# ANATOMY OF DIONYSIA I: FOLIAR SCLEREIDS

M. H. Bokhari* & P. Wendelbo**

ABSTRACT. An anatomical investigation of the leaves of 36 out of the 41 species of *Dionysia* (Primulaceae) showed that sclereids were of frequent occurrence. Three main types can be distinguished: dermal, terminal and diffused. Throughout the genus, sclereids provide a useful additional taxonomic character and are also of some help in trying to elucidate the phylogeny of the genus. Some of the results of this study are: *D. termeana* should be transferred from subsect. *Caespitosae* to subsect. *Bryomorphae*; two evolutionary lines within sect. *Anacamptophyllum* may be recognised—those with (Afghanistan-Pakistan) and without (Iran) sclereids; subsect. *Bryomorphae* has probably evolved from sect. *Anacamptophyllum*. Otherwise, the study does not conflict with the existing taxonomy and previously proposed phylogeny.

## INTRODUCTION

The genus *Dionysia* with 41 species is endemic to the Irano-Turanian floristic region; all the species are tuft-forming obligatory chasmophytes. It has already been shown that, on characters of external morphology, there are several discernible lines of progressive reduction, proceeding in a more or less parallel fashion in such characters as leaf size, nervation, inflorescence, number of seeds per capsule (Melchior 1943; Wendelbo 1961). These progressive reductional lines were considered to be part of a pattern of gradual xeromorphic adaptations of taxa occupying the drier inner ranges of the Iranian mountains. In an earlier paper Wendelbo (1971) investigated the anatomy of *D. microphylla* and *D. hedgei* and showed that they exhibited rather extreme adaptations to a xerophytic habitat. This small study proved to be so promising that the present authors decided to look into the anatomy of all the species of the genus. One of us (M.H.B) carried out the anatomical investigation.

The main purpose of this paper is to put on record some of the anatomical characters, especially sclereids, because these seem to provide useful characters for understanding the taxonomy and phylogeny of the genus.

We have followed the taxonomic treatment of *Dionysia* by Wendelbo (1964). A synopsis of the sectional classification is given below (species described after 1964 are interpolated).

DIONYSIA

1. Sect. Anacamptophyllum
    a. subsect. Mirae

*D. mira*

    b. subsect. Scaposae

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* Dept. of Biology, Pahlavi University, Shiraz, Iran.

** Göteborgs Botaniska Trädgård, S-41319, Göteborg, Sweden—previously at Ariamehr Botanic Garden, Tehran, Iran.

*D. bornmuelleri*; *D. teucrioides*; **D. paradoxa*; **D. balsamea*; *D. saponacea*; **D. lacei*; (*D. hissarica*)

c. subsect. Revolutae

*D. aretioides*; *D. leucotricha*; *D. revoluta*; *D. archibaldii*; *D. esfandiarii*; *D. oreodoxa*; *D. rhaptodes*

2. Sect. Dionysia

a. subsect. Caespitosae

(*D. bolivarii*); **D. caespitosa*; **D. diapensiifolia*; *D. termeana*; **D. gaubae*; **D. odora*

b. subsect. Bryomorphae

*D. sawyeri*; *D. haussknechtii*; *D. lamingtonii*; *D. iranshahrii*; *D. michauxii*; *D. zagrica*; *D. bryoides*; **D. curviflora*; *D. janthina*

c. subsect. Tapetodes

**D. denticulata*; **D. tapetodes*; **D. trinervia*; (*D. kossinskyi*)

d. subsect. Heterotrichae

**D. lindbergii*

3. Sect. Dionysiastrum

*D. microphylla*; *D. hedgei*; (*D. involucrata*); *D. freitagii*; *D. viscidula*; *D. afghanica*

Species marked with an asterisk have sclereids in their foliage; those in brackets have not been investigated.

## MATERIALS AND METHODS

This investigation is based entirely on the study of herbarium specimens. The techniques used for leaf clearing, preparing the herbarium material for section cutting and staining were the same as those previously used by Bokhari (1970). The techniques for macerating the tissue were the same as described for *Cyrtandra* (Bokhari & Burtt 1970). Morphology, range of variation and distribution of sclereids were studied from cleared leaves and hand sections. Individual sclereids were examined in more detail from macerated leaf lamina tissue. Permanent slide preparations are deposited at Pahlavi University, Shiraz; the appendix lists the specimens examined.

