OBSERVATIONS ON THE MUCILAGE OF SALVIA FRUITS

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ABSTRACT. The production of mucilage by wetted nutlets of *Salvia* species is a very widespread phenomenon among SW Asiatic members of the genus. It is shown that, in the species from Afghanistan, many have appreciable differences in their mucilage characters; morphologically distinct species tend to have the most distinct kinds of mucilage and allied species usually have similar mucilage features. In all the species examined, twisted or coiled threads are present; other cellular contents are also often present. The structure of the pericarp, mucilage formation in other Labiate genera and the biological function of mucilage are discussed. The taxonomic value of mucilage characters is considered and the conclusion reached that although occasionally valuable it is not an easy character to work with.

INTRODUCTION

The usefulness of nutlet characters for species and generic identification in the Labiatae has been demonstrated by Bilimovitsch (1935), Wojciechowska (1958 et seq.), Makarova (1967) and others. Wojciechowska carried out a nutlet study of eighteen European *Salvia* species and showed that there were sharply defined differences in the gross and detailed morphology of most species. She later (1966) extended her work to other genera of the Labiatae and showed that in these taxa also there were often profound differences at both generic and species level.

The present author (1968), during a taxonomic investigation of the Labiatae of Afghanistan, showed that most of the forty species of *Nepeta* could easily be recognised on macroscopic characters of nutlet size, shape, texture and areole pattern. In a taxonomically difficult genus, the nutlet characters of *Nepeta* species thus provided a useful character which had not previously been used in their identification. Subsequently the fruits of several other SW Asiatic genera were surveyed with a view to assessing the overall taxonomic worth of nutlet characteristics and although ideal comparative material was rarely at hand, *Salvia* appeared to be the only genus likely to produce interesting results. During this quick initial survey, it was noticed that all the nutlets of the *Salvia* species examined produced mucilage on wetting and that there were apparently differences between species. This suggested that a review of a selected number of species would be profitable to determine whether or not the differences were taxonomically significant. Accordingly, as the Afghan representation of *Salvia* covered a considerable range of the morphological variation within the genus, at least in the Old World, it was decided to consider in some detail the species from that country.

The following species, arranged in systematic order, were examined:

Subgenus	Section	Species
Salvia	*Physosphace* Bge.	1. *S. pterocalyx* Hedge
—	*Eusphace* Benth.	2. *S. cabulica* Benth.
Schraderia (Mönch) Briq.	*Hymenosphace* Benth.	3. *S. bucharica* M. Pop.

Sclarea (Mönch) Benth.	*Homalosphace* Benth.	4. *S. compressa* Vahl
		5. *S. leriifolia* Benth.
	—	6. *S. macrosiphon* Boiss.
	—	7. *S. spinosa* L.
	—	8. *S. moorcroftiana* Benth.
	—	9. *S. ariana* Hedge
	Gongrosphace Bge.	10. *S. ceratophylla* L.
	—	11. *S. sclarea* L.
	—	12. *S. rhytidea* Benth.
	Drymosphace Benth.	13. *S. nubicola* Sweet
	Plethiosphace Benth.	14. *S. virgata* Jacq.
		15. *S. nemorosa* L.
Viasala Briq.	*Eremosphace* Bge.	16. *S. aegyptiaca* L.
	—	17. *S. santolinifolia* Boiss.
	—	*18. *S. lacei* Mukerjee
	—	19. *S. trichocalycina* Benth.
Leonia (Llav. & Lex.) Benth.	*Notiosphace* Benth.	20. *S. plebeia* R.Br.

* Not yet recorded from Afghanistan.

No material was available of the other species in Afghanistan viz., *S. tetrodonta* Hedge, *S. maymanica* Hedge and *S. macilenta* Boiss.

General morphology of nutlets

As fig. 1 shows, there is a very remarkable range in size and shape of the nutlets. The extremes of size are represented by *S. leriifolia* with nutlets c. 6 × 6·2 mm and *S. plebeia* 1·0 × 0·7 mm. Most of the nutlets are more or less trigonous in transverse section but in *S. bucharica* and *S. leriifolia* they are round. The most common type of surface texture is smooth and somewhat glossy with fairly prominent reticulate venation; this type is found in *S. compressa*, *S. spinosa*, *S. moorcroftiana*, *S. ariana*, *S. sclarea* and *S. rhytidea*. In all these species the nutlets are more or less light brown in colour. In *S. pterocalyx* the nutlets are clearly compressed, smooth, matt and orange-brown; in *S. cabulica*, somewhat rough-matt; *S. bucharica*, rough-matt; in *S. leriifolia* and *S. ceratophylla*, rough-matt and black; in *S. nemorosa* and *S. virgata*, rough-matt and dark brown; in *S. aegyptiaca*, *S. santolinifolia*, *S. lacei* and *S. trichocalycina*, rough-matt and black sometimes glaucous; and in *S. plebeia* the nutlets are rough-matt and dark brown.

