VARIATION AND TAXONOMIC IMPORTANCE OF ANATOMICAL CHARACTERS IN LIMONIUM

M. H. BOKHARI*

ABSTRACT. Anatomical characters of vegetative parts of *Limonium* are investigated. A range of variation in endomorphic characters is surveyed and their taxonomic importance is evaluated. Some anatomical features which are reported here provide taxonomic characters that may be of great value in understanding and classifying this difficult genus. This work has revealed that we have a fresh set of endomorphic characters which can be reasonably used to supplement those commonly employed in classification. No attempt is made to reclassify this genus, but in the light of available endomorphic and exomorphic characters, some suggestions are made for improving its infrageneric classification.

INTRODUCTION

The anatomical structure of various plant organs in Plumbaginaceae has received attention from previous workers (Maury, 1886, Solereder, 1908, Metcalf & Chalk, 1950 and Labbe, 1962). Their work was of general type, and, practically in every case, the anatomical structures were investigated from a comparative point of view. In the present study, besides furnishing more information about variation in anatomical characters of *Limonium*, their taxonomic value, along with exomorphic characters, is discussed.

The material in this paper has largely been extracted from a Ph.D. thesis on the taxonomy of the Plumbaginaceae submitted at the University of Edinburgh.

MATERIAL & METHOD

The present study is entirely based on herbarium material. The techniques used for preparing material for sectioning leaves, scapes; leaf clearing; removing epidermis peels and staining are the same as those previously used (Bokhari, 1970). In all cases, hand sections were taken because it is the only practical rapid way of examining large amounts of material. Photographs and camera lucida drawings were made from the prepared slides; these are kept in the Herbarium, Royal Botanic Garden, Edinburgh. For convenience in reference I have followed the taxonomic treatment of *Limonium* by Boissier (1848) (see Table 1 for synopsis of sectional classification). Species of *Limonium* and other closely related genera investigated anatomically are arranged alphabetically below.

GONIOLIMON Boiss.

G. bessarianum (Schultes) Kusn.
G. collinum (Griseb.) Boiss.
G. dalmaticum (Presl.) Reichenb. & Reichenb. fil.

G. graminifolium (Aiton) Boiss.
G. heldreichii Halacsy
G. speciosum (L.) Boiss.
G. tataricum (L.) Boiss.

---

* Now at Biology Department, Pahlavi University, Shiraz, Iran.

TABLE 1

Classifications of the Genus Limonium Mill.

Then Known as STATICE		Genus LIMONIUM	
Boissier (1848).	Bentham & Hooker (1876).	Pax (1897).	Labbe (1962).
I. Sect. *Pteroclados*	I. Sect. *Schizopetalum*	A. Subgenus *Limonium*	I. Sect. *Sarcophyllum*
1. Subsect. *Odontolepideae*	II. Sect. *Goniolimon*	I. Sect. *Pteroclados*	II. Sect. *Eu-Limonium*
2. Subsect. *Nobiles*	(incl. *Circinaria*)	II. Sect. *Ctenostachys*	III. Sect. *Circinaria*
II. Sect. *Ctenostachys*	III. Sect. *Limonium*	III. Sect. *Plathymenium*	IV. Sect. *Pteroclados*
III. Sect. *Plathymenium*	IV. Sect. *Siphonantha*	IV. Sect. *Eu-Limonium*	V. Sect. *Ctenostachys*
1. Subsect. *Rhodanthae*	(incl. *Polyarthrion*	V. Sect. *Sphaerostachys*	VI. Sect. *Schizhymenium*
2. Subsect. *Chrysanthae*	*Myriolepis* *Eurychiton*)	VI. Sect. *Jovibarba*	VII. Sect. *Aristidella*
IV. Sect. *Limonium*		VII. Sect. *Circinaria*	VIII. Sect. *Jovibarba*
1. Subsect. *Genuinae*	V. Sect. *Psylliostachys*	B. Subgenus *Siphonantha*	IX. Sect. *Plathymenium*
2. Subsect. *Densiflorae*	VI. Sect. *Pterolimon*	I. Sect. *Eusiphonantha*	X. Sect. *Pterolimon* (= *Bakerolimon* Lincz.)
3. Subsect. *Dissitiflorae*		(incl. *Eurychiton*)	XI. Sect. *Cephalorrhizum*
4. Subsect. *Steirocladae*		II. Sect. *Psylliostachys*	(= *Cephalorrhizum* M. Pop. et Korov.)
5. Subsect. *Hyalolepidae*		III. Sect. *Pterolimon*	XII. Sect. *Tropidice* (= *Goniolimon* Boiss.)
6. Subsect. *Sarcophyllae*		C. Subgenus *Schizopetalum*	XIII. Sect. *Limoniopsis* (= *Limoniopsis* Lincz.)
V. Sect. *Sphaerostachys*			XIV. Sect. *Ikonnikovia* (= *Ikonnikovia* Lincz.)
VI. Sect. *Jovibarba*			XV. Sect. *Chaetolimon* (= *Chaetolimon* (Bunge) Lincz.)
VII. Sect. *Schizhymenium*			
VIII. Sect. *Schizopetalum* Boiss. (In Diagn. ser. 2(4): 67 1859).			XVI. Sect. *Psylliostachys* (= *Psylliostachys* (Jaub. et Sp.) Nevski)
IX. Sect. *Circinaria*			XVII. Sect. *Polyarthrion*
X. Sect. *Polyarthrion*			XVIII. Sect. *Myriolepis*
XI. Sect. *Myriolepis*			XIX. Sect. *Siphonantha*
XII. Sect. *Siphonantha*			XX. Sect. *Arthrolimon*
XIII. Sect. *Psylliostachys*			
Genus *Goniolimon*			

LIMONIOPSIS Lincz.
L. davisii Bokhari
L. owerinii (Boiss.) Lincz.