## GENERAL HISTOLOGY OF THE LAMINA

Before giving details of sclereids, it is necessary to give a brief description of the *Dionysia* leaf. Because the leaf anatomy of the genus shows a considerable range of variation, it is not possible to go into all the details of foliar histology; only the main general features of those species in which sclereids are found are mentioned now.

*Epidermis*. In all species, except *D. curviflora*, epidermal cells on both surfaces are barrel-shaped with a well-developed layer of cuticle. In *D. curviflora* the lower epidermis is sclerified in the upper region of the leaf (fig. 1e).

*Mesophyll*. In *D. paradoxa* and *D. balsamea*, palisade tissue is present on the upper and lower surfaces with spongy tissue in the middle—hence the leaves are isobilateral (fig. 1a, b). In *D. lacei*, the leaf is bifacial i.e. palisade tissue

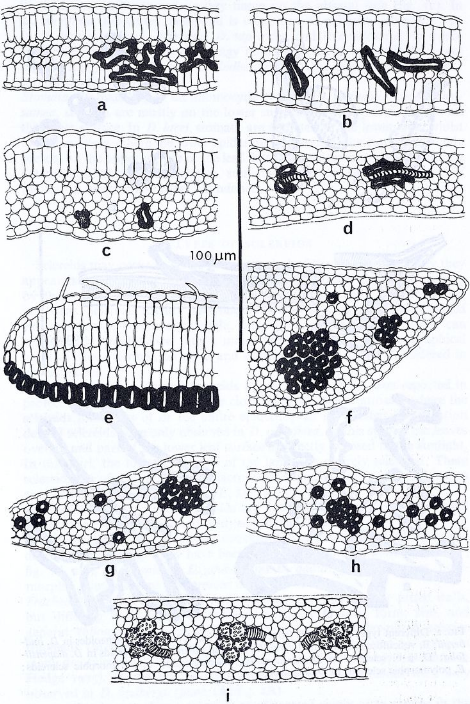

FIG. 1. Transverse sections of leaf laminas showing sclereids: a, *D. paradoxa*; b, *D. balsamea*; c, *D. lacei*; d, *D. diapensiifolia*; e, *D. curviflora*; f, *D. trinervia*; g, *D. tapetodes*; h, *D. denticulata*; i, *D. lindbergii*.

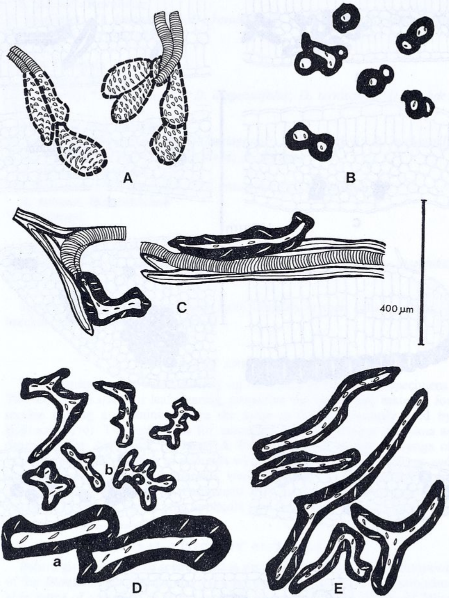

FIG. 2. Different types of sclereids from macerated leaf laminas: A, tracheoides in *D. lindbergii*; B, vesiculose sclereids in *D. lacei*; C, terminal polymorphic sclereids in *D. diapensiifolia*; D, a–b, sclereids in *D. paradoxa*—a, macrosclereids, b, polymorphic sclereids; *E*, polymorphic sclereids in *D. balsamea*.

is on the adaxial side and spongy tissue on the abaxial side (fig. 1c). In *D. curviflora*, the entire mesophyll is composed of palisade tissue (fig. 1e). In *D. diapensiifolia*, *D. trinervia*, *D. tapetodes*, and *D. denticulata*, the mesophyll is entirely made up of spongy tissue with large intercellular spaces (fig. 1d, f, g, h). Mesophyll in *D. lindbergii* (fig. 1i) is also composed of only spongy tissue.

