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ANATOMY OF DIONYSIA II. XEROMORPHIC FEATURES

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ABSTRACT. The xeromorphic characters found in the predominantly Irano-Turanian genus *Dionysia* (Primulaceae) are described and discussed, with particular reference to anatomical features of leaves. A cushion-like habit is common to most species but other xeromorphic features are found in various combinations according to species and, to a large extent, subsection or section. The additional features identified are: reduced leaves; revolute leaf margins; dense indumentum; sunken stomata; stomata in grooves or pits; thick cuticle and cutinized epidermis; extensive development of palisade at expense of spongy tissue; mesophyll of small, compactly arranged cells; tracheoides; and well developed mechanical tissues (sclereids and fibres).

The results of this study generally support the previous overall views on phylogeny and evolution within the genus, but with the new data some earlier suppositions are questioned.

INTRODUCTION

Dionysia is a genus of 43 fruticulose species endemic to the Irano-Turanian floristic region, but with an enclave in the mountains of Oman (Wendelbo, 1971). These species are loosely or compactly tufted chasmophytes growing on the cliff walls of the mountains of, and surrounding the Iranian highlands. In most cases the cliffs apparently remain dry during long periods of the year so that plants inhabiting them must tolerate conditions of adverse water balance. The different species of *Dionysia* show various, ± diverse morpho-anatomical features which have been considered in plants to be adaptations to a life in dry habitats (Pyykkö, 1966; Bocher & Lyshede, 1968, 1972; Fahn, 1974). *D. microphylla* and *D. hedgei* have already been investigated for their xeromorphic features by Wendelbo (1971), and the present work extends that study to most other species of the genus. Our previous paper on the anatomy of *Dionysia* (Bokhari & Wendelbo, 1976) dealt with the taxonomic significance of various types of foliar sclereids.

Xeromorphic features are those characters which are genetically fixed and are developed in plants connected with dry habitats (Bocher & Lyshede, 1972). All plants inhabiting hot and dry places have a more or less definite water economy strategy based upon an interaction of numerous physiological and morpho-anatomical characters which cannot be discussed in isolation. The morpho-anatomical characters have in reality a physiological basis. The main problem confronting plants of dry habitats is a condition of adverse water balance which is countered by various combinations of xeromorphic features. Besides the cushion habit which is more or less common to all *Dionysia* species, the remaining xeromorphic features have been found in differing combinations.

MATERIALS & METHODS

This study is mainly based on herbarium material which was revived and prepared for sectioning and clearing as described in Bokhari (1970).

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The appendix in Bokhari & Wendelbo (1976) lists the specimens of various species examined for xeromorphic features. Scanning through the anatomy of the different species a few special features have been discovered that can be compared to the conditions in *D. hedgei* and *D. microphylla* (Wendelbo, 1971). However the more common xeromorphic features, ± well-developed in the different species and in different combinations, are discussed here.

XEROMORPHIC FEATURES

CUSHION HABIT: Many plants living under adverse water balance conditions are cushion plants (*Acantholimon, Astragalus, Acanthophyllum* etc.). As with such plants, the stem of *Dionysia* branches almost at the base, producing many short, densely leafy twigs which are usually tightly gathered to form lax or compact cushions. These cushions create within themselves a special regime of moisture and temperature, while also minimizing evaporation, restricting the interchange of air within themselves, and effectively checking desiccation by dry hot winds (Zalensky, 1948). Under arid conditions a compact cushion is more advantageous than a lax cushion. In *Dionysia*, the specialized species inhabiting drier areas, besides possessing many other correlated xeromorphic features, are also the more compactly cushioned in habit; e.g. *D. tapetodes, D. trinervia, D. curviflora, D. janthina, D. rhaptodes*. A formation of soil from rock debris is collected inside the tufts, and in *D. tapetodes* there is a development of adventitious roots from the branches into this soil. The more loosely tufted species (especially *D. bornmuelleri*) are found on ± wet cliff walls.

REDUCTION IN LEAF SURFACE: One of the most distinct properties of xeromorphic leaves is their possession of a minimized external surface area in comparison to their volume (Weaver & Clements, 1938; Orshan, 1954). This feature is a highly effective adaptation to prolonged drought because it reduces the transpiring surface area of the plant, and is well exemplified by many *Dionysia* spp. (e.g. *D. afghanica, D. iranshahrii, D. lamingtonii, D. lindbergii, D. microphylla, D. trinervia, D. curviflora*, and *D. rhaptodes*). In addition, the leaves of these species are closely imbricate so that only a part of leaf surface is actually exposed to the atmosphere. A closely overlapping, small-leaved condition is an important xeromorphic feature in *Dionysia*; and in most species the lower parts of the branches are clothed by closely overlapping marcescent leaves, thereby precluding the possibility of water loss directly from the stem branches.

