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On xeromorphic adaptations in the genus *Dionysia* (*Primulaceae*)

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(Mit 2 Textabbildungen)

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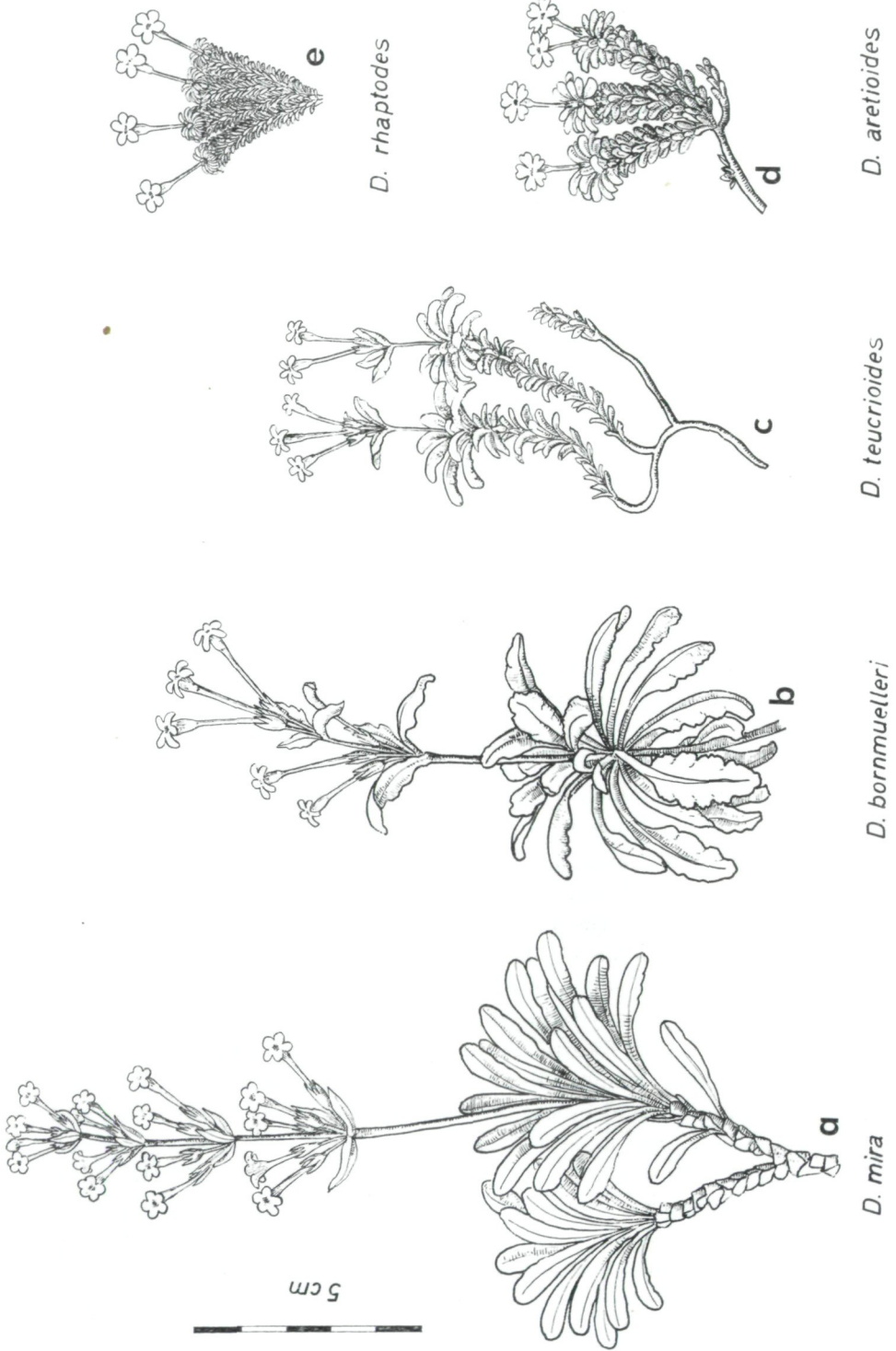
Abstract

Dionysia hedgei and *D. microphylla* are highly specialized species showing clear structural xerophytic adaptations. Well protected, clearly delimited stomatal grooves with a stomatal density of up to 1000 stomata pr. mm² occur in the leaves which otherwise have a thick-walled epidermis covered by a well developed cuticle. Clear progressive evolutionary trends towards a xerophytic life are found within the genus. The evolution of the genus *Dionysia* is closely connected with the geological and climatological development of the arid and semiarid Irano-Turanian region. *Dionysia* belongs to the strong element of endemic, autochthonous genera that characterize this floristic region.