LIMONIUM Mill.
L. anatolicum Hedge, IV 6*.
L. arborescens (Brouss.) O. Kuntze, I 2.
L. articulatum (Lois.) O. Kuntze, IV 4.
L. aureum (L.) O. Kuntze, III 2.
L. axillare (Forsk.) O. Kuntze, IV 6.
L. bellidifolium (Gouan) Dum., IV 3.
L. bicolor (Bunge) O. Kuntze, III 2.
L. bonduellii (Lostib.) O. Kuntze.
L. brassicifolium (Web. & Berth.) O. Kuntze, I 2.
L. cabulicum (Boiss.) O. Kuntze, VII.
L. californicum (Boiss.) Heller, IV 1.
L. carolinianum (Walt.) Britton, IV 1.
L. carnosum (Boiss.) O. Kuntze, IV 6.
L. chrysocomum (Kar. & Kir.) O. Kuntze, III
L. cordatum (L.) Mill., IV 4.
L. corymbulosum (Boiss.) O. Kuntze, IV 4.
L. cumanum (Ten.) O. Kuntze, IV 4.
L. cylindrifolium (Forsk.) Cufod., IV 6.
L. delicatulum (Gir.) O. Kuntze, IV 3.
L. dichotomum (Cav.) O. Kuntze, IV 5.
L. dictyocladum (Boiss.) O. Kuntze, IV 4.
L. dodartii (Gir.) O. Kuntze, IV 2.
L. dregeanum (Boiss.) O. Kuntze, IV 4.
L. dufourii (Gir.) O. Kuntze, IV 2.
L. duriusculum (Gir.) O. Kuntze, IV 3.
L. echioides (L.) Mill., VII.
L effusum (Boiss.) O. Kuntze, IV 1.
L. flexuosum (L.) O. Kuntze, III 1.
L. globuliferum (Boiss.) O. Kuntze, V.
L. gmelinii (Willd.) O. Kuntze, IV 1.
L. gougetianum (Gir.) O. Kuntze, IV 2.
L. iconicum (Boiss. & Heldr.) O. Kuntze IV 5.
L. imbricatum (Webb) F. T. Hubbard, I 2.
L. jovibarbum (Webb) O. Kuntze, VI.
L. leptophyllum (Schrenk) O. Kuntze, IV 6.
L. lilacinum (Boiss.) Wagenitz, IV 1.
L. linifolium (L.f.) O. Kuntze, IV 4.
L. lychnidifolium (Gir.) O. Kuntze, IV 2.
L. macrophyllum (Brouss.) O. Kuntze, I 2.
L. macropterum (Webb) O. Kuntze, I 2.
L. macrorhabdon (Boiss.) O. Kuntze, VIII.
L. meyeri (Boiss.) O. Kuntze, IV 1.
L. minutum (L.) O. Kuntze, IV 4.
L. minutiflorum (Guss.) O. Kuntze, IV 3.
L. mucronatum (L.f.) O. Kuntze, II.
L. myrianthum (Schrenk) O. Kuntze, IV 5.
L. occidentale (Lloyd) O. Kuntze, IV 2.
L. ovalifolium (Poir.) O. Kuntze, IV 2.
L. palmyrense (Post) Dinsm., IV 6.
L. pectinatum (Ait.) O. Kuntze, II.
L. perezii (Stapf) F. T. Hubbard, I 2.
L. puberulum (Webb) O. Kuntze, I 2.
L. pruinosum (L.) O. Kuntze, IV 5.
L. psilocladon (Boiss.) O. Kuntze, IV 3.
L. purpuratum (L.) L. H. Bailey, IX.
L. roseum (Sm.) Kuntze, IX.
L. reniforme (Gir.) O. Lincz. IV 4.
L. salsuginosum (Boiss.) O. Kuntze, IV 3.
L. scabrum (Thunb.) O. Kuntze IV 4.
L. sieberi (Boiss.) O. Kuntze, IV 3.
L. sinense (Gir.) O. Kuntze, III 2.
L. sinuatum (L.) Mill., I 1.
L. stocksii (Boiss.) O. Kuntze, IV 6.
L. suffruticosum (L.) O. Kuntze, IV 6.
L. tamaricoides Bokhari, IV 5.
L. thouinii (Viv.) O. Kuntze, I 1.
L. tubiflorum (Delile) O. Kuntze, XII.
L. virgatum (Willd.) Fourr., IV 4.

PSYLLIOSTACHYS (Jaub. & Sp.) Nevski (treated as a section of *Limonium* in Boissier's classification).
P. anceps (Regel) Roshk.
P. beludshistanica Roshk.
P. leptostachya (Boiss.) Nevski
P. spicata (Willd.) Nevski
P. suworowii (Regel) Roshk.
P. volkii Rech. f.

LEAF

Because the internal structure of the lamina and petiole was found to vary along the length of the leaf, all laminas and petioles were sectioned from the middle region.

Lamina. Only a few structural characters of diagnostic value are afforded by the leaf blade; the most important of these concern the structure of the epidermis, indumentum type, arrangement of chalk glands, venation pattern and the microscopic structure of the veinlets and veinlet-endings.

Epidermis. In transverse section, the epidermal cells have a broad lumen and are provided with a cuticle of varying thickness. The cells of the upper

---

* The numbers refer to the sections and subsections of Boissier's classification (1848) indicated on Table 1.

epidermis are essentially similar to the lower epidermis. There is some variation in the cuticle structure, but Fraine (1916) has reported that the thickness and nature of the cuticle varies with the habitat. The epidermis cell walls as examined from the epidermis peels are more or less smooth in *Limonium* (except Sect. *Psylliostachys*) and other genera. In Sect. *Psylliostachys* the cell walls are distinctly wavy.

Indumentum. The absence or presence of a particular type of indumentum is a distinctive character in some species. Simple unicellular hairs are quite common; stellate hairs are reported in *L. latifolium*, *L. puberulum* and *L. bourgaei.* Examination of cleared leaves and epidermal peels of these species revealed that the so-called stellate hairs are in reality tufts of simple, unicellular hairs, but as their bases are embedded in the thick cuticle, they appear 'stellate' in surface view.