INDUMENTUM: Hairiness is one of the most characteristic xeromorphic features of plants of arid regions. In *Dionysia* the hairs are of two types: long, simple articulated hairs, and glandular hairs which may be short or long. In many species the leaves are densely clothed with these hairs (Fig. 1). Indumentum has been considered to affect transpiration directly through its influence on the water diffusion boundary layer of the transpiring surface of a leaf (Johnson, 1975; Woolley, 1964). Indumentum has also been implicated in the temperature regulation of transpiring surfaces either by reducing the absorption of radiant energy or by

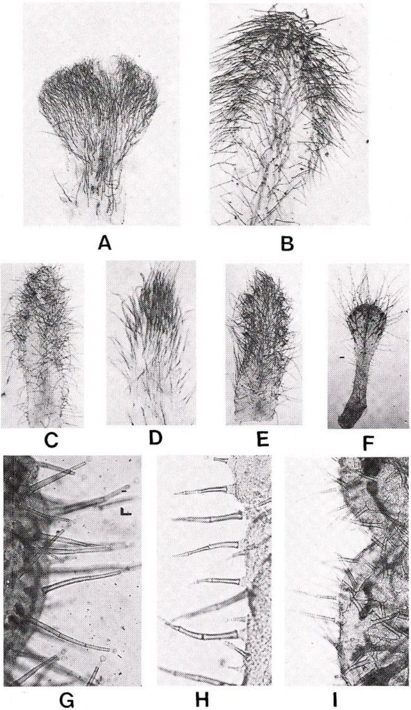

FIG. 1. A–F. Cleared leaves showing density of indumentum: A, *D. janthina*, ×20; B, *D. esfandiarii*, ×20; C, *D. aretioides*, ×10; D, *D. iranshahrii*, ×20; E, *D. leucotricha*, ×10; F, *D. lindbergii*, ×10. G–I. Dominant types of hairs on the leaves: G, *D. teucrioides*, ×200; H, *D. archibaldii*, ×200; I, *D. revoluta*, ×200.

reducing its dissipation once it has been absorbed. These postulated reductions are believed to result from the high reflectance property of indumentum. A dense cover of dead, air-filled trichomes which reflects radiation and produces an isolating layer on the surface has been described in a species of *Tetradymia* (Bocher & Lyshede, 1972). Atay (1958) studied the influence of the contents of ethereal oils in air on evaporation and transpiration, and found that the evaporation rate from a water surface was lowered by 8% when the air above contained a small amount of oils. In species of *Dionysia* an effect of this kind is possible because the glandular hairs are usually short and positioned close to stomatal openings, and are, in most cases, under a dense covering of simple, articulated hairs. In such a situation a layer of air over stomata could contain sufficient oils to reduce transpiration. This is likely to be much more pronounced in those species of *Dionysia* where stomata are confined to the stomatal grooves and stomatal pits; such as in *D. viscidula, D. freitagii* and *D. microphylla* (Figs 8A, B; 9A). In these species glandular hairs (farinipotent glands) are present on the 'floor', along the walls, and on the margins of the stomatal grooves and stomatal pits; and the glandular hairs which are on the margins arch over the grooves or pits, thereby also protecting the stomata.

PROTECTION OF STOMATA: The water loss from a leaf depends upon the temperature of leaf tissue. This temperature depends first and foremost on the intensity of light and radiation energy hitting the leaf epidermis and reaching the tissues, and secondly on the velocity of surrounding air currents. Volkens (1887, 1890) insisted on the important reduction in the transpiration rate which must result if water supply lags behind transpiration. As most of the water transpired by leaves is lost through stomata, so transpiration can be effectively reduced if stomata are protected against intense sunlight and dry air currents. In *Dionysia,* a dense indumentum can considerably reduce the effects of radiation and surrounding dry air currents: a covering of dead hairs projecting from the leaf surface keeps air currents well elevated above the stomata thus slowing down transpiration.

In the present investigation we discovered various structural characteristics for affording protection to stomata and these constitute important xeromorphic features.

a. *Sunken stomata.* These are found in many species, e.g. *Dionysia viscidula, D. freitagii, D. microphylla* and *D. michauxii* (Figs 8A, B; 9A, Aa, B, Ba). Stomata sunken below the level of the epidermal surface are well below the level of atmospheric turbulence, and plants with this characteristic have generally been found capable of reducing transpiration (Daubenmire, 1974:146).

b. *Stomata protected by revolute leaf margins.* In all species of subsect. *Revolutae* stomata are confined to the lower leaf surface, and hence protected from strong sunlight and dry air currents by the ± revolute leaf margins (Fig. 6A).

c. *Stomata in stomatal grooves or pits.* We have made a distinction between the stomatal grooves and stomatal pits which are both characteristically found on the adaxial leaf surfaces of species in sect.

