

# MORPHOLOGY AND TAXONOMIC SIGNIFICANCE OF FOLIAR SCLEREIDS IN LIMONIUM

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**ABSTRACT.** Foliar sclereids are highly specialized cells which because of their large size, bizarre form and thick secondary walls are sharply demarcated from neighbouring tissue elements. The data presented here is based upon the study of cleared leaves and macerated tissue of petiole and lamina. This is fully supplemented by cross and longitudinal hand sections. In the present investigation, the results of studies on form, structure and distribution of sclereids in mature leaves of *Limonium* are presented and their taxonomic significance evaluated. A leaf clearing technique is described which is equally useful for obtaining epidermal peels.

## INTRODUCTION, MATERIAL AND METHODS

The literature on Plumbaginaceae contains only two records of foliar sclereids in *Limonium*. Solereder (1908) states "Sclerenchymatous cells occur in the mesophyll of *Statice cylindrifolia* (*L. cylindrifolium*) in the form of branched 'spicular cells' (internal hairs)." Fraine (1916) noticed large numbers of sclereid groups, varying in size, which form a characteristic feature of leaf in *Statice binervosa* (*L. binervosum*). As far as I have been able to determine, no further study has been made on the foliar sclereids in *Limonium* and their taxonomic significance is unknown.

I became interested in the foliar sclereids of *Limonium* while determining the systematic position of *L. lilacinum*, a Turkish endemic which has been treated as an independent species and also as *Statice gmelinii* var. *lilacina* under Sect. *Limonium*. The morphology and distribution of sclereids in the petiole, together with other morphological and anatomical characters, supports its transfer to Sect. *Sphaerostachys* along with *L. globuliferum*. For convenience in reference I have followed the taxonomic treatment of *Limonium* by Boissier and the synopsis of the sectional classification is given below.

Boissier's (1848) classification of *Limonium* (then known as *Statice*)

- |                                   |                                       |
|-----------------------------------|---------------------------------------|
| 1. Sect. <i>Pteroclados</i>       | 5. Sect. <i>Sphaerostachys</i>        |
| a. Subsect. <i>Odontolepideae</i> | 6. Sect. <i>Jovibarba</i>             |
| b. Subsect. <i>Nobiles</i>        | 7. Sect. <i>Schizhymenium</i>         |
| 2. Sect. <i>Ctenostachys</i>      | 7a. Sect. <i>Schizopetalum</i> Boiss. |
| 3. Sect. <i>Plathymenium</i>      | (1859) (This section was created      |
| a. Subsect. <i>Rhodanthae</i>     | by Boissier later on in Boiss.,       |
| b. Subsect. <i>Chrysanthae</i>    | Diagn. Ser. 2, 4: 67, 1859).          |
| 4. Sect. <i>Limonium</i>          | 8. Sect. <i>Circinaria</i>            |
| a. Subsect. <i>Genuinae</i>       | 9. Sect. <i>Polyarthron</i>           |
| b. Subsect. <i>Densiflorae</i>    | 10. Sect. <i>Myriolepis</i>           |
| c. Subsect. <i>Dissitiflorae</i>  | 11. Sect. <i>Siphonantha</i>          |
| d. Subsect. <i>Steirocladae</i>   | 12. Sect. <i>Psylliostachys</i>       |
| e. Subsect. <i>Hyalolepidae</i>   |                                       |
| f. Subsect. <i>Sarcophyllae</i>   |                                       |

In the sections and subsections italicised no sclereids have been observed in any species.

Leaf-clearing techniques used by Bailey & Nast (1944) and by Foster (1955) were found to be unsatisfactory and time-consuming especially for thick-leaved species of *Limonium*. A modified and comparatively quicker clearing technique was used which could be equally useful for other plants. Herbarium leaves were soaked overnight in a 10% KOH solution with a few drops of  $H_2O_2$ . Next morning the leaves were washed with water and then allowed to stand in water with a few drops of  $H_2O_2$  for two hours; then after thoroughly washing with water, the leaves were either placed in "Eau de Javelle" for clearing or in F.A.A. for section cutting. Usually leaves will clear in an hour. The cleared leaves were boiled in water for five minutes; during boiling the upper epidermis becomes loosened and is peeled off automatically. It is possible with some skill to remove even the lower epidermis, leaving the vein reticulum and the mesophyll. This was stained with safranin dissolved in 50% alcohol for 5 minutes; excess stain was removed with 50% acidified alcohol and after thoroughly dehydrating with absolute alcohol the material was mounted in euparal. The above technique also proved to be very useful for removing the epidermis of *Acantholimon*, *Limonium* and other genera of Plumbaginaceae.