Stomata. In *Limonium* (except Sect. *Jovibarba*) and in other genera stomata are present on both surfaces in approximately equal numbers. In the monotypic Sect. *Jovibarba* stomata are confined to the lower epidermis. Paoli (1904) reported stomata only on the lower epidermis of *L. sinuatum* but I have thoroughly examined this species from different parts of its distribution range and have found stomata on both surfaces of the leaf. In narrow-leaved species of *Limonium* Metcalf & Chalk (1950) have reported that stomatal pores are parallel to the longitudinal axis of the leaf. This is not confirmed by the present study because in all the narrow-leaved species of *Limonium* and *Goniolimon* (*G. graminifolium*) examined, the stomatal pores were irregularly orientated. Stomata are usually level with the epidermis or slightly depressed but in species inhabiting dry localities, as in those of subsect. *Sarcophyllae*, they are deeply sunken below the epidermis. Stomata are anisocytic. In *L. imbricatum* stomata are reported to be anomocytic, but these are not truly anomocytic and their structure varies. In this species each stoma is encircled by 3–4 subsidiary cells which are structurally different from the neighbouring epidermal cells.

Chalk glands. These are present on both surfaces of the leaf, and are usually found depressed below the level of the epidermal cells, after the manner of the depressed stomata. In species inhabiting dry areas the glands are deeply depressed below the epidermis. The tuberulate appearance of the leaves which is a diagnostic feature of some species, such as *L. graecum*, is due to the fact that the epidermal cells adjoining the glands are considerably enlarged and become more or less elevated, forming structures known as 'tubercles'. This results in the sinking of glands in a depression at the top of these tubercles and in surface view glands appear as rosette-like structures formed by the radiating epidermal cells.

Mesophyll. The mesophyll is differentiated into palisade and spongy tissue. Isobilateral arrangement of the palisade is the usual condition in *Limonium*, but concentric type is found in thick-leaved species as in Subsect. *Sarcophyllae*. Dorsiventral arrangement is found in *L. jovibarbum* (Sect. *Jovibarba*), *L. sinuatum* (Sect. *Pteroclados*) and *L. effusum* (Sect. *Limonium*). The number of palisade layers is too inconstant to be of much taxonomic value. The arrangement of mesophyll was found useful in distinguishing critical species like *L. effusum* (meso-dorsiventral) and *L. gmelinii* (meso-isobilateral), but modification of mesophyll structure in relation to habitat has been recorded by Fraine (1916), who noticed that in *L. binervosum* normally isobilateral mesophyll is replaced by dorsiventral type in plants raised from seeds in cultivated ground.

Venation. In clearing and sectioning leaves for microscopic examination, I have noticed differences in the pattern of venation, structure of veinlets and veinlet-endings that appear to be of some taxonomic significance. In the species examined the pattern of venation can be classified into two main types: 1, Pinnate and 2, Palmate. Leaves with a typical pinnate vasculature are found only in Subsect. *Genuinae* (Sect. *Limonium*) and Subsect. *Nobiles* (Sect. *Pteroclados*). In this type there is a conspicuous midrib with a number of vascular bundles, giving comparatively tenuous principal lateral veins, which branch and extend diagonally towards the margin of the lamina (fig. 1a, c). In Sect. *Psylliostachys* and Subsect *Odontolepideae* (Sect. *Pteroclados*), which have sinuate to pinnatisect leaves, the pinnate venation is of special type. There is a distinct midrib having three vascular bundles; the lateral veins forming the reticulum are only produced from the two lateral vascular bundles while the middle bundle of the midrib remains more or less unbranched in the lamina (fig. 1b). In the palmate pattern, which is observed in the remaining sections of *Limonium* and in other genera, there are 3–5 veins in the lamina, and as seen in the cleared leaves these veins are in reality the continuation of petiolar bundles into the lamina. The lateral veins are usually arcuate and extend independently of the indistinct or distinct midvein. The vein-reticulum is formed by the branching of all the veins (fig. 1d, e).

STRUCTURE OF THE MIDRIB IN TRANSVERSE SECTION

In transverse sections of the leaf in the midrib region, the arrangement and number of vascular bundles varies considerably. In leaves with typical pinnate venation pattern, as in Subsect. *Nobiles* and Subsect. *Genuinae*, the midrib has a number of scattered bundles. The number of the constituent vascular bundles varies at different levels of the lamina, and there is always a tendency to decrease in number from the base of the lamina towards the apex. Subsect. *Nobiles* is characterized by possessing a central large 'compound' vascular bundle (for details of compound bundle see under 'petiole'), and a few scattered smaller bundles around the central one (fig. 1, c^1). In subsect. *Genuinae* bundles of various size are scattered in the midrib (fig. 1, a^1). In Subsect. *Odontolepidae* and Sect. *Psylliostachys*, which have a special type of pinnate venation (see relevant text), the midrib has 3 vascular bundles, a central large and 2 lateral smaller vascular bundles (fig. 1, b^1). In leaves with palmate vasculature, the midrib has only one vascular bundle (fig. 1, d^1, e^1) and if the midvein is more prominent than the lateral veins, there is always a group of collenchymatous cells below the vascular bundle.

Although the pattern formed by the minor veins and veinlets varies considerably, invariably the ultimate veinlets are composed of tracheary cells with helical or annular thickenings. In *Limonium* three types of veinlets and veinlet-endings are observed.

Type 1. The veinlets are slender and largely composed of 2–3 linear series of tracheary cells which become somewhat shorter in the terminal parts, but veinlet-endings are not very conspicuous. This type of veinlet and veinlet-endings is characteristic of some species such as *L. flexuosum* and *L. australis*.

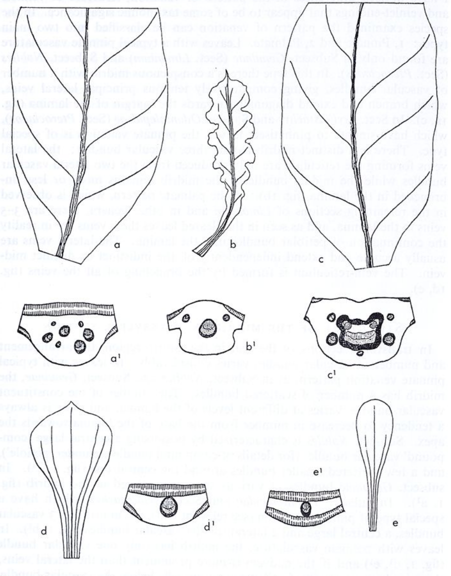

FIG. 1. Types of venation and transverse sections of midrib in *Limonium*. a-a1, *L. gmelinii*: a, part of cleared leaf; a¹, T.S. of midrib. b-b1, *L. sinuatum*: b, cleared leaf; b1, T.S. of midrib. c-c1, *L. arborescens*: c, part of cleared leaf; c1, T.S. of midrib. d-d1, *L. macrorhabdon*: d, cleared leaf; d1, T.S. of midrib. e-e1, *L. virgatum*: e, cleared leaf; e1, T.S. of midrib. All × 17.