Dionysiastrum. *Stomatal grooves* lie between the ridges produced by raised nerves and are open at one end (Figs 5C, 7A–C). *Stomatal pits* are similarly situated but are small, elongated or oblong cavities closed at both ends (Figs 5F, 7B–D). Both structures are found in *D. freitagii* (Figs 5F, 7B) and *D. hedgei* (Fig. 7C), but *D. viscidula* (Figs 5C, 7A) has only stomatal grooves. Conversely, the highly xeromorphic *D. microphylla* has just a few stomatal pits (Figs 7D, 9A). The stomata are mostly confined to the floors of the grooves or pits (Figs 5A, D; 8A, B) where they are also sunken below the epidermal surface (see above). In addition, the grooves and pits have their walls and floors provided with glandular hairs (Fig. 8A, B) and they are also filled with powdery farina. This combination of protective features is advantageous to plants during periods of water stress because the resistance to water vapours through the stomata is increased by lengthening the distance to the overall surface.

REVOLUTE LEAF MARGINS: These are characteristic of subsect. *Revolutae*, and provide an important xeromorphic feature in two ways. Firstly, by effectively protecting stomata (see above), and secondly, by considerably reducing the exposed, external surface of the leaf. From observations on *D. revoluta*, there is some evidence that these leaf margins become more revolute during dry hot days and under conditions of adverse water balance. Leaves collected at about 4 p.m. on a hot day were sectioned in the field and it was found that there was some shrinkage of cell walls of abaxial epidermal cells and neighbouring mesophyll cells in the revolute parts. This type of shrinkage could increase the inrolling of the leaf margin, but more experimental work is needed to corroborate this finding.

CUTICLE AND CUTINIZED EPIDERMIS: A thick cuticle and a cutinized epidermis are considered to be distinctive xeromorphic features as they are very common in plants of dry habitats. *Cuticle* is a layer of pure cutin (a fatty substance almost impermeable to water) deposited on the outer walls of the epidermal cells. *Cutinized epidermis* is formed by the deposition of cutin and wax in the intermicellar and interfibrillar spaces of cellulose of cell walls (Skoss, 1955; Treiber, 1955). The outermost walls of the epidermal cells which are impregnated with cutin and wax comprise what is called a *cuticular layer*. Many species of *Dionysia* have a thick cuticle and a strongly cutinized epidermis. In some species such as *D. revoluta* the adaxial epidermis has a thick cuticle and only the outermost walls of this epidermis are cutinized (Fig. 6A). In *D. microphylla* the abaxial epidermis has a thick cuticle and all its cell walls are strongly cutinized, but its adaxial epidermis has a thin cuticle and is not cutinized (Fig. 9A, Aa). In *D. michauxii* and many other species both sides have a cuticle overlaying an epidermis cutinized in its outermost walls only (Fig. 9B, Ba). In others such as *D. viscidula, D. freitagii* (Figs 5A, B, D, E; 8A, Aa, B, Ba) and *D. hedgei,* both surfaces have a well-developed cuticle and all walls of the epidermal cells very strongly cutinized. Well-developed cuticle and cutinized epidermis are also found in those species where leaf size is considerably reduced.

Stomatal transpiration is physiologically controlled and under water stress it can be checked by closing the stomata. Cuticular transpiration is generally less significant but it can often be fatal to a plant as it is beyond the reach of physiological control (Stålfelt, 1956). When stomatal transpiration is checked the reduction in cuticular transpiration from the epidermal walls can become decidedly important in resisting desiccation. In cutinized epidermis, wax plates are intimately interwoven with the highly polymerous meshes of cutin macromolecules, such that if the whole structure shrinks in a dry atmosphere it becomes practically impermeable to water. In xeromorphic leaves with strongly developed cuticle, initial dehydration by air is of fundamental importance since it results in the irreversible shrinkage of cuticular layers which become compact and almost impermeable to water (Gaumann & Jagg, 1936). Kamp (1930) established the important fact that cuticular transpiration is more or less inversely proportional to the thickness of the cuticle and cutinized walls, and Starr (1912) has assumed that cuticular transpiration takes place more abundantly from the side-walls of the epidermal cells. Therefore, it can be postulated that *Dionysia* species in which all the epidermal walls are strongly cutinized can control more effectively the cuticular transpiration than can those in which only the outer walls have cuticle and are cutinized. A thick cuticle and cutinized epidermis may also afford protection against the mechanical action of the wind; and they undoubtedly help to prevent the leaf from collapsing following water loss (Davies, 1955; Pisek, 1960).