The petiole and lamina material was macerated by Jeffrey's technique as outlined by Foster (1949) but staining and mounting was done in a modified way. After washing with water, the macerated material was dehydrated and was directly placed in safranin dissolved in absolute alcohol for future study. The material was taken from the stain, separated and mounted directly in euparal.

For convenience in reference the species investigated are listed below in alphabetical order. The figures in the brackets denote their sections and subsections respectively as given in the synopsis above.

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| <i>L. anatolicum</i> Hedge (4,f)                         | <i>L. dictyocladum</i> (Boiss.) O. Kuntze (4,d)        |
| <i>L. arborescens</i> (Brouss.) O. Kuntze (1,b)          | <i>L. dodartii</i> (Gir.) O. Kuntze (4,b)              |
| <i>L. articulatum</i> (Lois.) O. Kuntze (4,d)            | <i>L. dregeanum</i> (Boiss.) O. Kuntze (4,d)           |
| <i>L. axillare</i> (Forsk.) O. Kuntze (4,f)              | <i>L. dufourii</i> (Gir.) O. Kuntze (4,b)              |
| <i>L. bellidifolium</i> (Gouan) Dum. (4,e)               | <i>L. duriusculum</i> (Gir.) O. Kuntze (4,c)           |
| <i>L. bicolor</i> (Bge.) O. Kuntze (3,b)                 | <i>L. effusum</i> (Boiss.) O. Kuntze (4,a)             |
| <i>L. bonduellii</i> (Lestib.) O. Kuntze (1,a)           | <i>L. fruticans</i> (Webb.) O. Kuntze (1,b)            |
| <i>L. bourgeauii</i> (Webb) O. Kuntze (1,b)              | <i>L. globuliferum</i> (Boiss.) O. Kuntze (5)          |
| <i>L. brassicifolium</i> (Webb & Benth.) O. Kuntze (1,b) | <i>L. gmelinii</i> (Willd.) O. Kuntze (4,a)            |
| <i>L. cabulicum</i> (Boiss.) O. Kuntze (7)               | <i>L. gougetianum</i> (Gir.) O. Kuntze (4,b)           |
| <i>L. caesium</i> (Gir.) O. Kuntze (9)                   | <i>L. graecum</i> (Poir.) K. H. Rechinger (4,c)        |
| <i>L. californicum</i> (Boiss.) Heller (4,a)             | <i>L. griffithii</i> (Aitch. & Hemsl.) O. Kuntze (7,a) |
| <i>L. carolinianum</i> (Walt.) Britton (4,a)             | <i>L. iconicum</i> (Boiss.) O. Kuntze (4,e)            |
| <i>L. carnosum</i> (Boiss.) O. Kuntze (4,f)              | <i>L. imbricatum</i> (Webb) F. T. Hubbard (1,b)        |
| <i>L. chrysocomum</i> (Kar. & Kir.) O. Kuntze (3,b)      | <i>L. jovibarbum</i> (Webb) O. Kuntze (6)              |
| <i>L. coelicolor</i> K. H. Rechinger (7,a)               | <i>L. latifolium</i> (Sm.) O. Kuntze (4,e)             |
| <i>L. cordatum</i> (L.) Mill. (4,d)                      | <i>L. lilacinum</i> (Boiss.) Wagenitz (5)              |
| <i>L. corymbulosum</i> (Boiss.) O. Kuntze (4,d)          | <i>L. limbatum</i> Small (4,a)                         |
| <i>L. cumanum</i> (Ten.) O. Kuntze (4,d)                 | <i>L. linifolium</i> (L.f.) O. Kuntze (4,d)            |
| <i>L. cylindrifolium</i> (Forsk.) Cufod. (4,f)           | <i>L. lychnidifolium</i> (Gir.) O. Kuntze (4,b)        |
| <i>L. delicatulum</i> (Gir.) O. Kuntze (4,c)             | <i>L. macrophyllum</i> (Brouss.) O. Kuntze (1,b)       |
| <i>L. dichotomum</i> (Cav.) O. Kuntze (4,e)              | <i>L. macropterum</i> (Webb) O. Kuntze (1,b)           |
|  | <i>L. macrorhabdon</i> (Boiss.) O. Kuntze (7,a)        |