Type 2. In species where the veinlets are somewhat coarser, the veinlets as well as the veinlet-endings are composed of a number of short tracheary cells. This type is common in *Limonium*, but is usually most pronounced in thick-leaved species such as *L. globuliferum*.

Type 3. In this type veinlets are comparatively slender but the veinlet-endings are jacketed by usually large thick or thin-walled cells (terminal sclereids). The terminal sclereids are usually thick-walled and usually have a narrow lumen, but in *L. pectinatum*, these are much enlarged, thin-walled and have a broad lumen. In morphology they appear more like 'tracheoides' than like terminal sclereids.

Sclereids. For sclereid morphology and their taxonomic importance, see Bokhari 1970.

PETIOLE

In *Limonium* the petiole presents remarkable diversity in anatomical features, and this variation when taken in conjunction with other endomorphic and exomorphic characters may characterize sections, subsections or groups of species. The number and arrangement of vascular bundles varies at different levels and petioles should be sectioned at comparable places, especially in the middle part. The arrangement of the vascular bundles in the petiole is broadly classified into two types: type 1, with scattered vascular bundles and type 2 with the vascular bundles in an arc. When the vascular bundles are in an arc, the phloem is abaxial and the xylem adaxial, but when the vascular bundles are scattered, the phloem is not always oriented towards the abaxial side of the petiole.

Type I: *Petioles with scattered vascular bundles*. In the petioles of Subsect. *Nobiles* (Sect. *Pteroclados*), Subsect. *Genuinae* (Sect. *Limonium*) and Sect. *Sphaerostachys*, there are always numerous scattered vascular bundles. Subsect. *Nobiles* is unique in the genus in having 1–3 large vascular bundles which are 4–6 × larger than the numerous encircling bundles. These large vascular bundles were also observed by Labbe in *L. arborescens*, and he referred to them as 'steles.' The number, structure and shapes of these large bundles, which I call 'compound bundles', varies and is diagnostic of some species. In *L. arborescens* the compound bundle has 3–4 collateral vascular bundles arranged around a parenchymatous tissue and enclosed by a well-developed sheath of lignified fibres (Pl. 7b). In *L. macropterum* the compound bundle is concave in outline and there are two collateral vascular bundles around a parenchymatous tissue and enveloped by a common lignified fibrous sheath (Pl. 7c, d). In *L. brassicifolium* the compound bundle has a concentric layer of xylem and phloem around a parenchymatous tissue and enclosed by a lignified fibrous sheath. It must be emphasized that the number structure and shape of these compound vascular bundles varies considerably in different regions of the petiole in the same species, so it is essential that petioles of different species should be sectioned in comparable position for pointing out the similarities and differences in their anatomical features. The remaining smaller bundles in the petiole are collateral with well-developed layers of lignified fibres all around. The ground tissue of the petiole is parenchymatous and is not differentiated into a palisade layer towards the adaxial side.

In Subsect. *Genuinae* and Sect. *Sphaerostachys*, vascular bundles of various sizes are scattered in the petiole. In Subsect. *Genuinae*, in species inhabiting sea shores as well as inland salty flats such as *L. gmelinii*, there is interpolation of additional small bundles in the petiole of the plants from the latter habitat (Pl. 7g); perhaps an adaptation to more arid conditions. In this subsection the ground tissues is undifferentiated and there is usually a well-developed foliaceous margin (Pl. 7e, f). In Sect. *Sphaerostachys*, there is no foliaceous margin but the cells of the ground tissue towards the adaxial side and the flanks become palisade-like and there are groups of sclereids scattered in it. The vascular bundles have layers of fibrous tissue all round, but it is usually better developed on the upper and lower side. In Subsect. *Genuinae* all the fibres around the vascular bundles are lignified (Pl. 7h), but in Sect. *Sphaerostachys* the lignification of the fibres is confined to the lower region.

Type II: *Petioles with vascular bundles in arc*. This type shows great variation in number and arrangement of the vascular bundles. In Subsect. *Odontolepidae* the ground tissue is undifferentiated and the middle bundle is 5 × larger than the two lateral bundles. There is a ring of very small vascular bundles around the middle one (Pl. 7a). In the remaining sections of the genus (except for those with scattered bundles), there are 3–7 bundles occurring in a shallow or deep arc. In Sect. *Limonium* (except Subsect. *Genuinae*) the peripheral cells of the ground tissue are palisade-like and 3–5 main vascular bundles occur in an arc (Pl. 8c, d). In Subsect. *Sarcophyllae* the palisade tissue is more or less concentric (except in *L. cylindrifolium*) and the various species of this subsection are characterized by special anatomical features of petiole and leaf. For example in *L. stocksii* and *L. axillare* there are 3–5 distinct vascular bundles in a shallow arc, but in the former species there are groups of sclereids only in the undifferentiated part of the ground tissue, while in the latter sclereids are scattered singly in the palisade region. In the remaining species such as *L. suffruticosum*, *L. palmyrense*, *L. carnosum* and others, there are 3–5 vascular bundles and some of these are enclosed in a common lignified fibrous sheath (Pl. 8e, f). Some of these species have irregular groups of sclereids occurring in the palisade layer (Pl. 8e, f). *L. cylindrifolium* has 3–5 vascular bundles in a common fibrous sheath, but there is another mass of lignified strengthening tissue below the vascular bundles (Pl. 8g). The presence of an additional patch of fibrous tissue gives more strength to the small, narrow petiole for supporting the fleshy, terete leaf. This species is apparently unique in the genus in having filiform sclereids in the lamina which obliquely traverse the palisade and part of the spongy mesophyll from the apex downwards. In *L. roseum*, 7 main vascular bundles form a U-shaped deep arc in the petiole and the palisade tissue is confined to the flanks (Pl. 8a); in the remaining species of this section vascular bundles are in a shallow arc and the palisade is ± concentric. When the vascular bundles are quite distinct and in an arc, each bundle is surrounded by a lignified fibrous tissue which is comparatively well-developed in the upper and lower part of the bundle, but in the monotypic Sect. *Siphonantha* there is no fibrous tissue around the vascular bundles and only 1–3 lignified fibres are seen scattered in the phloem region (Pl. 8b).