MESOPHYLL TISSUE: Extensive development of palisade parenchyma at the expense of spongy parenchyma has been considered, in dicotyledons, to be a xeromorphic feature (Shield, 1950, 1951; Esau, 1965; Fahn, 1974; Wylie, 1951). Palisade parenchyma occurs in greatest amount in isobilateral leaves, in which such tissue is in both sides of the leaf or is the sole component of the mesophyll. Its cells are compactly arranged and have much smaller intercellular spaces than those of spongy parenchyma. Some species of sect. *Dionysiastrum,* such as *D. freitagii* (Figs 5D, E; 8B), have more than one layer of palisade in both sides of the leaf. In this section the presence of ridges on the adaxial side is a beneficial character since it increases the internal area of the leaf by accommodating more palisade tissue. In *D. michauxii* (Figs 2Ab; 9B) and some other species the mesophyll is entirely composed of palisade parenchyma. Intense light (Wylie, 1951; Hanson, 1917) and adverse water balance in soil (Amer & William, 1958) are two main causative factors suggested for the evolution of the extensive development of palisade tissue. Palisade parenchyma cells have two advantages. Firstly, chloroplasts in palisade tissues behind a highly diffusing epidermis are subjected to a light intensity which is directly proportional to the cell diameter, hence narrow palisade cells offer more protection to chloroplasts against intense illumination. Secondly, as the water supply becomes depleted there develops a resistance to flow, which is greater in passage from one cell to another than in minor veins (Maximov, 1929). Large intercellular spaces, as those of spongy parenchyma, handicap diffusion through the mesophyll. Thus, in xeromorphic leaves, narrow, well-developed palisade cells with small interstices minimize resistance to water flow in the mesophyll (Nius, 1931). According to Thoday (1931) decreased internal resistance in xeromorphic leaves is more significant than a reduction of surface area.

Extreme xerophytes have a highly compact mesophyll composed of small cells with small interstices, as is the case with highly specialized species such as *D. microphylla* (Fig. 9A), *D. tapetodes* (Fig. 4C), *D. denticulata* (Fig. 4E), and many others. The small cell size is also thought to possess significance chiefly as regards resistance to desiccation (Stålfelt, 1956), and according to Daubenmire (1974) it is quite possible that in a tissue composed of small cells, a given degree of dehydration has less tendency to pull the protoplast away from the cell wall and rupture plasmodesmata.

VENATION: A dense venation in leaf lamina is a xeromorphic feature found in many species, e.g. *Dionysia michauxii, D. lamingtonii, D. zagrica. D. diapensifolia, D. gaubae,* and *D. odora* (Fig. 2A, D–F). A copiously branched, dense network of venation is supposed to decrease the internal resistance to water flow in the mesophyll: an important facility for plants of hot, arid habitats, for no part of the mesophyll is then more than a very short distance away from the main channels of water supply. In species of *Dionysia* with considerably reduced leaves, the reduction in leaf surface is accompanied by a reduction in venation. For example, in *D. lamingtonii* (Fig. 2B), *D. zagrica* (Fig. 2C), and species like *D. microphylla, D. iranshahrii, D. afghanica* and *D. lindbergii,* the main vascular bundle of the leaf is branched in the upper half of the lamina only, and there is little or no subsequent branching.

TRACHEOIDS: In many genera of Dictotyledons differently shaped tracheid-like cells, frequently with pitted walls, terminate the veinlets. These are interpreted as water reservoirs and have also been called *storage tracheids* (Pirwitz, 1931; Solereder, 1908). In *Dionysia* they have been observed in *D. lindbergii* (Fig. 4F), *D. teucrioides* (Fig. 4H), *D. saponacea* (Fig. 4I) and in all species of subsect. *Revolutae*. In subsect. *Revolutae* they are developed in the revolute margins of the leaf (Fig. 6A–B) where they have added protection against strong sunlight.

MECHANICAL TISSUES: An abundant development of sclerenchyma is a common xeromorphic feature in plants of arid habitats and is thought to reduce the injurious effect of wilting (Stålfelt, 1956). In some *Dionysia* spp. there is a relatively large development of sclerenchyma in the form of fibres or sclereids. The sclerified tissues occur in association with vascular tissues, in the mesophyll, or in the epidermis.

a. *Fibres associated with veins*: in *D. michauxii* (Fig. 2A, Aa, Ab), *D. lamingtonii* (Fig. 2B) and *D. zagrica* (Fig. 2C), all veins in the upper half of the leaf lamina are accompanied by groups of fibres which form fibrous caps on the adaxial sides of the veins. The exact position of these fibrous caps is clear only in cross-sections of leaves (Fig. 2Aa, Ab).

b. *Sclereids associated with veins*: in species of sect. *Caespitosae* there is an extensive development of sclereids along the veins, as well as at the vein-endings, so that the entire vascular tissue is accompanied by sclerified tissue, e.g. *D. diapensifolia, D. gaubae* and *D. odora* (Fig. 2D–F, Da–Fa).