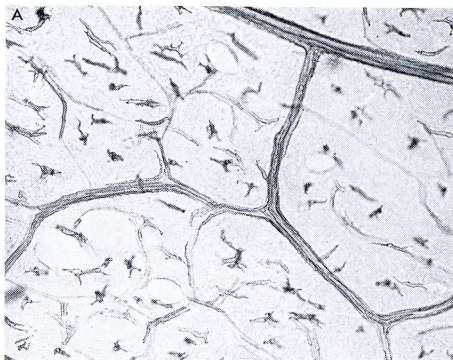


PLATE 3. A, diffused sclereids of *L. effusum*. B, terminal sclereids of *L. scabrum*.

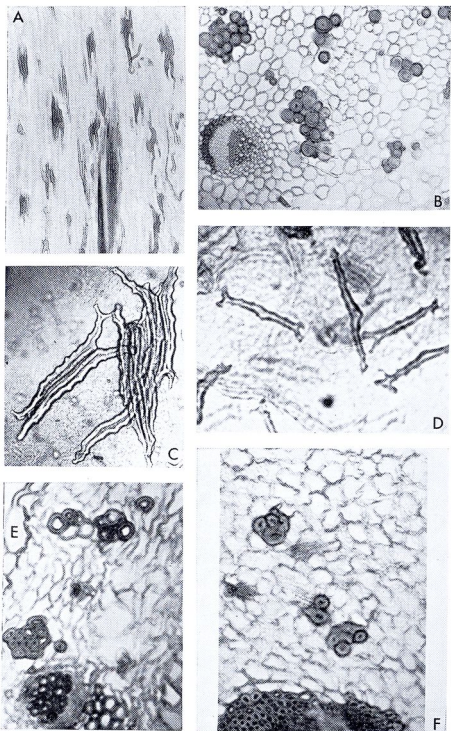


PLATE 4. A, longitudinal section of petiole of *L. lilacinum*. B, transverse section of petiole of *L. lilacinum*. C, sclereids of *L. imbricatum* from cleared leaf. D, sclereids of *L. arbore-sens* from cleared leaf. E, T.S. of leaf of *L. griffithii* showing sclereids with a broad lumen. F, T.S. of leaf of *L. macrorhabdon* showing sclereids with a narrow lumen.

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|--|---|
| <i>L. meyeri</i> (Boiss.) O. Kuntze (4,a)          | <i>L. psilocladon</i> (Boiss.) O. Kuntze (4,c)  |
| <i>L. mexicanum</i> Blake (4,a)                    | <i>L. roseum</i> (Sm.) O. Kuntze (8)            |
| <i>L. minutiflorum</i> (Guss.) O. Kuntze (4,c)     | <i>L. salsuginosum</i> (Boiss.) O. Kuntze (4,c) |
| <i>L. minutum</i> (L.) O. Kuntze (4,d)             | <i>L. scabrum</i> (Boiss.) O. Kuntze (4,d)      |
| <i>L. mucronatum</i> (L.f.) O. Kuntze (2)          | <i>L. sieberi</i> (Boiss.) O. Kuntze (4,c)      |
| <i>L. nashii</i> Small (4,a)                       | <i>L. sinense</i> (Gir.) O. Kuntze (3,b)        |
| <i>L. occidentale</i> (Lloyd.) O. Kuntze (4,b)     | <i>L. sinuatum</i> (L.) Mill. (1,a)             |
| <i>L. ovalifolium</i> (Poir.) O. Kuntze (4,b)      | <i>L. stocksii</i> (Boiss.) O. Kuntze (4,f)     |
| <i>L. palmyrense</i> (Post) Dinsm. (4,f)           | <i>L. suffruticosum</i> (L.) O. Kuntze (4,f)    |
| <i>L. perezii</i> (Stapf) F. T. Hubbard (1,b)      | <i>L. thuinii</i> (Viv.) O. Kuntze (1,a)        |
| <i>L. perfoliatum</i> (C. A. Mey.) O. Kuntze (4,e) | <i>L. tubiflorum</i> (Delile) O. Kuntze (11)    |
| <i>L. puberulum</i> (Webb) O. Kuntze (1,b)         | <i>L. virgatum</i> (Willd.) Fourr. (4,d)        |
| <i>L. pruinatum</i> (L.) O. Kuntze (4,e)           |   |