*Stomata*. Stomata are of an anomocytic type. In *D. paradoxa* and *D. balsamea*, stomata are mostly on the lower surface but a very few are also on the upper surface. In *D. lacei*, stomata are confined to the lower side, whilst in *D. curviflora*, where the lower epidermis is sclerified, the stomata are only present on the upper surface of the leaf. In species where mesophyll is entirely composed of spongy parenchyma, stomata are present on both surfaces of the leaf in more or less equal abundance.

## TYPES OF SCLEREIDS

Sclereids may occur in layers or clusters in leaf tissues but frequently they appear isolated among other types of cells from which they differ sharply by their thick walls and bizarre shapes; as isolated cells they are called idioblasts. Sclereids usually have thick walls, strongly lignified and provided with numerous, commonly simple, pits. Foliar sclereids in *Dionysia* can conveniently be classified into 3 main types from a purely topographical point of view: dermal, terminal and diffused. These are now considered in greater detail.

DERMAL SCLEREIDS. Dermal sclereids appear only to have been reported in protective foliar structures like the clove scales of *Allium sativum*, where the sclereids form part of or the entire epidermis. In the present investigation dermal sclereids were only observed in *D. curviflora*. In this species the leaves overlap and part of the lower leaf surface is directly exposed to the sunlight. In this part, the lower epidermis of the lamina is entirely sclerified. These sclereids are of a long, narrow, macrosclereid type and are tightly packed as seen in the cleared leaves (plate 1E, 2D; fig. 1e, 3D).

TERMINAL SCLEREIDS. These sclereids are confined to the ends of the small veins. Two types are observed: polymorphic and tracheoides.

*Polymorphic sclereids*. These vary considerably in size, form of cell body and degree of branching. They have been found in *D. diapensiifolia*, (plate 1F; fig. 1d, 2C), *D. caespitosa*, *D. gaubae* and *D. odora*. In these species, polymorphic sclereids were also noticed along the veins.

*Tracheoides*. These are idioblasts resembling tracheids in their pitted walls, but differing from typically tracheary elements in their form, size, and general topography. These have also been called circular-pitted storage tracheids (Metcalf & Chalk 1950). Tracheoides are reported to occur in many dicotyledon genera (Solereder, 1908; Bokhari & Burtt 1970; Bokhari & Hedge 1975). In the present investigation terminal tracheoides were only observed in *D. lindbergii* (plate 1A; fig. 2A).

DIFFUSED SCLEREIDS. These sclereids are dispersed singly or in groups in the leaf mesophyll and are of various types; there may be more than one type in the same species. The diffused sclereids found in this genus are classified into the following six types.

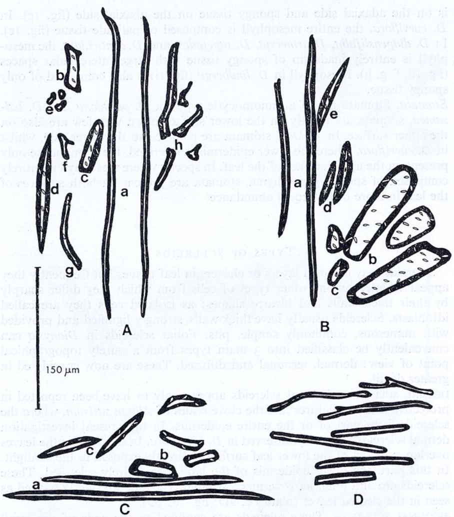

FIG. 3. Different types of sclereids from macerated leaf laminas. A, a–h, sclereids in *D. denticulata*: a, filiform sclereids; b–c, macrosclereids; d, fusiform sclereids; e–h, polymorphic sclereids. B. a–e, sclereids in *D. tapetodes*: a, filiform sclereids; b, large macrosclereids; c, brachysclereids; d–e, fusiform sclereids. C. a–c, sclereids in *D. trinervia*: a, filiform sclereids; b, macrosclereids; c, fusiform sclereids. D, epidermal thin macrosclereids in *D. curviflora*.