c. *Sclereids in the mesophyll*: in species of sect. *Tapetodes* there is abundant development of sclereids throughout the mesophyll. They are arranged parallel to the long axis of the leaf lamina and are not connected with the veins; e.g. *D. tapetodes* and *D. denticulata* (Fig. 4A–E). In *D.*

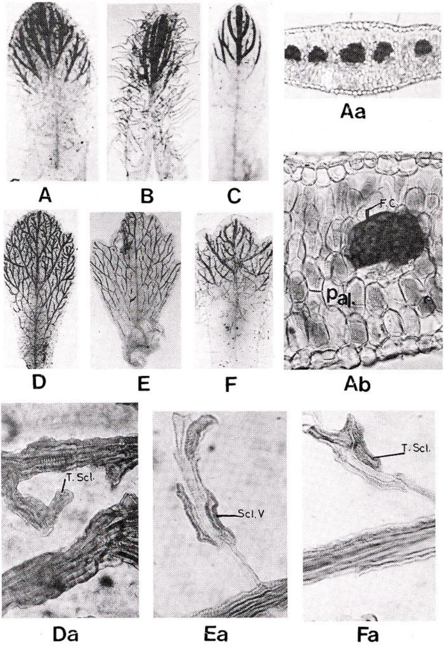

FIG. 2. A–F. Cleared leaves showing the presence of sclerified tissue along the veins: A, *D. michauxii*, ×15; B, *D. lamingtonii*, ×20; C, *D. zagrica*, ×15; D, *D. diapensiifolia*, ×10; E, *D. gaubae*, ×10; F, *D. odora*, ×15. Aa, Ab. Cross-section of leaf of *D. michauxii* showing fibrous cap on the adaxial side of the vascular bundles and mesophyll entirely of palisade tissue (×200 & ×800). Da–Fa. Part of cleared leaves showing position of sclereids (all ×800): Da, *D. diapensiifolia*; Ea, *D. gaubae*; Fa, *D. odora*. F.c. = fibrous cap; Pal. = palisade tissue; Scl. V. = sclereids along veins; T. Scl. = terminal sclereids.

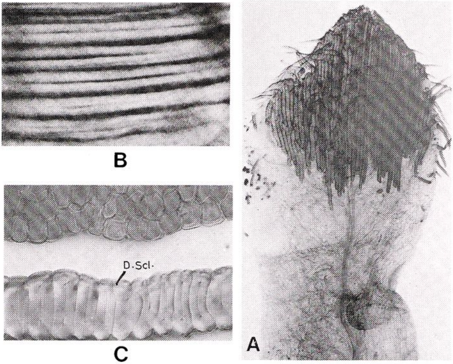

FIG. 3. *D. curviflora*: A, cleared leaf showing entire abaxial epidermis sclerified in the upper region, × 100; B, part of cleared leaves showing types of dermal sclereids, × 400; C, cross-section of leaf showing dermal sclereids, × 800. D. Scl. = dermal sclereids.

paradoxa (Fig. 4G) and *D. balsamea* of sect. *Anacamptophyllum* subsect. *Scaposae,* sclereids are irregularly scattered in the mesophyll.

d. *Sclereids in the epidermis*: dermal sclereids have been reported in *D. curviflora* (Bokhari & Wendelbo, 1976). In this species the leaves are closely overlapping, with only the apical part of the lower surface directly exposed to sunlight. Here the lower (abaxial) epidermis is entirely sclerified forming an efficient barrier against water loss (Fig. 3A–C).

The cell walls of fibres and sclereids are very thick and rich in cellulose, hemicelluloses and lignin. The question of the significance of mechanical tissue for xerophytes has been widely discussed in the literature. According to Porsch (1926) the entire physiological significance of lignification lies ultimately in the water retaining capacity of the cell wall. In fact the lignified cell wall is never completely desiccated, owing to its high water binding capacity. The presence of hemicelluloses with their high hydration capacity and water retentivity may be associated with drought resistance; and the high lignification of thick cell walls prevents collapse in states of high water loss (Davies, 1955). Lignification is now interpreted as an alternative to turgidity of fleshy tissue (Oppenheimer, 1960). The mechanical tissue also sustains the leaf, preventing wind from bending it, by which air containing water vapours could be pumped out of intercellular spaces.