In *Limonium* vascular anatomy of the petiole has probably arisen in response to the mechanical 'need', because numerous scattered bundles are

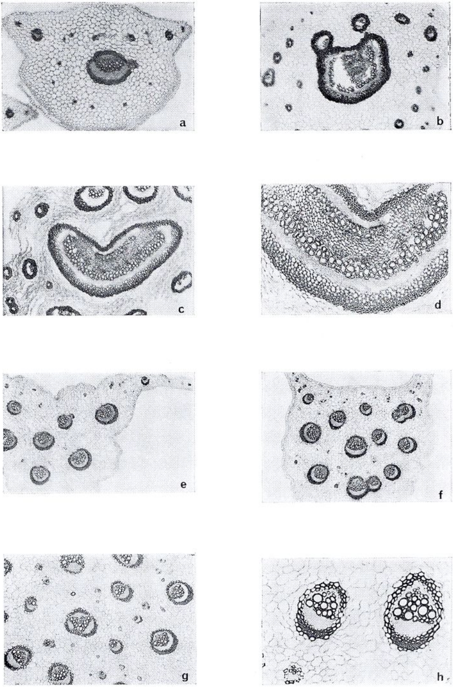

PLATE 7. Transverse section of petioles: a, *Limonium sinuatum* × 66, b; *L. arborescens* × 42; c, *L. macropterum* × 42; d, T. S. of 'compound bundles' of *L. macropterum* × 100; e, *L. effusum* × 42; f, *L. gmelinii* × 42; g, T. S. through central part of petiole of *L. gmelinii* × 42; h, vascular bundles in petiole of *L. meyeri* × 66.

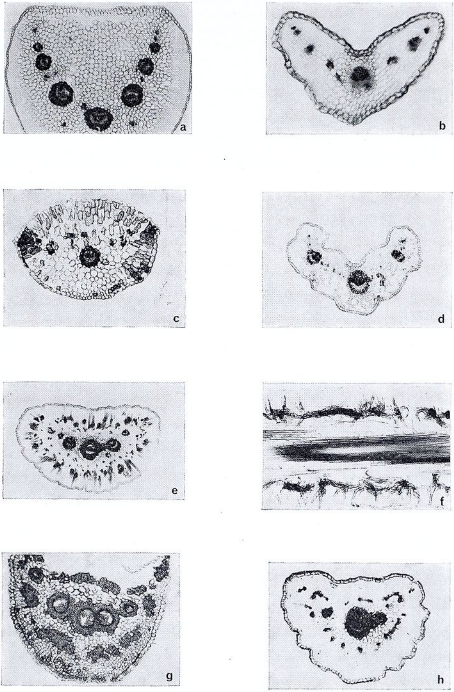

PLATE 8. Transverse section of petioles: a, *Limonium roseum*; b. *L. tubiflorum*; c, *L. sieberi*; d, *L. iconicum*; e, T. S. of petiole of *L. suffruticosum*; f, L.S. of petiole of *L. suffruticosum*; g, T.S. of petiole of *L. cylindrifolium*; h, T.S. of petiole of *L. carnosum*. a-f × 42, g × 66.

only found in large-leaved species as Sect. *Sphaerostachys*, Subsect. *Genuinae* and Subsect. *Nobiles*, while in small leaved species a few bundles occur in ± an arc. As increase in the number of bundles would automatically result in the increase of strengthening tissue, such petiole anatomy would be best suited to sustain the continuous vertical flexure resulting from the weight of the large lamina. If this is so, this feature appears to be mainly adaptive. But it is surely unwise to oversimplify a biological problem and to stress mechanical analogy too far; other factors have probably contributed towards the wide diversity of details in petiole, including the anatomy developed in the ancestral lines of present-day species.

Scape

There are some noticeable variations in scape anatomy, and these in conjunction with other anatomical and morphological features can provide characters of taxonomic value at various levels. In species having more or less terete scapes, the anatomy generally agrees with the findings of Fraine (1916). In such species, (except Subsect. *Genuinae* and Sect. *Sphaerostachys*), pith is surrounded by a ring of large, collateral, closed vascular bundles. The number of bundles in a ring depends upon the size of the inflorescence and decreases after the emission of each branch. The vascular bundles are partially embedded in a broad, lignified, fibrous zone (fig. 2a). Generally there is a second ring of very small vascular bundles present in the cortex immediately beyond the fibrous zone or embedded in the peripheral region of the fibrous zone. Around the fibrous zone is the cortex which is an assimilatory part of the scape. In the lower part of the scape (up to the first or second node), the assimilatory tissue is composed of a variable number of rounded parenchymatous cells, but in the upper part the outermost layer of these cells becomes palisade-like and the number of palisade layers increases in the branches.

In Subsect. *Genuinae* (Sect. *Limonium*) and Sect *Sphaerostachys* there are always two rings of large vascular bundles in the unbranched part of the scape as well as in the primary branches. There is a third ring of small bundles present immediately outside the fibrous zone. The bundles of the inner rings are partially embedded in the fibrous zone; those of the middle ring are usually embedded in it, but unlike other sections the fibrous zone is more or less lobed in its outline. The arrangement of the cortical tissue in the scape at different levels is the same as described earlier A few concentric medullary bundles are also observed in some species.