The genus *Dionysia* comprises 38 species of which no less than 34 grow in the area covered by K. H. RECHINGER's „Flora Iranica“. One species grows in the Jebel Akhdar Mts. of Oman, one in SE. Turkey and two in Tadjikistan (WENDELBO 1961; 1964; 1965; 1967; 1970). The genus must be considered endemic to the Irano-Turanian floristic region which probably has an exclave in the little known mountains of Oman.

All members of the genus are tuft-forming obligate chasmophytes. The comparatively large-leaved and loose-tufted species with well developed inflorescences considered to be the more primitive species, are found in the mountains surrounding the Iranian highlands (cfr. WENDELBO 1964, fig. 14). Most species form dense to compact tufts and have small comparatively thick, often pubescent leaves with strongly reduced nervation and an inflorescence reduced to one sessile flower per leaf rosette. These latter, phylogenetically more advanced, species are found in the inner, drier ranges of the mountains. The reduction in leaf size, in nervation and in size of inflorescence as well as the forming of dense tufts may be looked upon as adaptations to arid habitats (fig. 1a—e). Tufts of *D. tapetodes* BUNGE collected in the Paghman valley outside Kabul in Afghanistan in May 1962 — after the beginning of the dry summer period — were full of water that could be squeezed out. Possibly this is a form of water storage that may be common to several of the dense-tufted species.

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D. mira

D. bornmuelleri

D. teucroides

D. raptodes

D. aretioides

Abb. 1. Species of *Diomyisia* sect. *Anacamptophyllum* showing the gradual reduction from large-leaved and loose-tufted species with well developed inflorescences to small-leaved, densely tufted species with one-flowered inflorescences (a to e). Miranda Böppker del.

Structural characteristics considered to be adaptations to dry habitats are well known in many xerophytes. Such characteristics are usually connected with the stomata (cp. FAHN & DEMBO 1965; PYYKKÖ 1966; FAHN 1967; BÖCHER & LYSHEDE 1968). Little ecological-physiological work that directly demonstrates the significance of these structural changes for the water balance and the gas exchange of the xerophytes seems to have been done. But the many cases of convergency connected with „protection” of the stomata in xerophytes of unrelated families, demonstrate that these structural changes must have great significance. There was reason to suspect that such structural characteristics might also be present in some *Dionysia* species.

During an expedition to Afghanistan in 1962 the two species *D. hedgei* WENDELBO and *D. microphylla* WENDELBO were found at rather low altitudes in hot cliff walls which were fully exposed to the sun for a long part of the day. Most other species grow in shady cliff walls, often in gorges. The two mentioned species seem to represent extremes within the genus from an ecological point of view and are also taxonomically isolated within the genus (WENDELBO 1964). It thus seemed worth while to investigate these species more closely with respect to morphological and anatomical characteristics. Leaf sections were made with a freezing microtome from pressed dry material that had been soaked in water for some days. It was, however, difficult to obtain sections of such a quality that finer details could be demonstrated.