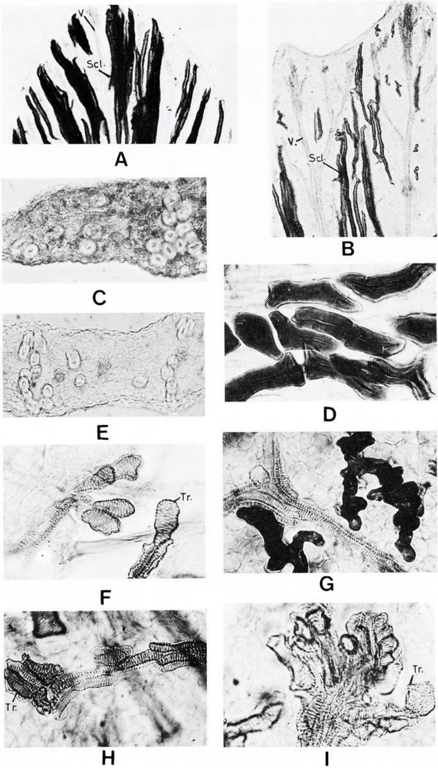

FIG. 4. A, part of cleared leaf of *D. tapetodes* showing sclereids in relation to veins, × 150; B, part of cleared leaf of *D. denticulata* showing sclereids in relation to veins, × 150; C, cross-section of leaf of *D. tapetodes* showing sclereids, × 400; D, cleared basal part of *D. tapetodes* leaf showing sclereids, × 800; E, cross-section of leaf of *D. denticulata* showing sclereids, × 400; F, part of cleared leaf of *D. lindbergii* with tracheoids, × 600; G, part of cleared leaf of *D. paradoxa* showing sclereids, × 800; H, part of cleared leaf of *D. teucrioides* with tracheoids, × 800; I, part of cleared leaf of *D. saponacea* with tracheoids, × 800. Tr. = tracheoids; Scl. = sclereids; V. = veins.

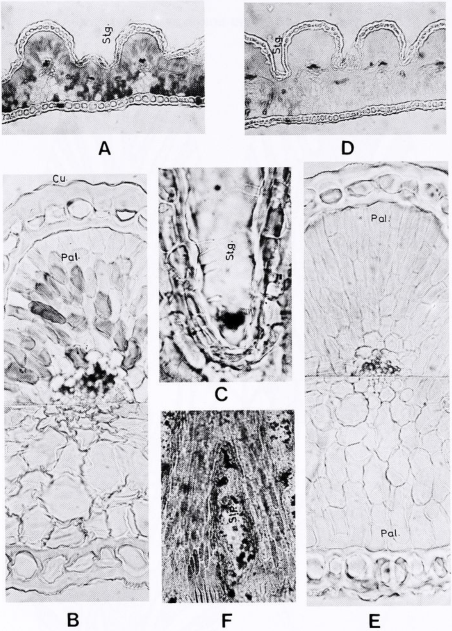

FIG. 5. A–C, *D. viscidula*: A, cross-section of leaf showing stomatal grooves, ×200; B, cross-section of leaf showing thick cuticle and palisade on the adaxial leaf surface, ×800; C, part of cleared leaf showing one stomatal groove, ×300. D–F, *D. freitagii*: D, cross-section of leaf showing stomatal groove, ×200; E, cross-section of leaf showing thick cuticle and palisade on both sides of leaf, ×800; F, part of cleared leaf showing one stomatal pit, ×300. Cu. = cuticle; Pal. = palisade; St. g. = stomatal groove; St. p. = stomatal pit.

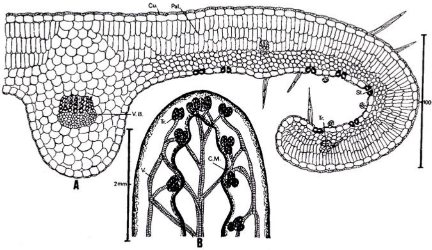

FIG. 6. *D. revoluta*: A, cross-section of leaf showing curved margin and distribution of stomata; B, upper part of leaf cleared to show the tracheoids protected by curved margins. C.M. = curved margin; Cu. = cuticle; Pal. = palisade; St. = stomata; Tr. = tracheoids; V. = vein; V.B. = vascular bundle.

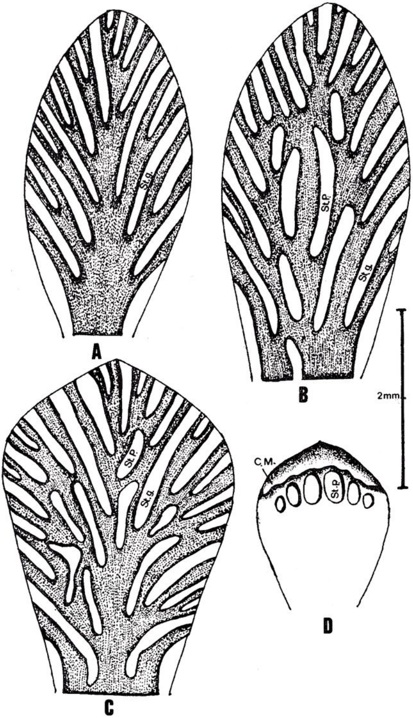

FIG. 7. Cleared leaves showing distribution of stomatal grooves and stomatal pits on the upper surface: A, *D. viscidula*; B, *D. freitagii*; C, *D. hedgei*; D, *D. microphylla*; C.M. = curved margin; St. g. = stomatal groove; St. p. = stomatal pit.

