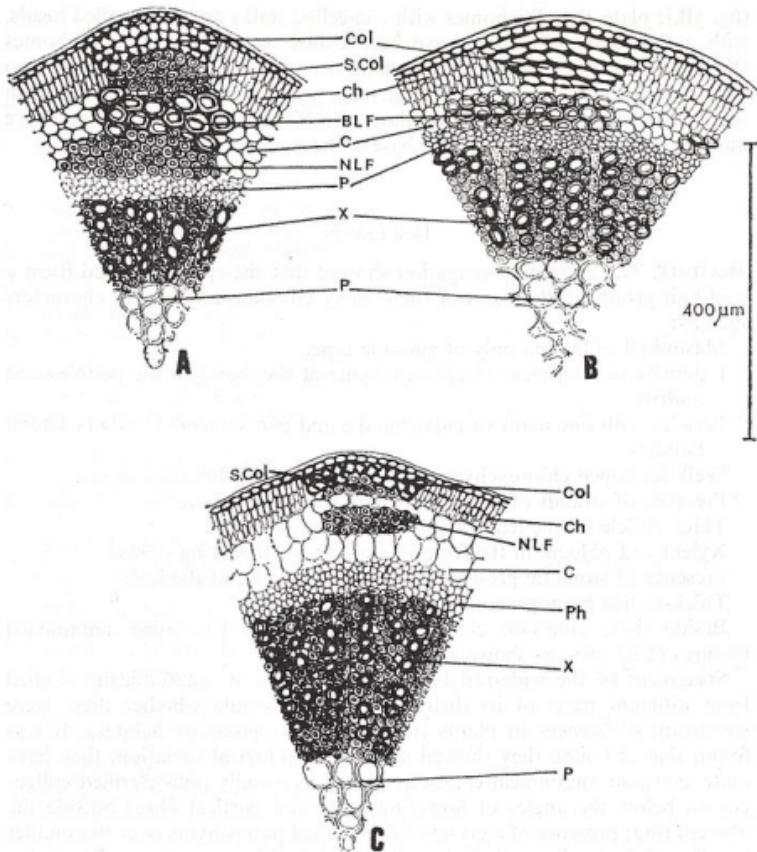


FIG. 6. Transverse sections of parts of flowering stems. A, *S. santolinifolia*; B, *S. deserti*; C, *S. aegyptiaca*.

BLF, broad-lumened fibres; C, cortex; Ch, chlorenchyma; Col, collenchyma; NLF, narrow-lumened fibres; P, pith; Ph, phloem; S.col, sclerified collenchyma; X, xylem.

Indumentum. Trichomes of different types are present on petiole, leaf lamina and flowering stems (fig. 3B a-k; plates 4F, 5).

Non-Glandular Trichomes. Mostly the hairs are non-glandular, 1-5-celled and simple (fig. 3B,a-h). 1-branched hairs were noticed in some specimens of *S. santolinifolia* (fig. 3B,h). Most of these hairs are thin-walled and non-cutinised but in *S. aegyptiaca* besides these thin-walled and non-cutinised hairs there are some 1-3-celled, thick-walled and strongly cutinised (fig. 3B, a-c); such hairs were noticed only on the lamina of *S. aegyptiaca* and were not observed in any other species of this group.

Glandular Trichomes. Hairs with a 1-celled stalk, 1-celled head and hairs with a 2-3-celled stalk and 1-celled head are quite common in these species

(fig. 3B,j; plate 4F). Trichomes with 1-2-celled stalks and 8-16-celled heads, with a thin layer of cuticle have been called terpene secreting trichomes (Kissler 1958). These characteristic glandular trichomes of Labiateae are also known as integumentary glands (Solereder 1908) and are quite common in the species examined (fig. 3B,k; plate 4F). There were found to be more numerous on the margin and at the base of the stomatal groove (fig. 3A).

DISCUSSION

ANATOMY. The present investigation showed that the species studied form a well-knit group on the basis of their many common anatomical characters such as:

Mesophyll of lamina only of palisade type.

Extensive development of chlorenchyma at the flanks of the petioles and midrib.

Petioles with one main vascular bundle and two smaller subsidiary lateral bundles.