Solely on the basis of general morphology, it would not be possible to distinguish the related and possibly introgressing *S. macrosiphon*, *S. spinosa* and *S. moorcroftiana* nor the species of sect. *Eremosphace*, *S. aegyptiaca*, *S. santolinifolia*, *S. lacei* and *S. trichocalycina*. The remaining species could be recognised by their nutlets.

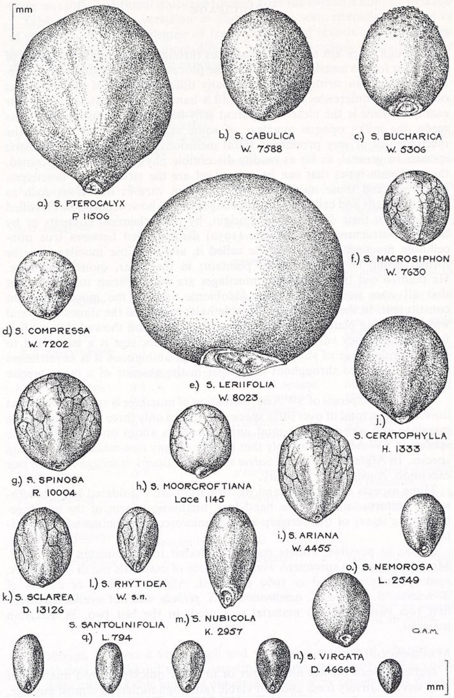

FIG. 1. Nutlets of Afghanistan species of *Salvia*. P—Podlech; W—Hedge & Wendelbo; R—Rechinger; H—Hewer; D—Davis; L—Lamond; K—Koeie.

MUCILAGE

GENERAL

Although there are numerous instances throughout the plant kingdom of seeds that form a mucilaginous coat in the process of germination, surprisingly little has been written about the many different kinds of mucilage that occur. These differences may, even with a hand lens, be quite striking. For example, there is the clear transparent jelly-like mucilage formed by cress seeds, the milky opaque mucilage of some sage species and there is the mucilage full of very prominent spiral inclusions as produced by *Blepharis* species. In general, as far as readily discernible physical form is concerned, the two main types that can be recognised are the structureless mucilages, like cress, and those mucilages which contain various inclusions such as spirals, threads and cell contents. Mucilages could, however, also be classified according to their developmental origin, by their chemical contents or by their fine structure. Muehlethaler (1950) distinguished between true non-cellulose mucilage, or slime as he called it, and cellulose mucilage. In the former group he cited flax and plantain; in the latter, quince and sage. He pointed out that chemically mucilages are very difficult to analyse but that all were polyuronides with aldobionic acid as the most important constitutent. In the same paper, Muehlethaler examined the slimes of several widely differing plants with an electron microscope and showed that in their fine structure they varied greatly. Clearly then, mucilage is a term used to cover a wide range of substances but although ambiguous it is nevertheless useful and is used throughout this paper in the absence of a more precise terminology.

In the *Salvia* species of SW Asia, formation of mucilage is apparently almost universal. In a total of over forty species examined only three failed to produce mucilage and although this total only represents about one fifth of all the species in SW Asia it is unlikely that there are many non-mucilage producing species. In Afghanistan all the *Salvia* species produced mucilage in, with one exception, considerable quantity.

Three aspects of mucilage and its formation are considered here: macroscopic features visible with a hand lens, anatomical form of the mucilage-producing layers of the pericarp and the microscopic structure of the mucilage.

As far as possible, nutlets recently collected in Afghanistan were used. Mostly, herbarium specimens were the source of materials but in some cases, seed specially collected in 1969 was used. Afghan material of nutlets of *S. sclarea*, *S. virgata*, *S. nemorosa* and *S. plebeia* was not available; in the first two cases, Turkish material was used, in the last two, W Pakistan material.

MACROSCOPIC FEATURES

Nutlets placed on wet filter paper or in water quickly formed mucilage if they were relatively fresh and still viable (although nutlets of almost any age, if they have been mature at some time, will eventually form mucilage). In most cases mucilage production starts almost immediately; in some species, e.g. *S. aegyptiaca*, the bulk of the mucilage is formed after only a few minutes but in others the time taken is somewhat longer. In all the species examined there was little additional mucilage formed after the first half hour of wetting.

Table I shows the variation in three readily seen characters—quantity of mucilage, colour or degree of transparency and texture. These features are by their very nature most difficult to define precisely and observable differences cannot readily be expressed in words.