1\. *Vesiculose*. These are sclerotic parenchymatous cells which are usually unbranched but variously lobed. They are little different from the neighbouring cells and do not show intrusive growth. These have only been observed in *D. lacei* (plate 1B; fig. 1c, 2B).

2\. *Brachysclereids*. These are more or less isodiametric in form having uniform thick walls and are only noted at the leaf base of some specimens of *D. tapetodes* (plate 2B; fig. 3Bc).

3\. *Fusiform sclereids*. The sclereids grouped under this category are unbranched with fusoid ends. They vary considerably in size and exhibit great variation in cell forms. These are very common towards the leaf margin in

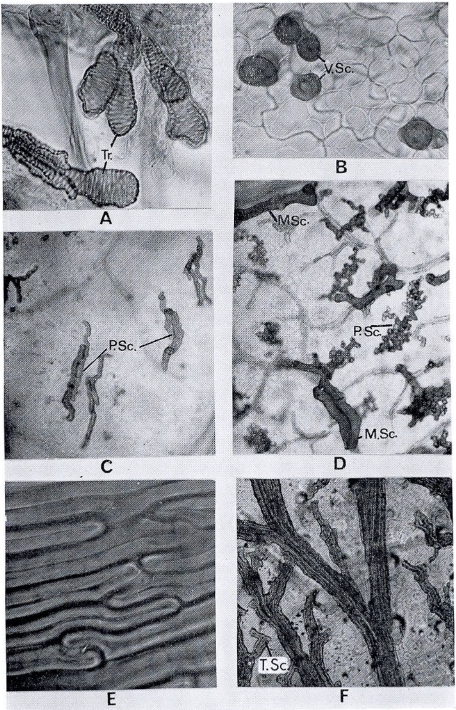

PLATE I. Parts of cleared leaf laminas showing sclereids: A, *D. lindbergii*; B, *D. lacei*; C, *D. balsamea*; D, *D. paradoxa*; E, *D. curviflora*; F, *D. diapensiifolia*.
M.Sc. = macrosclereids; P.Sc. = polymorphic sclereids; T.Sc. = terminal sclereids; V.Sc. = vesiculose sclereids.

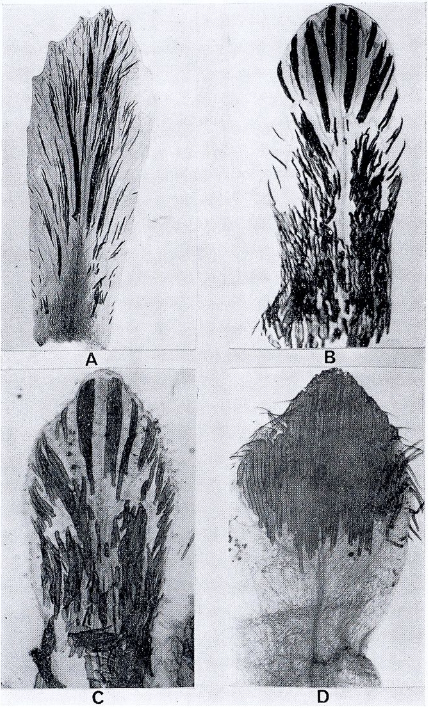

PLATE 2. Cleared leaf laminas. A, *D. denticulata*; B, *D. tapetodes*; C, *D. trinervia*; D, *D. curviflora*.

*D. tapetodes* and *D. trinervia*. In a closely related species, *D. denticulata*, there are only a few fusiform sclereids along the margin of the leaf (plate 2A, B, C; fig. 3Ad, Bd–e, Cc).