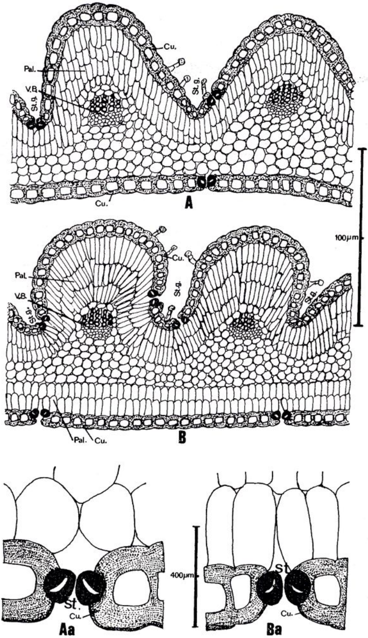

FIG. 8. A, cross-section of leaf of *D. viscidula*; B, cross-section of leaf of *D. freitagii*; Aa, part of lower epidermis of *D. viscidula* with sunken stomata; Ba, part of lower epidermis of *D. freitagii* with sunken stomata. Cu = cuticle; Pal. = palisade; St. = stomata; St. g. = stomatal groove; V.B. = vascular bundle.

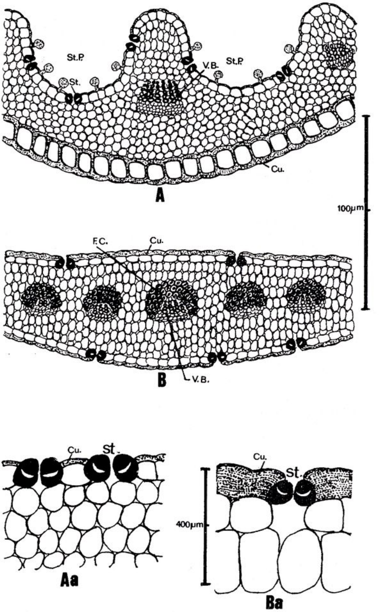

FIG. 9. A, cross-section of leaf of *D. microphylla* showing stomatal pit and thick-walled abaxial epidermis; B, cross-section of leaf of *D. michauxii* showing fibrous caps on the adaxial side of vascular bundles and mesophyll of all palisade tissue. Aa, part of upper leaf epidermis of *D. microphylla* showing thin-cuticle and stomata at level with the epidermis; Ab, part of upper leaf epidermis of *D. michauxii* showing thick cuticle and sunken stomata. Cu. = cuticle; F.C. = fibrous cap; Pal. = palisade tissue; St. = stomata; St. p. = stomatal pit; V.B. = vascular bundle.

INFRAGENERIC CLASSIFICATION/XEROMORPHIC FEATURES

1. sect. **Anacamptophyllum**

a. subsect. **Mirae**: the single species, *D. mira,* exhibits the least specialization in the genus. However, it shows some xeromorphic features: (1) raised nerves on lower side of the leaf enclosing certain areas in which stomata are confined; (2) trichomes covering both leaf surfaces.

b. subsect. **Scaposae**: all species have trichomes covering both leaf surfaces but other xeromorphic features are not common to all species. *D. bornmuelleri* has raised nerves on lower side of the leaf enclosing areas in which stomata are confined. *D. teucrioides* and *D. saponacea* have groups of tracheoids in the leaf. *D. paradoxa* and *D. balsamea* have diffused sclereids in the leaf mesophyll. *D. lacei* shows no additional specialized xeromorphic features.

c. subsect. **Revolutae**: revolute leaf margins lead to considerable reduction in exposed leaf surface. This character is accompanied by: (1) stomata confined to abaxial leaf surface and mostly located below the revolute margins; (2) well-developed cuticle and outer walls of the adaxial epidermal cells cutinized; (3) presence of tracheoids in the revolute margins. In *D. rhaptodes,* besides all the aforementioned characters, the leaf is considerably reduced so it is the most specialized species of this section.