Well-developed chlorenchyma in the cortex of the flowering stems.

Presence of strands of cortical fibres in the flowering stems.

Thick cuticle on the leaf, petiole and flowering stems.

Xylem and phloem in the form of rings in the flowering stems.

Presence of stomatal grooves on the lower surface of the leaf.

Thick-walled homogeneous pith.

Beside these common characters, each species has some anatomical features of its own, as shown in table 1.

Specimens of the wide-ranging *S. aegyptiaca* were anatomically studied from different parts of its distribution to determine whether there were significant differences in plants from different regions or habitats. It was found that although they showed some morphological variation, they have quite constant anatomical characters: such as usually non-sclerified collenchyma below the angles of flowering stem; few cortical fibres outside the phloem ring; presence of a group of thin-walled parenchyma over the smaller bundles of the lamina and thick-walled, cutinised hairs on the lamina. Some differences were however noticed between specimens from Iran, Afghanistan, Pakistan and those of the Canary Islands, Morocco and Tunisia. Those from the east of the species range tended to be more densely hairy, and have more stomatal grooves and stomata per unit than those of the Canary Islands, Morocco and Tunisia.

It is also clear from the anatomical evidence that all the species examined possess a number of xeromorphic features which are of great advantage to them in their natural desert habitat. One of the obvious features is the xeromorphic leaf structure with the small ratio of external leaf surface to volume. The reduction of the external surface is often accompanied by certain changes in the internal structure (Weaver & Clements 1929). This is shown by the reduction in the size of the cells, greater density of stomata per unit area and increased development of palisade tissue. All our species are found in regions where there is intense sunlight and scarcity of water during the long dry spell in the summer season. Intense illumination and retardation of water flow due to water deficiency results in the increased development of palisade

TABLE I

CHARACTER	SPECIES							
	ae	de	er	sa	te	tr	la	ma
A. Cortical fibres all narrow-lumened.								
B. Cortical fibres all broad-lumened.								
C. Cortical fibres broad-lumened as well as narrow-lumened.	A	B	C	C	C	C	A	A
A. Collenchyma at the angles of stems not becoming distinctly sclerified.								
B. Collenchyma at the angles of stem becoming distinctly sclerified.	A	A	B	B	B	B	B	B
A. Petiole distinctly winged.								
B. Petiole not distinctly winged.	A	A	A	A	B	B	A	A
A. A group of thin-walled parenchyma cells over smaller bundles.								
B. Such parenchyma groups absent.	A	B	B	B	B	B	B	B
A. 1-3-celled thick-walled cutinised trichomes present.								
B. Such trichomes absent.	A	B	B	B	B	B	B	B
A. Midrib adaxial fibres absent.								
B. Midrib adaxial fibres present.	A	A	B	B	B	B	A	A
A. Midrib abaxial fibres narrow-lumened.								
B. Midrib abaxial fibres broad-lumened								
C. Midrib abaxial fibres both narrow and broad-lumened.	A	B	A	C	A	C	B	B
A. 4 strands of cortical fibres below the angle of stem well-developed but cortical strands of fibres all around phloem poorly developed.								
B. 4 well-developed strands of cortical fibres below the angles of stem. Cortical strands of fibres all around the phloem also well-developed.	A	B	B	B	B	B	B	B
A. Long axes of the epidermal cells parallel to the surface of leaf.								
B. Long axes of the epidermal cells at right angles to surface of leaf.								
C. Long axes of the epidermal cells parallel as well as right angles to the surface of the leaf.	A	A	B	C	A	A	A	A

Abbreviations: ae, *Salvia aegyptiaca*; de, *deserti*; er, *eremophila*; sa, *santolinifolia*; te, *tebesana*; tr, *trichocalycina*; la, *lacei*; ma, *macilenta*.

tissue (Shield 1950). In these species the reduction in leaf size is compensated by the extensive development of chlorenchyma in the midrib, petiole and in the stem which are also provided with stomata. The increase in the number of stomata and increased development of palisade in leaf and chlorenchyma in the midrib, petiole and the stem certainly results in an increase of photosynthetic activity.