TABLE I

	Mucilage/seed width ratio	Colour	Other remarks
1. *S. pterocalyx*	0·7 width of seed or more.	milky-opaque	loose soft texture with no definite margin.
2. *S. cabulica*	0·3	translucent	rather soft texture; inclusions visible.
3. *S. bucharica*	0·3	transparent	firm texture; inclusions visible, mainly at base of nutlets.
4. *S. compressa*	1·3	transparent-translucent	soft texture; firm at centre, loose at periphery.
5. *S. leriifolia*	<0·1	transparent	dark brown inclusions at periphery of mucilage.
6. *S. macrosiphon*	0·5	translucent	firm texture; no inclusions visible.
7. *S. spinosa*	0·5	translucent	firm texture; no inclusions visible.
8. *S. moorcroftiana*	0·5	translucent	firm texture; no inclusions visible.
9. *S. ariana*	no adequate fruits available		
10. *S. ceratophylla*	0·5	brownish opaque	firm texture.
11. *S. sclarea*	0·5	transparent-translucent	firm texture.
12. *S. rhytidea*	0·5	translucent	firm texture.
13. *S. nubicola*	0·5	translucent-opaque	firm texture; peeling strips of outer epidermis present.
14. *S. virgata*	0·7	translucent-opaque	firm texture; prominent inclusions.
15. *S. nemorosa*	0·7	transparent	softish texture; inclusions visible.
16. *S. aegyptiaca*	1·1	milky opaque	
17. *S. santolinifolia*	no adequate fruit available		
18. *S. lacei*			
19. *S. trichocalycina*	1·0	translucent	soft texture; regular fine structure apparent, peeling epidermis.
20. *S. plebeia*	1·0	translucent	soft texture; regular fine structure apparent peeling epidermis.

Although this was a very rough and superficial method of comparison it nevertheless brought out some interesting features very clearly. A few species had quite unmistakable kinds of mucilage, others were recognisably different and the remainder not or scarcely distinguishable.

In the first category came *S. pterocalyx* and *S. plebeia;* the former with its thick, loose, wet cotton-wool-like mucilage was quite unlike anything else and the latter appeared equally unique on account of the thin regularly

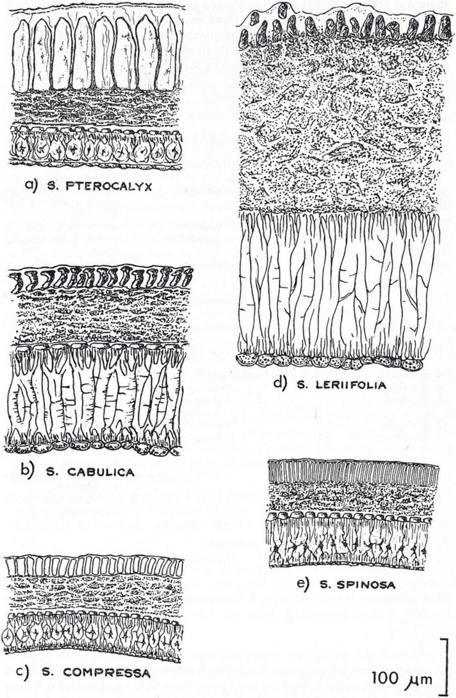

FIG. 2. Transverse sections of nutlets of *Salvia* species. The sections were cut from the same collections as those illustrated in fig. 1. The structure of the testa is not shown.

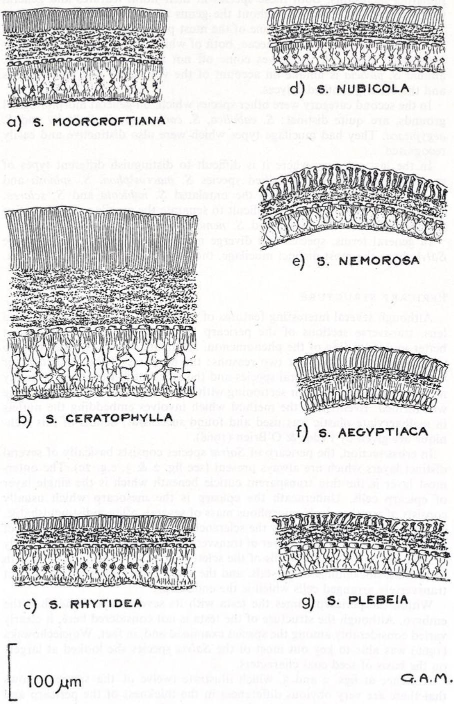

FIG. 3. Transverse sections of nutlets of *Salvia* species. The sections were cut from the same collections as those illustrated in fig. 1 except for *S. moorcroftiana* which was prepared from *W*. 8884.

radiating inclusions. Both these species in their floral features and general facies are most distinct throughout the genus and quite without any close allies. *S. pterocalyx* is florally one of the most primitive Salvias in that there is little differentiation of the thecae, both of which bear fertile pollen; it has a six-sided stem and the leaves come off not in pairs but in threes. The annual *S. plebeia* is unique on account of the very small c. 5 mm corollas and the blunt 3-toothed calyces.