### CLASSIFICATION OF SCLEREIDS

Though remarkable fluctuations occur in sclereid position in some species, foliar sclereids in *Limonium* can be conveniently classified into two main groups from a purely topographical point of view (Foster 1955): I, Diffused; II, Terminal. In the 'diffused' pattern the sclereids occur as solitary or clustered idioblasts distributed in the tissue of the petiole and lamina unrelated to veinlets or veinlet ends (plate 3,A). In contrast the 'terminal' sclereids lie in direct contact with the tracheary elements of the veinlet endings (plate 3,B; 6,F).

#### I. DIFFUSED SCLEREIDS

These sclereids typically occur as idioblasts dispersed singly or in groups in the tissue of petiole and lamina, and, as cross and longitudinal sections of these organs indicate, these are separated from one another by parenchymatous elements (plate 4,A & B). The distribution of sclereids in the various tissues of petiole and lamina, as will be discussed elsewhere, is a useful taxonomic character. Diffused sclereids occur in species belonging to Sect. *Pterocladus* subsect. *Nobiles*; Sect. *Limonium* subsect. *Genuinae* and subsect. *Sarcophyllae* and Sect. *Sphaerostachys*.

*Distribution of sclereids in petiole.* In *Limonium* petiole the ground tissue is usually undifferentiated and the sclereids are dispersed singly in Subsect. *Nobiles* but in Subsect. *Genuinae*, these may occur singly or in groups. In Sect. *Sphaerostachys* there is a palisade layer toward the abaxial side and sclereids occur singly or in groups in the lacunose spongy tissue. In Subsect. *Sarcophyllae* the palisade tissue is usually concentric and sclereids may occur singly or in groups, confined either to the palisade or to the spongy tissue. The distribution of sclereids in the petiole is a useful character at species level in this subsection. (plate 5,A-H).

*Distribution of sclereids in lamina.* The sclereids in the lamina may be irregularly scattered in the mesophyll as in *L. effusum* and *L. lilacinum* (fig. 1,B) but in all the species belonging to Subsect. *Nobiles* these are confined to the palisade tissue (fig. 1,A). Just as there are interesting variations in the morphology and distribution of sclereids in the petiole of the species belonging to Subsect. *Sarcophyllae*, likewise their morphology and distribution in the lamina show taxonomically interesting types in different species.

*Types of diffused sclereids.* The majority of species with the diffused pattern develop more or less branched sclereids which vary widely in respect to the



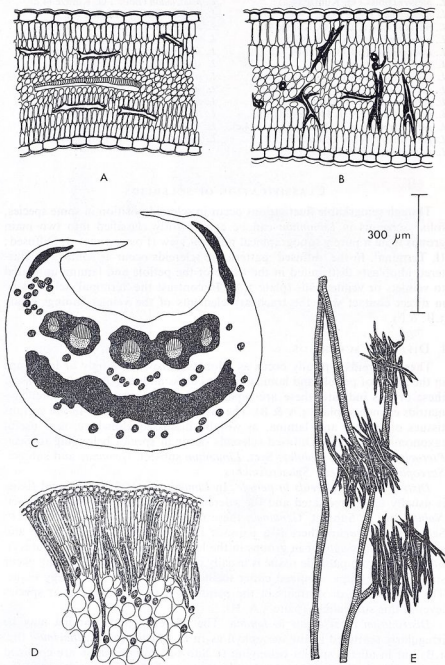


FIG. 1. A, transverse section of lamina of *L. arborescens*. B, T.S. of lamina of *L. lilacinum*. C, T.S. of petiole of *L. cylindrifolium*. D, T.S. of part of lamina of *L. cylindrifolium*. E, petiolar sclereids of *L. ovalifolium*.