In some species, especially in Subsect. *Steirocladae* and Subsect. *Hyalolepidae* (Sect. *Limonium*), there are numerous repeatedly forked sterile assimilatory branches in the lower part of the scape. In these branches the assimilatory tissue is much more developed; palisade cells are longer and occur in 2–3 layers. The tuberculate appearance of these branches in some species is due to the fact that the epidermal cells surrounding the chalk glands are considerably enlarged, resulting in the sinking of the gland in a depression, e.g. in *L. iconicum*.

In *Limonium* species with a winged scape, the general arrangement of the tissue is similar to that in the terete scape, but the main assimilatory parts of

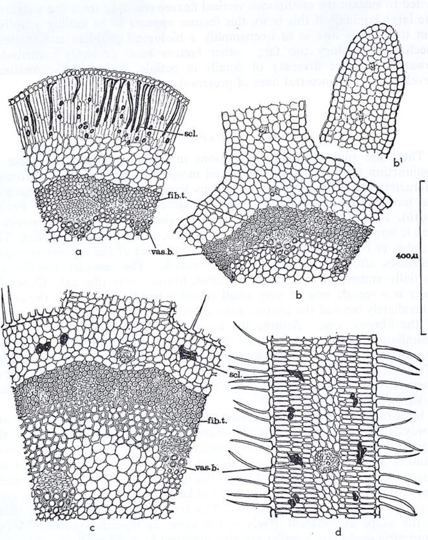

FIG. 2. Transverse sections of part of scapes. a, *Limonium cylindrifolium*. b-b1, *Psylliostachys beludschistanica*: b, part of scape; b1, terminal part of wing. c-c1, *Limonium imbricatum*: c, part of scape; c1, middle part of wing. fib.t. = fibrous tissue; scl. = sclereids; vas.b. = vascular bundles.

the scape are the wings. Winged scapes are characteristic of Sect. *Pteroclados* and some species belonging to Sect. *Ctenostachys* and Sect. *Psylliostachys*. In Sect. *Pteroclados* there are two inner rings of vascular bundles and a third outer ring of small bundles. In Subsect. *Odontolepidae*, 1–2 outermost layers of cortical cells become palisade-like and palisade tissue is also well-developed in the wings, but in Subsect. *Nobiles*, though the palisade tissue is well-developed in the wings the cortical cells in the non-winged part of the scape remain usually undifferentiated. In *L. mucronatum* (Sect. *Ctenostachys*) and winged species of Sect. *Psylliostachys*, in addition to a ring of small vascular bundles in the cortex, there is only one inner ring of large vascular bundles. In *L. mucronatum* there are 2–3 layers of palisade in the wings as well as in the non-winged parts of the scape. In species of Sect. *Psylliostachys* the assimilatory tissue in the winged as well as non-winged part of the scape is not clearly differentiated (fig. 2b, b^1).

Sclereids. In species where either foliar sclereids are absent or terminal sclereids are present in the leaves, the sclereids are found to be absent in the scapes. But species with diffused foliar sclereids invariably possess sclereids in the cortical region of the scape. The distribution pattern of sclereids in the scape is found to follow that of sclereid distribution in the leaf of the respective species. For example, in *L. lilacinum* and *L. brassicifolium* the sclereids are present singly or in groups in the petiole, and have the same arrangement in their scapes. In *L. suffruticosum* sclereid groups are irregularly scattered in the petiole as well as in the scape. In *L. stocksii* there are groups of sclereids arranged parallel to the long axis of the petiole and the scape. In *L. cylindrifolium*, the sclereid arrangement in the scape (fig. 2a) is the same as in the leaf lamina.

In the preceding account, the range of variation and the taxonomic importance of some anatomical features is discussed. Though certain anatomical characters appear to be quite distinctive of some sections, subsections or species, it must be emphasized that the present findings are based only on the limited number of species examined in each section. The primary aim of the present work is to find new and neglected endomorphic characters and correlate them with exomorphic ones. Within prescribed limits anatomical characters in *Limonium* show, in fact, immense variety and constancy, and it is this which gives them their real taxonomic value, for we have a fresh set of characters which might be used to supplement those commonly employed in classification.

The variation of characters which are reported here should encourage others to seek to add further to the scanty knowledge of endomorphic characters and test the validity of the present findings.

SUGGESTIONS FOR THE IMPROVEMENT OF INFRAGENERIC CLASSIFICATION

At present there is no satisfactory taxonomic treatment of *Limonium* on a world basis. Boissier (1848) divided the genus into 12 sections and a number of subsections. Bentham & Hooker (1876) divided the genus into a smaller number of (6) sections; Pax (1897) recognized 3 subgenera and 10 sections. Since then some Soviet workers have given generic rank to some sections and species of *Limonium*: *Psylliostachys* (Jaub. & Sp.) Nevski, 1937 (Sect. *Psylliostachys*); *Limoniopsis* Lincz., 1952 (*Limonium owerinii* Boiss.). and *Bakerolimon* Lincz., 1967 (Sect. *Pterolimon*). Recently Labbe (1962), on the basis of his morphological and anatomical study of 63 species of *Limonium* and related genera, has recognised 20 sections and relegated some of the established genera to sections of *Limonium*. The classificatory schemes are compared in Table 1.

On the basis of available morphological and anatomical data, in the following account some changes are suggested for improving the infrageneric classification, and for this purpose Boissier's classification is used as a basis for discussion.

Sect. *Pterocládos* is a well-knit natural section and is accepted by most authors. Its two subsections, *Odontolepidae* and *Nobiles*, besides their diagnostic exomorphic characters, also have a distinctive venation pattern and petiolar anatomy (Pl. 7a–d & fig. 1b, b^1, c–c^1). Subsect *Nobiles* has a group of nine shrubby species and is endemic to the Canary Islands. Stapf (1906) treated *L. frutescens* as a 'form' of *L. arborescens*, *L. bourgaei* as a 'form' of *L. puberulum*, and *L. macropterum* as a variety of *L. brassicifolium*. In *L. arborescens* and *L. frutescens* there is a continuous range of variation of morphological characters, and the subacaulescent habit of the latter is believed to be a modification in response to habitat conditions. These two species share similar anatomical features. Similarly *L. puberulum* and *L. bourgaei* are indistinguishable in their morphological features and have the same type of indumentum and leaf anatomy; hence Stapf seems justified in his taxonomic treatment of these species. But his treatment of *L. macropterum* is not sustained by anatomical features. In *L. macropterum* the structure and shape of the compound vascular bundle of the petiole (Pl. 7c, d) is quite different from that of *L. brassicifolium*. If we were to accept *L. macropterum* as a variety of *L. brassicifolium* it would be very difficult to explain the differences in their petiolar anatomy, especially when both species have been reported to grow in the same locality. Stapf remarked that some morphological differences between these species, like the narrow wings on the scape, subfloral auricles and the denser indumentum of *L. macropterum* seem to be fairly constant. But as these morphological features of *L. macropterum* are correlated with a distinctive petiolar anatomy, it seems to stand to reason to treat it as a distinct species.