In the second category were other species which, on general morphological grounds, are quite distinct: *S. cabulica*, *S. compressa*, *S. leriifolia* and *S. aegyptiaca*. They had mucilage types which were also distinctive and easily recognised.

In the last category where it is difficult to distinguish different types of mucilage came the closely allied species *S. macrosiphon*, *S. spinosa* and *S. moorcroftiana* together with the unrelated *S. nubicola* and *S. sclarea*. With a hand-lens it would be difficult to separate the mucilages of these five species. Likewise *S. virgata* and *S. nemorosa* were very similar.

In general terms, species that diverge most from a hypothetical average *Salvia* have the most distinct mucilage, those that are near it have the least.

PERICARP STRUCTURE

Although several interesting features of mucilage can be seen with a hand lens, transverse sections of the pericarp are essential in order to give a better understanding of the phenomenon. Adequate sections of the pericarp were difficult to obtain for two reasons: the hardness of the fruit together with the small size of several species and the fact that in the course of many methods of preparation for sectioning with a microtome, unwanted mucilage was formed. Eventually, the method which involves embedding the nutlets in methacrylate plastic was used and found successful; details of this technique are given by Feder & O'Brien (1968).

In cross section, the pericarp of *Salvia* species consists basically of several distinct layers which are always present (see fig. 2 & 3, e.g. 2c). The outermost layer is the thin transparent cuticle beneath which is the single layer of epicarp cells. Underneath the epicarp is the mesocarp which usually consists of a rather dark amorphous mass of several, often indistinguishable, cell layers. This is followed by the sclerenchyma tissue. It usually consists of a distinct uppermost single layer of transversely arranged cells, the irregularly shaped vertically arranged cells of the sclerenchyma layer itself, usually with inclusions, thickenings or crystals, and the single innermost layer of distinct transversely arranged cells which is the endocarp.

Within the pericarp comes the testa with its several layers and then the embryo. Although the structure of the testa is not considered here, it clearly varied considerably among the species examined and, in fact, Wojciechowska (1966) was able to key out most of the *Salvia* species she looked at largely on the basis of seed coat characters.

A glance at figs. 2 and 3, which illustrate twelve of the species, shows that there are very obvious differences in the thickness of the pericarp and in the proportions of its individual layers.

The most distinct species in general facies proved in general to have the most distinctive pericarps. For example, the long broad epicarp cells of

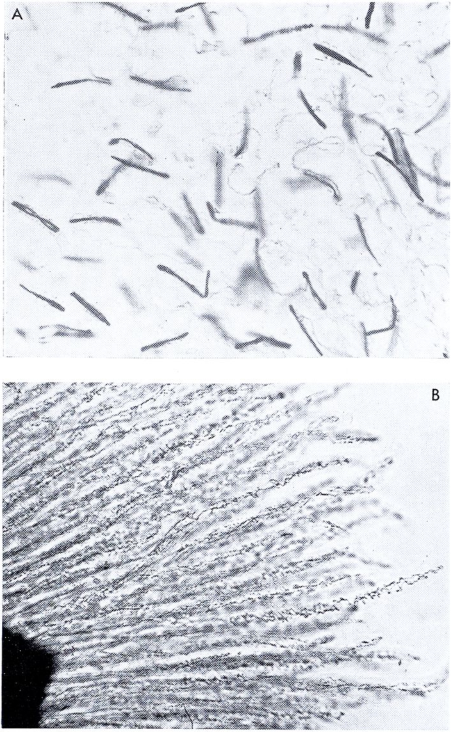

PLATE 7. Mucilage of A, *S. ceratophylla* (c. × 200) and B, *S. nubicola* (c. × 1000) showing inclusions and spirals.

S. pterocalyx, the short stub-like contents of the epicarp in *S. cabulica*, the distinct short, broad clear cellular structure of the epicarp in *S. compressa*, the dense, thick dark brown mesocarp layer of *S. leriifolia* and the elongated narrow epicarp cells of *S. ceratophylla* were all most distinctive features. *S. nemorosa*, *S. aegyptiaca* and *S. plebeia* were also distinct enough in their pericarp structure: *S. nemorosa* on account of the epicarp, *S. aegyptiaca* because of the clear cellular structure of the epicarp with black pigments in the cuticle and *S. plebeia* on account of the sclerenchyma layer. *S. spinosa*, *S. moorcroftiana*, *S. macrosiphon* (not illustrated), *S. rhytidea* and *S. nubicola* were very similar and not readily distinguishable.