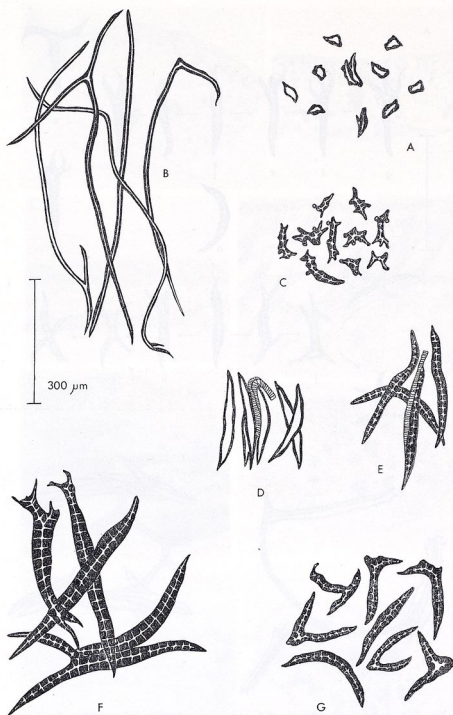


FIG. 2. Sclereids from macerated lamina showing morphological diversities in different *Limonium* species. A, *L. puberulum*. B, *L. cylindrifolium*. C, *L. ovalifolium*. D, *L. griffithii*. E, *L. coelicolor*. F, *L. stocksii*. G, *L. suffruticosum*.

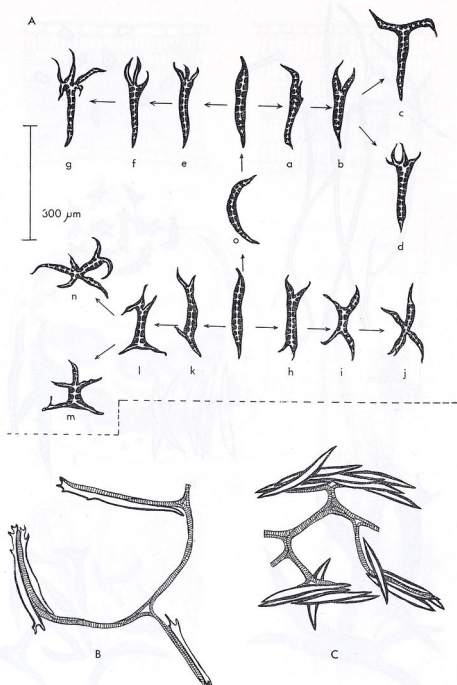


FIG. 3. A, polymorphic sclereids of *L. globuliferum* showing different lines of cell specialisation. B, terminal sclereids of *L. dodartii*. C, terminal sclereids of *L. griffithii*.



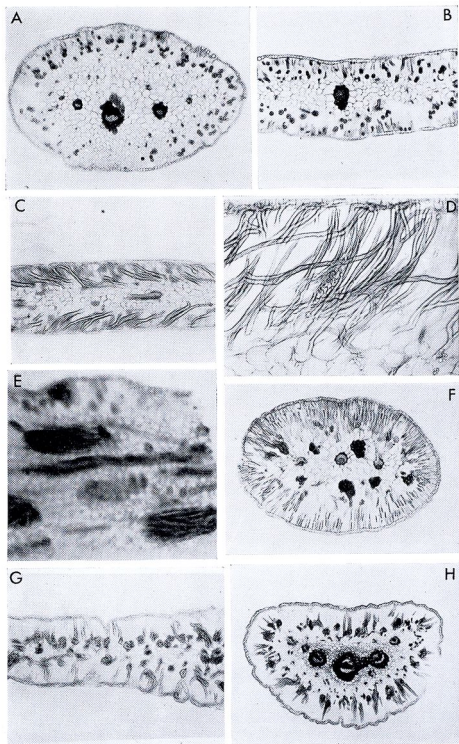


PLATE 5. A-C, leaf sections of *L. axillare*: A, transverse section of petiole; B, T.S. of lamina; C, longitudinal section of lamina. D, L.S. of part of lamina of *L. cylindrifolium*. E-F, *L. stocksii*: E, L.S. of petiole; F, T.S. of petiole. G-H, *L. suffruticosum*: G, T.S. of lamina; H, T.S. of petiole.