Sect. *Limonium*, which is further divided by Boissier into six subsections, appears to contain the most heterogeneous group of species. In this section, Subsect. *Sarcophyllae*, containing closely allied species, appears to be out of agreement with the other subsections morphologically and anatomically. Linczevski (1952) raised this subsection to sectional rank, i.e. Sect. *Sarcophyllum* (Boiss.) Lincz., a decision which is supported by exomorphic and endomorphic characters. Subsect. *Genuinae* contains, (except *L. lilacinum*), morphologically and anatomically (venation and petiolar anatomy), a group of well-knit species. *L. lilacinum*, a Turkish endemic, is not closely related to the other species of this subsection. On the basis of the under-mentioned morphological and anatomical features, I have treated this species under Sect. *Sphaerostachys*, because it appears to be more closely related to *L. globuliferum* of Sect. *Sphaerostachys* than to any other species of Sect. *Limonium* Subsect. *Genuinae*.

Morphological and Anatomical characters of

Sect. *Sphaerostachys*	Sect. *Limonium* Subsect. *Genuinae*
Leaves with usually a distinct crisp-undulate margin.	Leaf margin not crisp-undulate.
Vein reticulum indistinct.	Vein reticulum distinct.
Petioles without a foliaceous margin.	Petioles with foliaceous margin.
Development of palisade at the adaxial and lateral sides of the petiole.	Ground tissue undifferentiated up to the middle of the petiole.
Presence of large number of groups of sclereids in the ground tissue of the petiole.	Sclereids usually absent or rarely few sclereids scattered in the ground tissue.
In the fibrous sheath around the vascular bundles, lignification is confined to the lower region.	All the fibres of the fibrous sheath are lignified.
Palmate venation as seen from the cleared leaves.	Pinnate venation pattern.

In the remaining 4 subsections, though all the species belonging to Subsect. *Steirocladae* have terminal foliar sclereids, such sclereids are also found in some species of the other 3 subsections. The leaf and scape anatomy is also uniform in all these subsections. The examination of a large number of species has revealed that the characters used by Boissier to separate Subsect. *Densiflorae* from *Dissitiflorae* and Subsect. *Steirocladae* from *Hyalolepidae* no longer hold good. I am convinced that these pairs of subsections cannot be kept distinct from each other. I think it is reasonable to combine Subsect. *Densiflorae* and *Dissitiflorae* into one subsection, characterised by few or no sterile branches and by its larger spikelets, and to combine Subsect. *Steirocladae* and *Hyalolepidae* as another subsection, characterised by the presence of numerous, repeatedly branched sterile branches in the lower scape region, and smaller spikelets.

L. latifolium is placed under Subsect. *Hyalolepidae* by Boissier, but its characters, such as large leaves, pinnate venation, numerous scattered bundles in the petiole, and two rings of large vascular bundles in the scape, clearly suggest that this species is more closely related to the species of Subsect. *Genuinae* than to any other species of Subsect. *Hyalolepidae*.

Sect. *Limonium*, which contains some morphologically and anatomically well-knit subsections such as Subsect. *Sarcophyllae* and *Genuinae*, is not further divided into subsections by Bentham & Hooker and Pax, a situation which is far from satisfactory. As Subsect. *Sarcophyllae* has already been given the rank of a separate section, it seems convenient to recognize only 3 subsections: i.e. 1, subsect. *Genuinae*; 2, Subsect. *Densiflorae* including (Subsect. *Densiflorae* & *Dissitiflorae*); 3, Subsect. *Steirocladae* including (Subsect. *Steirocladae* & *Hyalolepidae*).

Sections *Schizhymenium* & *Schizopetalum*. Sect. *Schizhymenium* is the most heterogeneous section of Boissier, containing 3 unrelated species, i.e. *L. owerinii*, *L. echioides* and *L. cabulicum*. Linczevski has treated *L. owerinii* as a separate genus, *Limoniopsis* Lincz. *L. echioides*, by its annual habit, structure of spikelet and calyx, leaf anatomy and in its distribution range, is out of agreement with other species of the sections and differs strikingly in its linear stigmas. Baker (1953) examined this species throughout its range and found that it has B pollen or is male sterile and always possesses 'cob' stigmas; this combination of pollen and stigma is unknown elsewhere in the genus. On this basis, as has been suggested by Baker, it is quite reasonable that this species should be removed from the association of *L. cabulicum* and treated as a section of its own. Sect. *Schizopetalum* was created by Boissier (1859) to accommodate *L. macrorhabdon*, and one of the important characters of this section was the bifid nature of the limb of the petal. Other species like *L. griffithii* and *L. gilesii* have been discovered since then, and there is no doubt that morphologically and anatomically they are closely related to *L. macrorhabdon*. It is also now clear that the bifid petal character has no sectional significance. If we accept *Limoniopsis* (*L. owerinii*) as an independent genus and place *L. echioides* in a section of its own, we are only left with *L. cabulicum* in Sect. *Schizhymenium*. In habit *L. cabulicum* is extremely close to *L. griffithii*, and its rosette leaves and inflorescence are very like those of *L. macrorhabdon*. All species of Sect. *Schizopetalum* and *L. cabulicum* have dimorphic pollen and asymetrically oblong-capitate stigmas, and also share more or less the same leaf anatomy. The similarity in exomorphic and endomorphic characters, geographical distribution and the general arrangement in pollen and stigma characters of Sect. *Schizopetalum* and *Schizhymenium* (excluding *L. owerinii* and *L. echioides*) suggest these two sections might well be united.