MUCILAGE STRUCTURE AND RELATION TO EPICARP CELLS

When a fruit is wetted, water is rapidly absorbed by the outer layer of the pericarp, the cells of the epicarp swell, the cuticle ruptures and the contents of the epicarp cells are expelled in a mucilaginous form. The contents may be exuded in a mucilaginous tube or sheath which encloses the long continuous spiral threading within which solid cell contents may be present. Sometimes the sheath is clearly visible and is ejected in the straight form shown in plate 7B; more often a sheath is not apparent and the only obvious epicarp contents are the threads or coils which are expelled like a rapidly unwinding spring. In the latter case, the end-result is like that shown in plate 7A where the threads are much tangled and the only parts where clear coiling remains is around the dark-coloured cell contents. In almost all cases the expulsion of the mucilage occurs so quickly, and cannot easily be retarded, that it is very difficult to follow the process with accuracy.

Although as already pointed out in the section dealing with macroscopic features, it is far from easy to define mucilage differences, the following characters may be used: 1, method of ejection; 2, degree of coiling; 3, shape and breadth of coils; 4, form of inclusions. Most of these features are illustrated in figs. 4 and 5.

1. Although in the samples examined, *S. nubicola*, as represented by *Koeie* 2957, was the only species in which an obvious mucilage sheath was apparent (fig. 5d), this may in fact be the general method of mucilage ejection and in other species the sheath although present disintegrates almost immediately after emerging from the epicarp. No range of *S. nubicola* was available to test whether or not this was a constant specific feature but it was interesting to note that in the non-Afghan *S. viridis* L., mucilage production was apparently always in the form of definite persistent sheaths, emerging from individual cells.

2. In several species, *S. pterocalyx* (fig. 4a), *S. cabulica* (fig. 4b), *S. leriifolia* (fig. 4d), *S. aegyptiaca* (fig. 5g), the coils remain more or less tightly rolled with relatively little splitting into individual thin threads. In all the remaining species the threads are loosely and usually irregularly coiled. The coils are usually tightest around the inclusions in these species (as in fig. 5e). In *S. rhytidea* (fig. 5c) and some other species the main threads split up into smaller ones. *S. plebeia* has the characteristic threads with terminal caps shown in fig. 5h; this species is also apparently different from all the other Afghan species in that very little mucilage appears to be shot out when the coiled threads emerge.

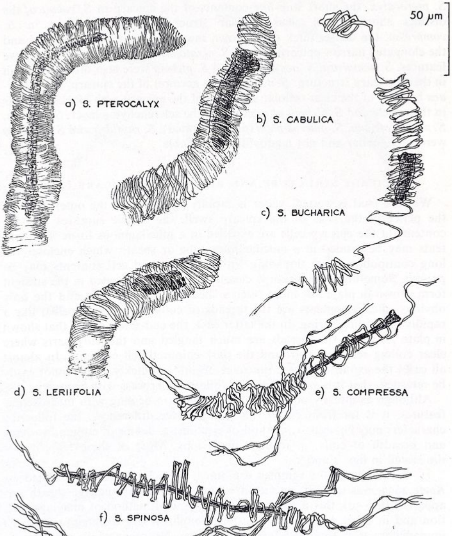

FIG. 4. Structures apparent in mucilage formed by nutlets of *Salvia* species. The preparations were made from the same collections as in fig. 1. except for *S. moorcroftiana* which was prepared from *W*. 8884.

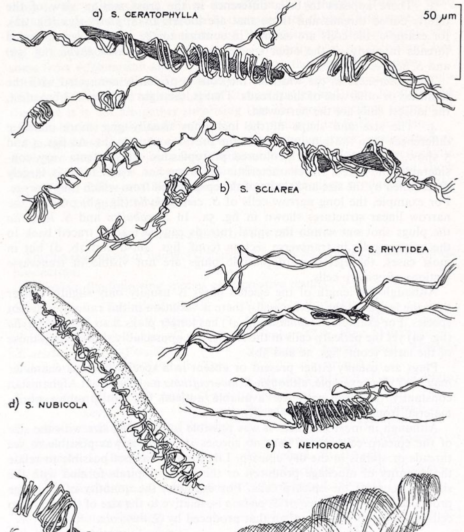

FIG. 5. Structures apparent in mucilage formed by nutlets of *Salvia* species. The preparations were made from the same collections as in fig. 1 except for *S. sclarea* which was prepared from *Archibald* 2584.