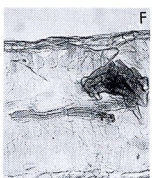
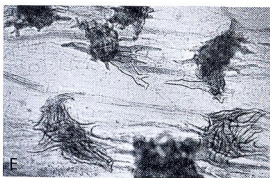


PLATE 6. A, mamillate sclereids of *L. ovalifolium*. B, transverse section of leaf of *L. stocksii*. C, sclereids of *L. griffithii*. D, vesiclose sclereids of *L. puberulum*. E, petiolar sclereids of *L. ovalifolium*. F, T.S. of leaf of *L. salsuginosum* showing terminal sclereids at the terminus of short veinlet.

form of cell body and extent of branches. In marked contrast to it there are two extremes. At one extreme there are vesiculose types which broadly resemble parenchymatous cells in form; at the other, are remarkably filiform sclereids, resembling fibres in their form and more or less unbranched nature. All these types, however, cannot be sharply demarcated because of the intergradations and a strong tendency to fluctuation within many of the entities which have been studied. Under these circumstances a morphological classification of diffused sclereids in *Limonium* is attempted here which not only includes the outstanding types but also the intergradations which exist between them.

1. Vesiculose sclereids. The sclereids treated under this type are characterized by their more or less parenchymatous forms and rudimentary branches. In the simplest case the vesiculose sclereids are sphaeroidal cells usually unbranched or provided with short appendages. These are very common in *L. puberulum* where these are found intermixed with other types (plate 6,D; fig. 2,A) and very rarely found in other species of Subsect. *Nobiles*.

2. Spindle-shaped sclereids. The sclereids grouped under this type are mostly unbranched with fusoid ends and rarely show a tendency to branch at one or both ends. These vary considerably in size in different species and exhibit great variations in cell form. In maceration these appear straight, L-shaped, C-shaped or V-shaped. These are the characteristic petiolar sclereids but also found in the lamina of the majority of species belonging to Subsect. *Sarcophyllae* (fig. 2,F, G).

3. Polymorphic sclereids. Under this term I have attempted to group a complex series of sclereids, varying considerably in size, form of cell body and degree of branching. On one hand, are specialized columnar or "Osteosclereids", usually showing a tendency to lobe dichotomously or trichotomously at one or both ends. These may be present singly (plate 4,D) or mostly in groups of two or more (plate 4,C), in different species. At the other extreme there are bizarre irregularly branched cells approaching "Astrosclereids". In most of the species with polymorphic sclereids, all the gradations from osteosclereids to astrosclereids are found in one and the same species. These sclereids have recurved fusoid branches of various degrees and a narrow lumen of uniform width. There are so many intermediate forms of these sclereids that any attempt to classify them rigidly into minor types is precluded. All the variations shown by these sclereids, however, can be traced back to unbranched sclereids possessing fusoid ends; from this basic type they exhibit distinct lines of cell modification. Along one line there is a dichotomy or trichotomy at one end only, which may undergo further branching resulting in the formation of columnar bodies with slender fusoid branches produced nearly from the middle of the cell. (fig. 3A, a-g). Along the other line the dichotomy (rarely trichotomy) occurs at both ends and by further branching, more or less astrosclereids are produced (fig. 3A, h-n). In rare cases the sclereids remain unbranched and variously curved (fig. 3A, o).

4. Filiform sclereids. This type is only observed in *L. cylindrifolium*. These are characterised by their slender, greatly elongated form and their characteristic orientation within the leaf. Most of these sclereids have contact with the epidermis and obliquely traverse the palisade and part of

spongy mesophyll from the apex downward. In cross and longitudinal section of the leaf, the mesophyll appears to be permeated by numerous fibre-like cells (fig. 1,D; plate 5,D). In maceration, most of these sclereids are unbranched, curved or bent at one end by which they abut against the inner walls of epidermal cells (fig. 2,B).

## II. TERMINAL SCLEREIDS

Rao (1951) has questioned the use of the term 'Terminal' for sclereids merely because of their position in the mature leaf. His ontogenetic study has revealed that initials of the seemingly terminal sclereids arise away from the procambial strands. These are in fact transformed cells of the spongy parenchyma and their eventual terminal position is due to the juxtaposed development of the nerve endings. As the development of sclereids has not been followed in the present study, the term 'Terminal sclereid' is used purely on a topographical basis. Such sclereids are noticed in Sect. *Schizopetalum*, in all species of Sect. *Limonium* subsect. *Steirocladae* and in a few species of subsect. *Densiflorae* and subsect. *Dissitiflorae*. The species with terminal sclereids in the lamina also possess sclereid groups in the petiole, showing distinct relation to the veins (plate 6,E; fig. 1,E). The number and size of the sclereid groups in the petiole were found to increase with the increase in size and thickness of the leaf lamina.