4. *Macrosclereids*. Under this category are included sclereids which are long, unbranched, straight, or curved having ± blunt ends, and uniform thick cell walls. They may be isolated or in groups. In *D. denticulata*, *D. tapetodes* and *D. trinervia*, the macrosclereids are straight and occur singly scattered throughout the mesophyll (fig. 3Ab–c, Bb–Cb). In *D. paradoxa*, these are straight, or curved, occurring singly or in groups and are found dispersed throughout the mesophyll along with numerous polymorphic sclereids (plate 1D; fig. 2Da).

5. *Polymorphic sclereids*. Diffused polymorphic sclereids are found in *D. balsamea*, *D. paradoxa* and *D. denticulata*. There are many different shapes of sclereids under this category. On the one hand, there are somewhat vesiculose or columnar sclereids which are variously lobed or recurved but showing little tendency towards branching. These types of sclereids are found in *D. balsamea* (plate 1C; fig. 2E). A few such sclereids are also found scattered throughout the lamina in *D. denticulata* (fig. 3Ae–h). At the other extreme, there are bizarre irregularly branched cells approaching astrosclereids. These sclereids are a dominant type in *D. paradoxa*, occurring together with macrosclereids in the lamina (plate 1D; fig. 2Db). There are so many intermediate forms of this type of sclereid that any attempt to classify them rigidly into minor types is precluded.

6. *Filiform sclereids*. These are characterised by their slender, greatly elongated form and their characteristic orientation within the leaf lamina. Filiform sclereids are found in *D. tapetodes*, *D. trinervia* and *D. denticulata* (plate 2A, B, C; fig. 3Aa, Ba, Ca). In *D. tapetodes* and *D. trinervia* these sclereids are mostly in the form of 3–5 compact strands occurring in between the vascular bundles. These strands are oriented parallel to the long axis of the leaf. Besides these strands there are also some isolated filiform sclereids in the lamina of these species. In *D. denticulata*, filiform sclereids do not from definite compact strands but run ± parallel to the long axis of the leaf.

## DISCUSSION AND CONCLUSIONS

*Dionysia* seems to be an unusual genus in having three different main types of sclereids in the lamina, i.e. dermal, terminal and diffused. The small amount of literature on foliar sclereids indicates that, except in *Limonium*, there are usually either terminal or diffused sclereids in a genus and not all three together. As is clear from the preceding account foliar sclereids, in general, do provide some characters that may be of help in understanding the phylogeny and taxonomy of the genus. Some of the more interesting results are now discussed.

1. *D. balsamea* and *D. paradoxa*, which were considered to be very closely related by Wendelbo (1964:7) show clear anatomical differences in the material examined. In *D. paradoxa*, macrosclereids and mostly branched polymorphic sclereids are found intermixed in the mesophyll, while in

*D. balsamea* there are no macrosclereids and the polymorphic sclereids are mostly unbranched.

2. *D. lacei* is a very distinct species in its sclereid morphology. Vesiculose types of sclereids are found only in this species.

3. In all the species studied of subsect. *Caespitosae*, except *D. termeana*, polymorphic terminal sclereids were observed. Polymorphic sclereids were also noticed along the veins of all these species, again except *D. termeana*. It was also possible to distinguish closely related species within the subsection on the basis of the sclereid morphology.

4. *D. termeana*, because it lacks sclereids and has obcordate corolla lobes, should be transferred from subsect. *Caespitosae* to subsect. *Bryomorphae*. In the original description, Wendelbo (1970:306), noted that it differed from all the other species of subsect. *Caespitosa* in the obcordate corolla lobes and a calyx split to the base. With its comparatively large, toothed leaves and several-seeded capsule, this species should now be considered as a primitive member of subsect. *Bryomorphae*. It appears to be most closely related to *D. bryoides* and *D. haussknechtii*. Further evidence for this relationship is found in the fact that the only spontaneous hybrid known in the genus is between *D. termeana* and *D. bryoides* (Grey-Wilson 1974: 693).

5. All species of subsect. *Bryomorphae*, except *D. curviflora*, lack sclereids. The dermal sclereids of *D. curviflora*, found in the epidermis near the apex of the underside of the leaf, are not met with in any other species of the genus. As this species appears to be closely related to other species of its group on morphological characters, there is no reason to transfer it to a separate group on anatomical characters alone. The dermal sclereids must be considered to have originated in this taxon as part of a syndrome connected with xeromorphic adaptations. The group *Bryomorphae* may thus be considered a natural one.