Dionysia microphylla

The plants form very dense tufts from which the short scapes with leafy bracts and one to four verticils of flowers protrude (WENDELBO 1965, tab. 7, fig. 2). The leaves are c. 2 mm in diameter, suborbicular in outline, somewhat saucer-shaped and densely imbricate forming a globular rosette (fig. 2A). The stomata are found in 4–6 elliptic grooves below the apex on the adaxial, concave side of the leaf (fig. 2B–D). A few stomata on the adaxial surface are also found in groups near the leaf margin at the broadest part. The epidermis consists of thick-walled celles with well-developed cuticle on the abaxial exposed side (fig. 2C–D), whereas it is somewhat thinner on the side turning inwards and is thin, without a cuticle in the stomatal grooves. The largest groove is 0,61 mm long and 0,18 mm broad and contain about 80 stomata; the smallest is 0,36 mm long and 0,19 mm broad with c. 45 stomata. This is equal to about 1000 stomata pr. square mm which is a much higher number than any previously reported for a leaf. Small farinipotent glands c. 0,07 mm long are found in the stomatal grooves which are usually filled with white powdery farina. The nervation of the leaf is much reduced (fig. 2B).

Dionysia hedgei

The comparatively large obovate-spathulate leaves, 5–9 mm long and 2–3,5 mm broad (fig. 2E), form relatively open leaf rosettes. The inflorescence is a several-flowered umbel subtended by leafy bracts and raised above the