Laminar terminal sclereids show varying degrees of form, structure and arrangement in different species. In *L. dodartii* (fig. 3,B); *L. gougetianum* and *L. griffithii* (fig. 3,C) the sclereids have a broad lumen. The orientation of sclereids in the lamina also varies considerably. In Sect. *Schizopetalum* their orientation is usually along the long axis of the leaf (plate 6,C; fig. 3,C) while in other species with terminal sclereids, they are irregularly oriented in the mesophyll. In *L. ovalifolium* the variously curved and tuberculate sclereids are arranged in such a manner that usually these appear 'mamillate' in cleared leaves (plate 6,A) and their structure can be examined only in maceration. In *L. lychnidifolium*, *L. ovalifolium* and Sect. *Schizopetalum* very rarely a few diffused sclereids were also observed. Two main types of terminal sclereids occur: spindle-shaped and polymorphic. 1. *Spindle-shaped sclereids*. These are mostly unbranched, with broad or narrow lumen and are confined to Sect. *Schizopetalum*. (fig. 2,D, E). 2. *Polymorphic sclereids*. They vary considerably in form and structure and show various degrees of branching. Sometimes these are provided with small tubercles which give them a mamillate appearance (fig. 2,C).

## TAXONOMIC SIGNIFICANCE

As has already been described, topographically there are two types of sclereids in *Limonium* which are restricted to particular sections or sub-sections. They provide useful taxonomic characters, and in some cases can be safely used for identification at sectional, subsectional and particularly at species level. Some particular features of interest are listed below.

1. Boissier (1848) treated *Goniolimon* as a separate genus and distinguished it from *Limonium* by its capitate stigmas, papillose style and  $\pm$  cuspidate inner bract. Later on it was found that Sect. *Schizhymenium* and Sect. *Schizopetalum* of *Limonium* have also subcapitate to capitate stigmas. On

this basis alone Mobayen (1964) has transferred *L. griffithii* from Sect. *Schizopetalum* to *Goniolimon*. The lack of papillose style and cuspidate inner bract in *L. griffithii* does not justify this transfer. The morphology of sclereids in *L. griffithii* also speaks against it and supports its previous position under Sect. *Schizopetalum*. Spindle-shaped terminal sclereids only have been noted in Sect. *Schizopetalum*, and in *L. griffithii* the sclereids have a broad lumen and most of them are oriented along the long axis of the leaf. In *Goniolimon* most of these species are without sclereids but in the few species (as *G. speciosum*) which possess sclereids they always have a narrow lumen and their orientation is irregular.

2. *L. lilacinum* and *L. globuliferum* have numerous sclereid groups dispersed in the lacunose spongy tissue of the petiole (plate 4,A, B). The structure and distribution of sclereids and other anatomical and morphological characters clearly show that *L. lilacinum* is more closely related to *L. globuliferum* of Sect. *Sphaerostachys* than to any species of Sect. *Limonium* subsect. *Genuinae* to which it was previously assigned.

3. Diffused polymorphic sclereids are usually irregularly dispersed in the mesophyll of the lamina (fig. 1,B) but in all the species of Subsect. *Nobiles* the sclereids are generally confined to the palisade tissue (fig. 1,A).

4. Subsect. *Nobiles*, endemic to the Canary Islands, is further divided by Boissier (1848) into 3 groups on the character of the inner bract. Group I with two species, i.e. *L. arborescens* and *L. fruticans*, has a keeled inner bract and the keel is vertically dilated. Both species possess thin-walled,  $\pm$  osteosclereids dispersed singly in the palisade (plate 4,D). Group II with 4 species has a dorsally convex inner bract; *L. macrophyllum* and *L. macropterum* are without sclereids; the remaining two species, *L. imbricatum* and *L. brassicifolium* are characterised by possessing thick-walled,  $\pm$  branched osteosclereids with distinctly sinuous walls occurring mostly in pairs or groups (plate 4,C). Group III has a truncate bract and contains three species. Here sclereids are not found in *L. bourgeauii*; *L. puberulum* is unique in having mostly vesiculose sclereids (plate 6,D); *L. perezii* has osteosclereids like group I. The variation in sclereids of group III shows that the bract character on which the grouping is based is not a useful taxonomic character.