6. The present investigation has revealed that there is no difference between *D. tapetodes* and *D. trinervia* in their sclereids. Both species have compact strands of filiform sclereids and a large number of fusiform sclereids along the margin of their leaves. In the initial survey, *D. tapetodes* seemed to be distinct in possessing brachysclereids at the basal part of the leaf, while such sclereids were absent from *D. trinervia*. However, by examining more leaf specimens of *D. tapetodes* it was found that this distinction did not hold, because in some leaves of *D. tapetodes* sclereids were lacking from the basal part of the leaf. Unfortunately we were not able to examine leaf specimens of *D. denticulata* from different localities. At present, this species seems to be rather distinct from *D. tapetodes*, and *D. trinervia*, as it has ± loose filiform sclereids and also possesses some polymorphic sclereids which have not been found in the other two species. The loose arrangement of filiform sclereids in *D. denticulata* could be due to the comparatively large size of the lamina. It is possible that if a larger number of leaf specimens were examined the anatomical differences between *D. denticulata* and *D. tapetodes* and *D. trinervia* might disappear. The close relationship between these three species forming subsect. *Tapetodes*, as well as the distinctness of the group, is substantiated by the anatomical investigations.

7. *D. lindbergii* (Wendelbo 1961:78) was granted a monotypic subsection, *Heterotrichae*, because of several unusual features. Wendelbo later (1964: fig. 13 & p. 15) suggested that there might be a relationship between it and

species of *Dionysiastrum*. However, the present study did not support this since all the species of sect. *Dionysiastrum* lack sclereids and *D. lindbergii* is the only species in the genus with terminal sclereids.

8. It is of great interest from a phytogeographical point of view that both *D. bornmuelleri* and *D. teucrioides*, considered to be the most primitive species of the north-west migration branch of the genus (Wendelbo 1961: 24ff), both lack sclereids as do all the species of subsect. *Revolutae* which are considered as being derived from the former branch. *D. balsamea*, *D. paradoxa* and *D. lacei*, which are the primitive large-leaved species of the north eastern migratory branch, have sclereids as do the species of *Tapetodes* which are thought to have evolved from them. *D. saponacea*, the most advanced of the large-leaved north-eastern species, lacks sclereids and thus disturbs this otherwise very clear pattern.

9. Wendelbo (1961:25) suggested that subsect. *Bryomorphae* had its origin within subsect. *Caespitosae*. As the species of the first section lack sclereids, and those of the second have them, it seems more likely that both of these groups have arisen from sect. *Anacamptophyllum* where sclereids are absent. The sclereids of subsect. *Caespitosae* are so different from those of the north-eastern species that there is no reason to propose a connection here.

10. *D. mira*, which was considered to be the most primitive of the species of the genus, lacks sclereids. This Omani species has a powdery farina which, in the genus, it only shares with *D. microphylla* and *D. hedgei*, the two most primitive species of sect. *Dionysiastrum*; the species of this section also lack sclereids. It may not be too much to hope that a new species of the genus with a several-flowered inflorescence, large leaves lacking sclereids and with powdery farina will be found in the mountains of southern central Afghanistan —the missing link to connect the species of sect. *Dionysiastrum* with *D. mira*. So many finds corroborating earlier theories on the phylogeny of this genus have been made since the monograph of the genus was published 15 years ago, that this would not be too much of a surprise.

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## APPENDIX

*Dionysia* species investigated; listed in alphabetical order.

*D. afghanica*: Afghanistan, prov. Maymana, Darreh Zang, Grey-Wilson & Hewer 1308. *D. archibaldii*: Iran, C. Zagros mts, Hewer 2089, 2095. *D. aretioides*: Iran, Sarii 7887, Wendelbo & Shirdelpur 11710, 15224.

*D. balsamea*: Afghanistan, prov. Herat, Hedge, Wendelbo & Ekberg, W. 7801. *D. bornmuelleri*: Iraq, district Mosul, Sharanish, Rechinger 11485. *D. bryoides*: Iran, S Zagros mts, Kuh-i-Dinar, Hewer 2053, 2054. *D. bryoides × termeana*: Iran, S Zagros mts, Kuh-i-Dinar. Hewer 2051, 2055.