2. sect. **Dionysiastrum**: there are stomatal grooves or stomatal pits, in the floor of which the stomata are mostly confined. This character is associated with: (1) thick cuticle or cutinized adaxial and abaxial epidermis (except *D. microphylla* in which only the abaxial side has a cutinized epidermis and thick cuticle); (2) stomata sunken below the epidermis; (3) extensively developed palisade parenchyma at the expense of spongy parenchyma (except *D. microphylla* in which the mesophyll is composed of small, compactly arranged cells); (4) presence of glandular hairs in the stomatal grooves and stomatal pits. *D. microphylla* has very small, densely overlapping leaves with a few stomatal pits on the adaxial concave side of the lamina, and is regarded as the most highly specialized species in this section.

3. sect. **Dionysia**

a. subsect. **Caespitosae**: all the species investigated have a densely branched network of veins with accompanying sclereids. These species also have: (1) well-developed cuticle and cutinized outer walls of the adaxial and abaxial epidermis; (2) sunken stomata; (3) mesophyll entirely of small compactly arranged cells.

b. subsect. **Bryomorphae**: no single xeromorphic feature is common to all species. In *D. michauxii, D. lamingtonii* and *D. zagrica* the veins in the upper half of the lamina are always accompanied by fibrous caps on their adaxial sides, and in addition these species have: (1) sunken stomata; (2) thick cuticle and cutinized outer walls of abaxial and adaxial epidermis; (3) mesophyll of small compactly arranged cells. *D. janthina* has: (1) leaves considerably reduced, densely clothed on both sides with trichomes; (2) mesophyll of small-sized, compact cells; (3) sunken stomata; (4) thick cuticle and cutinized outer walls of abaxial and adaxial epidermis. In *D.*

curviflora: (1) leaves very small, closely overlapping, and densely clothed with trichomes on the adaxial surface; (2) abaxial epidermis of apical portion of the lamina entirely sclerified with very thick walls; (3) stomata confined to the adaxial surface of upper epidermis of the overlapping leaves; (4) mesophyll entirely composed of palisade; (5) sunken stomata. In the remaining species of this subsection such combinations of xeromorphic characters are not found. *D. curviflora* appears to be the most specialized species of the subsection.

c. subsect. **Tapetodes**: all species characterized by the presence in the mesophyll of sclereids which have no connection with the veins and are orientated parallel to the long axis of the leaf. These species have also: (1) sunken stomata; (2) mesophyll of small-sized, compactly arranged cells; (3) thick cuticle and cutinized outer walls of the abaxial and adaxial epidermis. *D. trinervia* with reduced leaves and nervation is the most specialized species of this subsection.

d. subsect. **Heterotrichae**: the single species, *D. lindbergii* has small leaves and reduced nervation. This character is accompanied by: (1) leaves densely clothed with trichomes on both sides; (2) well-developed cuticle and cutinized epidermis on both surfaces; (3) small-sized compact mesophyll cells; (4) tracheoides in leaf.

As we have seen in all sections having xeromorphic species, there is a general trend in the reduction of the leaf surface, and in most cases the small leaves are also densely clothed with trichomes. These two xeromorphic features are of considerable importance to the water economy of plants

SOME PHYLOGENETIC CONSIDERATIONS

The present study generally supports the supposed phylogeny and evolution as proposed by Wendelbo (1961, 1964). It is quite clear from the above-mentioned account that most of the species in stage III of his diagram (Wendelbo, 1961, fig. 7; 1964, fig. 12) are morphologically and anatomically the more highly specialized group of species. But in *D. bryoides* and *D. haussknechtii* we could not find the combination of these specialized characters which have been found in other species, or group of species, of this stage. In his supposed phylogeny and relationship of the eastern species (Wendelbo, 1964, fig. 13), *D. viscidula* is shown at a higher evolutionary level than *D. hedgei* and *D. microphylla*. The present study has revealed that, anatomically, *D. viscidula* is the least specialized species in sect. *Dionysiastrum* because its leaves have only stomatal grooves and are bifacial (i.e. palisade tissue is confined to the adaxial side of the leaf); whereas in *D. hedgei* and *D. freitagii* these stomatal grooves are interspersed with the stomatal pits and the leaves are isobilateral in which well-developed palisade tissue is present in both sides. Stomatal pits are decidedly more specialized structures than the stomatal grooves and there is no doubt that the isobilateral condition is more specialized than the bifacial one. So it appears that *D. viscidula* is at a lower evolutionary level than *D. hedgei* and *D. freitagii*. One can confidently say that *D. microphylla* is a highly specialized species in this section, as is evident from its reduced leaf size, and closely overlapping leaves with concave adaxial surfaces (only parts of abaxial surfaces being directly exposed to sunlight). It has only a few stomatal pits, which are restricted to the adaxial concave side, and, in which the stomata are confined. Furthermore, the epidermal cells of the adaxial side are strongly cuticulized and cutinized. Anatomically, *D. afghanica* is not related to any other species of sect. *Dionysiastrum*: its leaves are very much reduced but are without stomatal grooves or stomatal pits; its position under this section seems doubtful.

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