5. In Subsect. *Sarcophyllae*, the sclereids are either spindle-shaped or filiform. The arrangement and distribution of sclereids in the petiole and lamina are useful taxonomic characters at species level. In *L. axillare*, sclereids are dispersed singly in the petiole and lamina. These are restricted to the palisade tissue and are oriented  $\pm$  parallel to the long axis of the leaf (plate 5,A-C). In *L. stocksii*, the sclereids in the petiole occur in groups, run parallel to the long axis of the petiole and are confined to the spongy tissue (plate 5,E, F) but in the lamina their orientation becomes irregular and they are  $\pm$  free (plate 6,B). *L. suffruticosum*, *L. anatolicum* and *L. palmyrense* have irregular groups of sclereids occurring in the palisade tissue of the petiole (plate 5,H) but in the lamina these sclereid groups are irregularly dispersed in the palisade as well as the spongy tissue (plate 5,G). In *L. carnosum*, sclereids were not noticed. *L. cylindrifolium* is unique in the genus on account of its filiform sclereids. In the petiole, sclereids are dispersed singly in the ground tissue (fig. 1,C) while in the lamina long slender fibre-like sclereids permeate the palisade and part of the spongy mesophyll (plate 5,D; fig. 1,D).



6. In Sect. *Schizopetalum*, sclereid morphology is also useful at species level. In *L. macrorhabdon* and *L. coelicolor* the sclereids have a narrow lumen. (plate 4,F; fig. 2,E). *L. griffithii* can be easily distinguished from the two above-named species by its sclereids having a broad lumen (plate 4,E; fig. 2,D). In *L. macrorhabdon*, sclereids are usually absent from the lamina while in *L. coelicolor* there are abundant sclereids with a narrow lumen in the lamina.

7. Thin-walled terminal sclereids were only noticed in two closely related species of Subsect. *Densiflorae*, i.e. *L. dodartii* (fig. 3,B) and *L. gougetianum*. *L. ovalifolium* appears to be unique in its polymorphic terminal sclereids, which are tuberculate, variously curved and grouped in such a manner as to appear mamillate in cleared leaves (plate 6,A).

#### DISCUSSION

The literature on foliar sclereids shows that throughout the phanerogams there are usually either terminal or diffused sclereids in a genus. *Limonium* is interesting in possessing both terminal and diffused sclereids without much overlapping. In all the comparisons which were made between the leaves of the same specimen, variations in sclereids were found to be very slight. Even between different specimens of the same species, little difference is found in sclereid morphology and distribution.

The plainest evidence for the parallel development of the sclereids is afforded by the 'diffused polymorphic' types and 'terminal sclereids'. Diffused polymorphic types are found in few species of Sect. *Limonium* subsect. *Genuinae* and most species of Sect. *Pteroclados* subsect. *Nobiles*. On the basis of other characters these two sections are not closely related, hence their sclereids have apparently had a separate origin. Terminal sclereids are found in Sect. *Limonium* subsect. *Steiroidae*, subsect. *Densiflorae*, subsect. *Dissitiflorae*, Sect. *Schizopetalum* and in genus *Goniolimon*. All these are plainly not closely related, so these are clear examples of the independent development of like forms. It is a noteworthy point that in Subsect. *Nobiles* which is endemic to the Canary Islands although the species are obviously closely related there are great variations in the sclereid morphology.

The present study represents the first attempt to illustrate the variations in form, size and structure of sclereids, and also what appears to be the general trend in their distribution in *Limonium*. This is by no means a complete survey and indeed it is quite possible that examination of a wider range of leaf material than has been undertaken in this study would reveal even more interesting variations. As far as the present investigation shows, there is no sharp demarcation between various form types, but the vesiculose and filiform types surely represent the two extremes in cell specialization at the two ends of a continuous morphological series.

The great variety of forms in the genus and their relative constancy in certain entities, makes sclereid morphology a very valuable taxonomic character. The more distinctive types of sclereids and their distribution may indicate the section, subsection and even the species to which the specimens belong. However, owing to the occurrence of like forms in different entities, and the tendency for the majority of species in a subsection to have nearly the same sclereid morphology, this character, like most others, cannot be relied upon alone but must be used in conjunction with others.



The only comprehensive account of the genus *Limonium* is already over 100 years old (Boisser, 1848). It is hoped that, in any future attempt at the taxonomic revision of *Limonium* which is so badly needed, the character of sclereid morphology and distribution will be given due consideration.

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