TAXONOMY. The anatomical studies have clearly illustrated the basic similarity in internal structure of all the species examined, but have not yielded much in the way of new information for the taxonomist. Several species are, however, on anatomical evidence, very close to each other, such as *S. tebesana*, *S. trichocalycina* and *S. santolinifolia*, and their status needs to be re-assessed.

All the species of the group are dwarf in stature, with small, often few, leaves, and reduced flowers. The main available characters for separating them on gross morphological features are: leaf shape and degree of revolution; and calyx shape and indumentum. Nutlets, which are generally a most useful and reliable character in the genus, are very similar in all of them, but those of *S. aegyptiaca* are somewhat more elongated and trigonous.

Summing up the existing anatomical and morphological information about this interesting group of species, the following synopsis of relationships and distinctness includes all the species in the alliance, including the three not anatomically studied.

1. *S. aegyptiaca*; *S. gabriellii* probably synonymous. Clearly distinct from the other sub-units.
2. *S. deserti*.
3. *S. eremophila*.
4. *S. santolinifolia*; *S. tebesana*, probably the same, and the earliest name; *S. trichocalycina*, very close; *S. lacei*, close but differing in leaf shape; *S. chudaei*, allied but clearly distinct.
5. *S. macilenta*; *S. bazmanica* apparently close. Probably should be placed along with the related species.

ACKNOWLEDGMENTS

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APPENDIX I

Species investigated, listed in alphabetical order.

S. aegyptiaca. *Canary Islands*. Tenerife: Santa Cruz, J. Ball; Santa Cruz, Bourgeau. Gran Canaria: Maspalomas, Bramwell 1245. *Morocco*: Marrakech to Chemaia, Davis 54115; Sous valley, Taroudannt to Irherm, Davis 48900. *Algeria*: Biskra, Balansa. *Tunisia*: Matmata, Davis 48088. *Egypt*: lower Egypt, Wadi el Obdi, Davis 6308 B. *Palestine*: Wadi Kelt, Davis 4054. *Iraq*: Negev, Wheeler-Haines. *Oman*: Muscat, Rubens 102. *Iran*: Fars, Kahurestan to Lar, Davis 56202; near Kangan, E of Dayyer, Davis 56078; Bandar Khomyer, Davis 56139; Baluchistan, Tangue Sarhé, Sharif 414E (as *S. gabrieli*). *Afghanistan*: Jalalabad to Chigha Serai, Lamond 2536. *Pakistan*: Peshawar to Torkham, Lamond 1597; Rawalpindi, R. R. Stewart 28587. *India*: New Delhi ridge, New Delhi, Muluka s.n.

S. deserti. *Sinai*: Mt Sinai, Schimper 184; Wadi Berra, Tadmor 53452. *Transjordan*: Wadi Ithm, Davis 9244.

S. eremophila. *Iran*: Farsistan, Niris, Bornmüller 4316; Tehran, Kashan to Natanz, Wendelbo & Foroughi TARI 11418; Fars, Kahurestan to Lar, Davis 56204.

S. lacei. *Pakistan*: Baluchistan, Quetta, Cheppar Rift, Lace 3976 (type).

S. macilenta. *Iran*: Baluchistan, Tangue Sarhé, Sharif 414E bis; Bandar Abbas, Rudan, Wendelbo & Foroughi TARI 15603.

S. santolinifolia. *Iran*: Zahedan to Birjand, Grey-Wilson & Hewer 341; E of Lar, Grey-Wilson & Hewer 90; E of Bandar Lengeh, Davis 56159; SW Nasratabad Sipi, Lamond 105. *Afghanistan*: Fariah, Dilaram, Hedge, Wendelbo & Ekberg 7662. *Pakistan*: Peshawar to Cherat, Lamond 1572. *India*: Kutch Nakhtrana, S. K. Jain 61965.

S. tebesana. *Iran*: prope Meibut, inter Jesd et Isfahan, Bunge (type).

S. trichocalycina. *Afghanistan*: Nangarhar, Khyber pass, Hedge & Wendelbo 7418; Torkham to Jalabad, Lamond 1904; *Pakistan*: Torkham, Lamond 1622.