*D. caespitosa*: Iran, Bakhtiari Country, Wendelbo 1754, Iranshahr & Moussavi, Iranshahr 8133E. *D. curviflora*: Iran, Foroughi 7896, 7898, Yazd, Shirkuh, Archibald 1146.

*D. denticulata*: Afghanistan, prov. Bamian, Panjao, Hedge & Wendelbo, W. 4995. *D. diapensiifolia*: Iran, Shiraz, Bokhari 421.

*D. esfandiarii*: Iran, Fars, Abadeh, Termé & Izadyer 8128E.

*D. freitagii*: Afghanistan, prov. Balkh, Ali Kuh. Hedge, Wendelbo & Ekberg, W. 8497; Kuh e Elburz, Grey-Wilson & Hewer 833.

*D. gaubae*: Iran, Lorestan, near Khorramabad, Archibald 1633.

*D. hedgei*: Afghanistan, prov. Mazar-i-Sharif, Kuhe Elburz. Hedge & Wendelbo, W. 3888; Grey-Wilson & Hewer 836. *D. haussknechtii*: Iran, Wendelbo & Assadi, 16427.

*D. iranshahrii*: Iran, Bakhtiari, Kuhe Pashmaku, Iranshahr.

*D. janthina*: Iran, Yazd, Shir Kuh, Archibald 1153.

*D. lacei*: Pakistan, Beluchistan, Torkhan Pass, Lamond 1258. *D. lamingtonii*: Iran, Shahreza, Hewer 1109. *D. leucotricha*: Iran, Wendelbo & Assadi 16465. *D. lindbergii*: Afghanistan, prov. Maymana, Darreh Zang, Hedge & Wendelbo, W. 3740.

*D. michauxii*: Iran, Shiraz, Bokhari 429. *D. microphylla*: Afghanistan, prov. Maymana, Darreh Abdullah, Hedge & Wendelbo 3710; Darreh Zang, Hedge & Wendelbo 3721. *D. mira*: Oman, Jebel Akhtar massif, Deacock 16.

*D. odora*: Iran, Wendelbo & Assadi 16761; Kermanshah, Moussavi & Safai (Evin). *D. oreodoxa*: Iran, Kerman, Kuhe Hosseinabad. Archibald 1165.

*D. paradoxa*: Afghanistan, Kapisa near Sarobi, Hedge, Wendelbo & Ekberg 7496.

*D. revoluta*: Iran, Bakhtiari, Moussavi (Evin). *D. rhaptodes*: Iran, Wendelbo & Foroughi.

*D. saponacea*: Afghanistan, prov. Ghorat, Kuhe Tscheling-Safed, Rechinger 19093.

*D. tapetodes*: Afghanistan, prov. Takhar, Darreh-i-Ransch, Ekberg, W. 9128; prov. Badakhshan, Khumbak Bala, Hedge & Wendelbo 9454; prov. Parvan, Panjshir Valley. Wendelbo 5273. Iran: Mashad, Ardagh-Tolgher Iranshahr, Rowshan 8703. *D. termeana*: Iran, prov. Fars, Sisakht, Kuhe Daena, Termé & Izadyer 8131; Hewer 2054, 1994; Zarghani; Riazi 10327. *D. teucrioides*: Turkey, Cheese & Watson 68, 3169B (Cultivated at Botanic Garden, Göteborg). *D. trinervia*: Afghanistan, prov. Orozgan, Rechinger 35240.

*D. viscidula*: Afghanistan, prov. Maymana, Darreh-Zang, Hedge & Wendelbo, W. 3722.

*D. zagrica*: Iran, S. Zagros mts, Kuhi-Sehqua, Hewer 2023.

In addition to the herbarium specimens listed, a quantity of fresh or preserved material of *D. michauxii*, *D. bryoides*, *D. revoluta* and *D. diapensiifolia* was examined. These four species are common around Shiraz.