3. There appears to be a difference in the cross section view of the tightly coiled threads and those that are looser. In *S. pterocalyx* (fig. 4a), for example, the coils are circular in contrast to the more or less 4-angled threads in many of the other species such as in *S. ceratophylla* (fig. 5a) and *S. sclarea* (fig. 5b).

The differences in the width of the coils is primarily connected with the tightness or otherwise of the threads. That is, the tight coils are the broadest, the loosest coils are the narrowest.

4. The size and shape of the inclusions usually give more concrete differences than those mentioned in the previous paragraphs. As figs. 4 and 5 show, these usually dark-coloured protoplasmic cell contents vary considerable and often are characteristic for a species. Their form is largely determined by the size and shape of the epicarp cell from which they emerge. For example, the long narrow cells of *S. ceratophylla* (fig. 3b) produce the narrow linear structures shown in fig. 5a. In *S. cabulica* and *S. leriifolia* the plugs shot out within the spiral threads can be readily traced back to the epicarp cells in transverse section (conf. figs. 4b, d and 2b, d) but in most cases, the ejected protoplasmic plugs are not visible in transverse sections of epicarp cells.

Although the length of the ejected plugs is usually only slightly longer than the length of the epicarp cells, there is variation in this ratio in different species. For example, *S. spinosa* (fig. 4f) has longer plugs than *S. ceratophylla* (fig. 5a) yet the pericarp cells in the former are appreciably shorter than those of the latter (conf. figs. 2e and 3b).

Plugs are usually either present or absent in a species but this character may vary. For example, although *S. moorcoftiana* material from Afghanistan constantly (at least with the available nutlets) did not produce plugs, material from W Pakistan normally did.

Although in most instances it was possible to link plug size with the size of the epicarp cells, there were no species in which it was possible to see threads or spirals in the dry epicarp. Likewise, it was not possible to relate the quantity of mucilage produced or the kind of spirals formed with the size or shape of the epicarp cells. For example, the quantity of mucilage produced by *S. aegyptiaca* or *S. plebeia* is, relative to the size of their epicarp cells, considerably greater than that produced by *S. nubicola*.

VARIATION WITHIN A SPECIES

In the few species where there were several gatherings of ripe fruits from different localities in Afghanistan such as *S. macrosiphon*, *S. ceratophylla* and *S. aegyptiaca*, there was a general similarity in the form of the mucilage. For example, in four gatherings of *S. ceratophylla* the structure was basically the same as that illustrated in fig. 5a; there were considerable differences in the lengths of the ejected cell contents in the different gatherings but in the degree of coiling of the threads and in the thickness of the strands there was general uniformity.

S. aegyptiaca was also considered throughout its total range, from NW Africa to W Pakistan, and although there was little material to study, specimens from Morocco, Egypt, Israel, Iraq, Afghanistan and W Pakistan gave fairly similar results. The feature common to them all were spirals like those in fig. 5g consisting of fine threads; in the gatherings from the west of the range the spirals were clearly composed of threads and were rather loose, but those from Afghanistan and W Pakistan had tighter spirals and the individual threads less obvious. The majority had no inclusions but some from Afghanistan and W Pakistan did, as the illustration shows.

Both *S. aegyptiaca* and *S. ceratophylla* are stable species varying relatively little in their general morphological characteristics and their habitats and therefore it is not altogether surprising that the basic mucilage forms, and presumably the anatomical structure of the pericarp, are fairly uniform.

No adequate material of a widespread and polymorphic species such as *S. virgata* was available but a brief comparison of material from a mesophytic locality in C Europe and some from the dry steppe of Turkey did show appreciable differences in the quantity of the mucilage produced and the degree of coiling of the threads.

OTHER GENERA AND SPECIES EXAMINED

During the course of this work, many other species were tested for mucilage production.

In *Salvia*, the following species gave positive results:

S. aethiopis L. (Turkish material)
S. algeriensis Desf. (NW Africa)
S. amasiaca Fr. & Bornm. (Turkey)
S. aristata Benth. (Persia)
S. brachyantha (Bordz.) Pobed. (Turkey)
S. caespitosa Montb. & Auch. (Turkey)
S. cyanescens Boiss. & Bal. (Turkey)
S. desertii Dcne. (Israel)
S. dominica L. (Israel)
S. eigii Zoh. (Israel)
S. euphratica Montb. & Auch. (Turkey)
S. frigida Boiss. (Turkey)
S. halophila Hedge (Turkey)
S. indica L. (Israel)
S. judaica Boiss. (Israel)
S. lanigera Poir. (Israel)
S. limbata C.A. Mey. (Turkey)
S. merjamie Forssk. (cult., Uganda origin)
S. nilotica Vahl (cult., Uganda origin)
S. pinnata L. (Turkey)
S. scabiosifolia Lam. (Crimea)
S. syriaca L. (Turkey)
S. taraxacifolia Coss. (Morocco)
S. triloba L. fil. (Israel)
S. verbascifolia M. Bieb. (Turkey)
S. verbenaca L. (Israel)
S. verticillata L. (Turkey)
S. viridis L. (incl. *S. horminum* L.; Israel)