Species belonging to Sect. *Circinaria* are unique in the genus in possessing a circinate style. Because of their capitate stigma, Bentham & Hooker included these species under their Sect. *Goniolimon*, but this settlement is too obviously artificial to be satisfactory. Boissier's treatment of these species under a separate Sect. *Circiniaria* is the most tenable one. In spite of distinct morphological characters of this section, there is no anatomical feature of diagnostic value; however, within the section, *L. roseum* can be easily distinguished from the other species by its characteristic petiolar anatomy, see (Pl. 7a and relevant text).

Sect. *Pterolimon* contains two closely related species, *L. plumosum* (Phil.) O. Kuntze and *L. peruvianum* O. Kuntze. They are shrubs with narrow scale-like leaves on the branches and spicate inflorescence. With five calyx nerves and feathery awns, they are of a type not to be seen elsewhere in the genus. They have monomorphic pollen and the structure of pollen is of special type (Baker 1953a, p. 444). Unfortunately it has not been possible to examine any material of this section. On the basis of their shrubby habit, narrow scale-like leaves, plumose excurrent calyx nerves, and characteristic ornamentation of pollen grains, Linczevski is justified in elevating this section to generic rank, i.e. *Bakerolimon* Lincz.

In Boissier's classification of *Limonium*, 4 sections have a gamopetalous corolla and the corolla is funnel-shaped to hypocrateriform. Of these four, Sect. *Psylliostachys* requires special mention. This section contains tiny-flowered steppe herbs and has many distinctive exomorphic and endomorphic features, most of which are not shared by any section of *Limonium*, i.e. sinuate to pinnatisect-margined leaves, glandular calyx tube and ex-current nerves, special pinnate venation (see relevant text) and wavy epidermal cells.

The union of Sect. *Psylliostachys* with Sect. *Eusiphonantha* and *Pterolimon* into a single subgenus, as suggested by Pax, is quite untenable and was based simply on the greater than usual union of the petals. On the basis of the above-mentioned characters the generic status given to Sect. *Psylliostachys* (*Psylliostachys* (Jaub. & Sp.) Nevski) by Nevski is justified.

DISCUSSION

Classificatory schemes for *Limonium* have been proposed by various workers (Boissier 1848, Bentham & Hooker 1876, Pax 1897, Labbe 1962), but none of these approaches perfection. Boissier's classification, though over a hundred years old, is the most detailed scheme and the only one in which a published attempt has been made to place all the species known at that time. Indeed, there is no argument about the naturalness of some of his sections, like Sect. *Pterocladus* and others, a fact which is also supported by endomorphic characters. But it is also evident from the preceding account that, owing to the discovery of many new species and extensive recent collecting, some of his sections, like Sect. *Limonium*, *Schizhymenium* and a few others, contain a heterogenous collection of species and are certainly unnaturally circumscribed. Sect. *Psylliostachys* and some others such as Sects. *Pterolimon* and *Arthrolimon* (these two were not known to Boissier, but were treated under *Limonium* by subsequent authors) appear to be out of place in this genus. In the light of exomorphic and available endomorphic characters, some suggestions are made for improving the infra-generic classification of the genus. Labbe, after examining 63/300 species of the genus, recognised 20 sections in *Limonium*, and has relegated some accepted genera like *Goniolimon*, *Chaetolimon*, *Psylliostachys*, *Ikonnikovia*, *Cephalorrhizum* and *Limoniopsis* to sections of this genus. This taxonomic decision is decidedly a step backwards, because it is unreasonable to expect a single genus like *Limonium* to accommodate all the above-mentioned groups of plants.

A thorough study of this genus in the light of data from all sources (exomorphic, endomorphic, pollen and stigma types), on a world-wide basis is needed before proposing any classificatory system. The approach of Soviet work in treating some sections and species of *Limonium* as distinct genera appears to be a step in the right direction for a better taxonomic treatment of *Limonium* sensu lato, although I prefer to treat *Ikonnikovia kaufmanniana* (Regel) Lincz. as a *Goniolimon* species.

REFERENCES

BAKER, H. G. (1953a). Dimorphism and monomorphism in the Plumbaginaceae. II: Pollen and Stigma in the genus Limonium. *Ann. Bot.* 17: 433–445.

— (1953b). Dimorphism and monomorphism in the Plumbaginaceae. III: Correlation of geographical distribution patterns with dimorphism and monomorphism in Limonium. *Ann. Bot.* 17: 615–627.

BENTHAM, G. & HOOKER, J. D. (1876). *Genera Plantarum* 2: 623–628.

Boissier, E. (1848). Plumbaginaceae in DC., *Prodr.* 12: 620–696.

— (1846–59). *Diagnoses Plantarum Orientalum Novarum*, vol. 1–2.

Bokhari, M. H. (1970). Morphology and taxonomic significance of foliar sclereids in Limonium. *Notes R.B.G. Edinb.* 30: 43–53.

Fraine, E. De (1916). The morphology and anatomy of genus Statice as presented at Blakeney Point. Part I. *Ann. Bot.* 30: 239–282.

Labbe, A. (1962). *Les Plumbaginacees. Structure, devélopment, repartition, conséquences en systematique.* Grenoble.

Linczevski, I. (1952). in *Fl. U.R.S.S.* 18: Addenda 12.

Maury, P. (1886). Études sur l'organization et la distribution geographique des Plombaginacees. *Ann. Sci. Nat. ser.* 7, 4: 1–134.

Metcalf, C. R. & Chalk, L. (1950). *Anatomy of the Dicotyledons*, 2 Vols. Oxford.

Paoli (1904). Contributio allo studio della eterofillia. *Nuovo Giorn. bot. Ital.* 11: 217–219.

Pax, F. (1897). Plumbaginaceae in Engler & Prantl, *Die natürlichen Pflanzenfamilien* 4, 1: 116–125.

Solereder, H. (1908). *Systematic anatomy of the dicotyledons.* vol. I & II.

Stapf, O. (1906). The Statice of Canaries of the subsection Nobiles. *Ann. Bot.* 20. I. 205–212: II. 301–310.