S. forskahlei L. (Turkey), *S. glutinosa* L. (Turkey) and *S. grandiflora* Etl. (Turkey) did not produce mucilage.

Among other genera, the following produced mucilage:

Dracocephalum kotschyi Boiss. (Persia)
— *thymiflorum* L. (Persia)
Lallemantia canescens (L.) F. & M. (Turkey)
— *iberica* (Stev.) F. & M. (Turkey)
— *peltata* F. & M. (Turkey)
Lallemantia royleana (Wall.) Benth. (Afghanistan)
Lavandula stoechas L. (Turkey)
Nepeta sewerzowii Rgl. (Afghanistan)
Prunella vulgaris L. (Afghanistan)

The samples of the following species did not produce mucilage:

Audibertia humilis Benth. (N America)
Dorystoechas hastata Boiss. & Heldr. (Turkey)
Eremostachys acaulis Rech. fil. (Afghanistan)
— *labiosa* Bge. (Afghanistan)
Hypogomphia turkestana Bge. (Afghanistan)
Meriandera bengalensis Benth. (India)
Nepeta cataria L. (Afghanistan)
— *micrantha* C.A.M. (Afghanistan)
— *pinetorum* Aitch. & Hemsl. (Afghanistan)
— *rechingeri* Hedge (Afghanistan)
— *rugosa* Benth. (Afghanistan)
Perovskia atriplicifolia Benth. (Afghanistan)

Although this was a cursory survey partly limited by the amount of available material, several interesting features came to light. Of the three Salvias that did not produce mucilage, two of them, *S. glutinosa* and *S. forskahlei* are mesophytic species entirely restricted to damp woodland localities. *S. glutinosa* is constantly non-mucilaginous throughout its wide geographical range from S and C Europe through the Balkans to Turkey and N Persia; its close ally *S. nubicola* which can be considered as its eastern replacement from Afghanistan to Bhutan has, at least in Afghanistan, regularly mucilaginous nutlets.

Four of the genera placed close to *Salvia* in most generic arrangements of the family, *Audibertia*, *Dorystoechas* (monotypic), *Perovskia* and *Meriandera*, had, in the species examined, non-mucilaginous nutlets.

The three genera of the tribe Nepeteae that were examined, the closely allied *Nepeta*, *Lallemantia* and *Dracocephalum*, gave most interesting results and suggested that further investigation would be worthwhile. In *Nepeta*, only one of the six Afghan species proved to have mucilaginous nutlets; this was *N. sewerzowii*, rather anomalous in the genus and sometimes placed in the separate genus *Drepanocaryum* Pojark. The mucilage produced by this species was almost structureless. In contrast, the examined species of *Dracocephalum* and *Lallemantia* had a very characteristic structural mucilage consisting of distinct straight tubes with small circular grain-like inclusions arranged singly or in rows. Because the status of some of the genera in Nepeteae is uncertain, some being separated only on unit characters, any additional character such as mucilage that could be used to assess their inter-relationships would be valuable. It was surprising that among the Afghan Nepetas which are usually species of very arid regions, so few produced mucilage. Murbeck (1919) also found that very few of the NW African *Nepeta* species were mucilaginous; only one out of seven gave mucilage.

Biological function of the mucilage

Various suggestions have been put forward to explain the function of the mucilage surrounding seeds and fruits. Murbeck (1919) discussed most of the older theories such as its importance as an aid to dispersal, in root penetration, as a water reservoir at germination time and its function in anchoring the seed. More recently Lukyanov (1959) and Gutterman *et al.* (1967) have proposed other functions. Lukyanov in his paper on the mucilage of *Salvia* *sclarea* measured the water intake of seeds with and without pericarp, the effect of different ions on the mucilage production and the germinating capacity of the seed under varied conditions. His reasoning is not always clear to follow but his conclusions based on these characters can be summarised in two of his sentences. "The germination of fallen seeds of *S. sclarea* can start in autumn when the rainy period sets in, which involves the hazard of the mortality of the young seedlings before they are properly established in the event of a subsequent cold spell. However a considerable proportion of the seeds do not germinate in the autumn since under the effect of the increased concentration of the soil solution the permeability of the pericarp decreases and the seeds fall into a state of dormancy from which they emerge in the spring of the following year when conditions are more favourable". He states in fact that the principal function of mucilage is to protect seeds from premature germination. Gutterman *et al.* in their interesting paper on the Acanthaceous *Blepharis persica* propose that, in addition to other functions, the mucilage layer in combination with excess water acts as an oxygen barrier and prevents germination.

Whatever the more complex functions of the mucilage may be, its role as an anchoring device must be of considerable importance. *Salvia* nutlets placed in damp soil are, when the mucilage is produced, soon strongly bound to surrounding soil particles. These particles adhere tightly to the pericarp even when the soil dries off and can only be separated with some difficulty. In arid conditions, where rainfall is scant and the soil surface layers are unstable, any device which helps to fix the seed in the substrate and aids germination must be of great biological value. This a mucilaginous layer appears to do in two ways. It both helps to prevent the seed from being blown about on the soil surface and from working down too deep into the soil as a result of the increased size of the fruit and its surrounding layer of mucilage and attached soil particles. This coat of particles also acts as a protective barrier in that it shelters the seed and provides a more amenable micro-environment in which to germinate.

ECOLOGY AND MUCILAGE

The prevalent belief that mucilaginous seeds are more frequent among species from desert or arid zones does have some basis in fact even though there are plenty species from temperate mesophytic regions, and even some from the tropics, that produce mucilage. For example, Murbeck (1919) in his survey of North African species from an arid area found that in the Labiatae 30% of them had mucilaginous seeds contrasted with a 12% total among Scandinavian species of the family. However, Bilimovitsch (1935) dealing with the Labiatae of part of European Russia found that about 50% of the species had mucilaginous seeds; if this figure is correct, it is a surprisingly high total. In the arid country of Afghanistan, no exact count of mucilaginous species in the Labiatae has been made but from random sampling of different genera a rough figure of 35% was reached.

Most of the *Salvia* species from Afghanistan grow in dry, hot, stony places. One species is mesophytic, the widespread tropical and subtropical weed, *S. plebeia;* three others, *S. sclarea*, *S. rhytidea* and *S. nubicola*, grow in association with trees or shrubs or at streamsides or else occur in areas of somewhat higher rainfall. The case of *S. plebeia* is of special interest in that as a mesophytic species it produces as much mucilage relatively as any of the Afghan species including the more or less desert group of species in Sect. *Eremosphace.* It was also of interest that these species and *S. plebeia* have the smallest nutlets among the Afghan species and produce the greatest quantity of mucilage whereas the species with the largest and heaviest nutlets, *S. leriifolia,* produced the least mucilage.

It would be interesting to investigate in more detail the connections in a species between mucilage production and habitat but the impression gained from a study of fruit gatherings of the same species from different habitats within Afghanistan was that the mucilage characters are linked with the taxon rather than its habitat.

GENERAL CONCLUSIONS

Mucilage features throughout the Labiatae are obviously of great interest *per se* and in at least some genera can be of some taxonomic value both at specific and generic level. In the *Salvia* species considered, there were appreciable differences between many species and their mucilage features do provide an extra taxonomic character. Normally however mucilage adds little to existing taxonomic knowledge in that distinctive mucilage is produced by a morphologically distinct species, such as *S. pterocalyx,* or by a group of allied distinctive species such as those of sect. *Eremosphace.* But among the examined Afghan species there were some points of general interest. The fact, for example, that *S. nubicola* produced mucilage whereas its ally, the SW Asiatic and European *S. glutinosa* did not. It was also of much interest that the Persian *S. aristata,* considered as a possible ally of the remarkable *S. pterocalyx,* though very different from it in many ways, produced very similar mucilage to the Afghan species; this supported the contention that they should be placed in the same section.

As a character for practical use, mucilage has drawbacks. The range of variation within a species, for example, is not adequately known. Furthermore, ideal material is rarely available and even when it is, differences of mucilage types are often very difficult to express or illustrate because of the nature of the substance.

The pericarp or in particular the epicarp, whence the mucilage comes, provides, as Wojciechowska has so clearly shown, a more precise character but it has the disadvantage of requiring considerable time to prepare material and, also, as is the case with mucilage, little is known about variation within a species.

In comparing mucilages it is important to study them by similar methods and also to use fruits that are ripe and mature. The production of mucilage is largely if not entirely a physical phenomenon. That is, it is not dependent on living cells. Nutlets from a specimen of *Salvia viridis* collected in 1777 still produced some mucilage; others that had been immersed in absolute alcohol, embedded in methacrylate, then dissolved out in acetone still produced mucilage. But in these cases, the mucilage is somewhat atypical and for comparative purposes fresh fruits are essential.

Further work on the detailed structure of mucilage, threads and spirals would certainly be rewarding; although eventually with special techniques, the scanning electron microscope may prove most useful, much still remains to be learned from observations with optical methods.

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