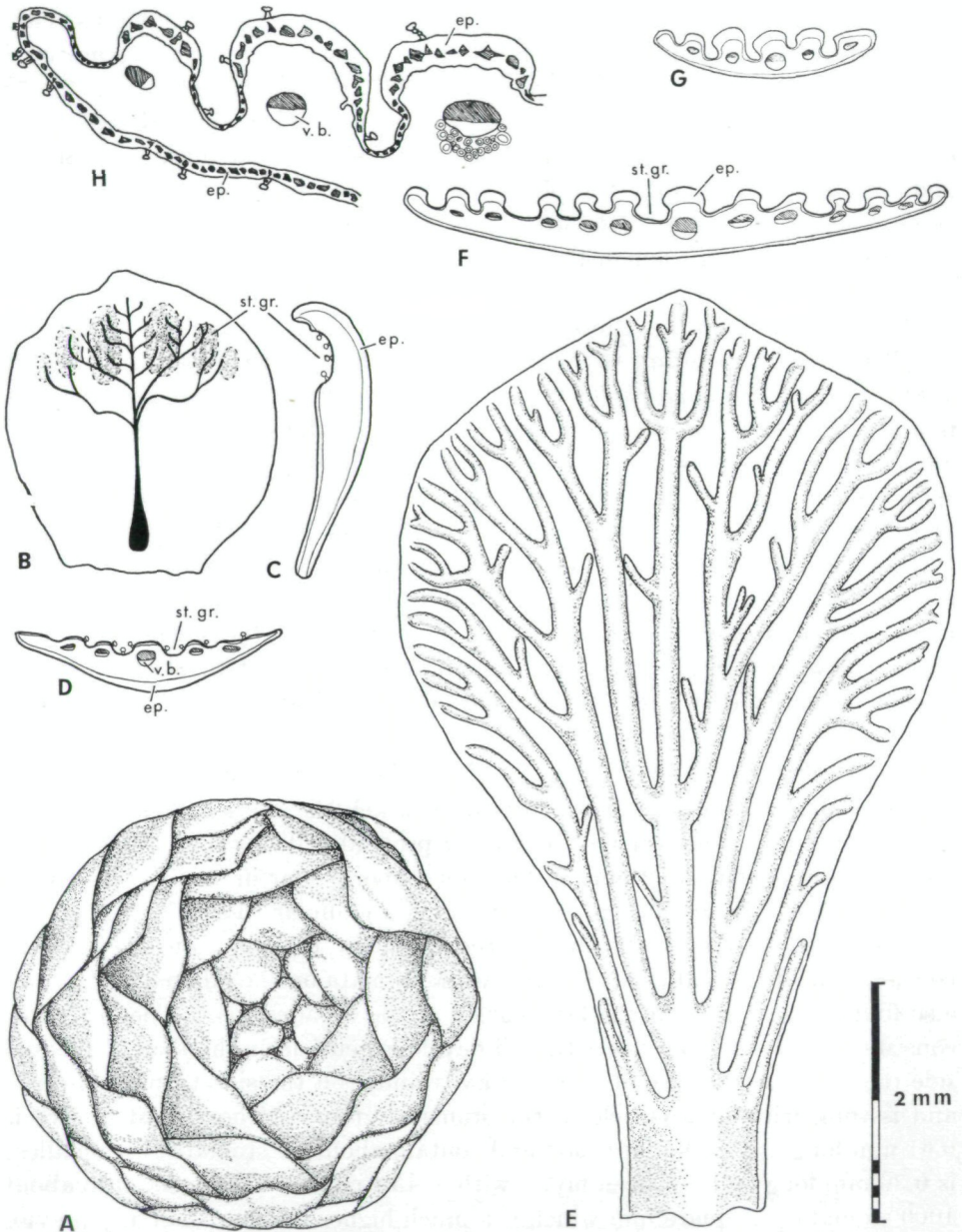


Abb. 2. A—D. *Dionysia microphylla*: A. Sterile leaf rosette from above; B. Nervation of leaf (stomatal grooves indicated by grey tone); C. Longitudinal section of leaf with stomatal groove; D. Transversal section of leaf through the stomatal grooves. E—H. *Dionysia hedgei*: E. Upper side of leaf showing the ridges between which the stomatal grooves are situated; F. Section through broadest part of leaf showing stomatal grooves and ridges with their thick epidermis; G. Section near base of leaf; H. Detail of leaf section. ep. — epidermis; st. gr. — stomatal grooves; v. b. — vascular bundles. A—G: X 16; H: X 60. Kari KRISTOFFERSEN del.

foliage on a well developed scape (WENDELBO 1965, fig. 2). The stomata are found on the upper side of the leaves in grooves formed between ridges which are thickest in their upper part and here have an epidermis of thick walled cells and a thick cuticular layer (fig. 2F—H). Farinipotent glands are found in the grooves which often are more or less filled with white powdery farina. The underside of the leaf also has an epidermis with comparatively thick-walled cells and a well-developed cuticle.

Discussion

In *D. hedgei* air chambers are formed by the stomatal grooves on the upper side of the leaf. Although no experiments could be made on living material there is reason to believe that in a state of water deficiency the leaf will bend together somewhat, resulting in a closing of the stomatal grooves. A rather similar leaf anatomy is found for example in such Argentinian xeromorphic species as *Condalia microphylla* CAV. of *Rhamnaceae* (PYYKKÖ 1966: 496; fig. 61), *Nassauvia nivalis* POEPP. & ENDL. of *Compositae* (l. c.: 522; fig. 94) and in several grasses e. g. *Stipa bella* PHIL. (l. c.: 527; fig. 115). The Mediterranean *Nerium oleander* of *Apocynaceae* (FAHN 1967: fig. 93, 1) also has a similar structure.

In *D. microphylla*, the system is somewhat different. Here the well-protected abaxial side which is without stomata is exposed. Air chambers are partly formed by the stomatal grooves of the adaxial leaf side inside the rosette and also by open space between the closely imbricate leaves. It has not been possible to get a sensible estimate of the volume of the air chambers but judging from the sections of the leaves it seems that the stomatal grooves formed between the ridges of the upper leaf side of *D. hedgei* may have a capacity that is as large as that of the substomatal air chambers and the inter-cellular space together.

The powdery farina which these two species share with many species of the closely related genus *Primula* may have a certain function in protecting the leaf against water loss by transpiration. In the two species discussed here the farina fills up the stomatal grooves; in *Primula* species where it is best developed in young leaves it covers stomata and thus protects the young leaves against water loss.

From a taxonomic and phylogenetic point of view the rather specialized features of *D. hedgei* and *D. microphylla* are not without importance. They suggest that these taxa have a rather long evolutionary history and thus are of considerable age. Certain groups of *Dionysia* such as subsect. *Tapetodes* and subsect. *Caespitosae* give an impression of being phylogenetically rather young because all stages in the evolution are represented by more or less closely related species within relatively limited geographical areas. But here we may have a rather remarkable case where the different stages in the development of a genus have been preserved due to their chasmophytic way of life. DAVIS (1951)

already pointed out that many relicts of great age in the Mediterranean have found their refugia in cliff walls during changing periods.

No doubt *Dionysia* is closely related to *Primula* but it shows several parallel progressive adaptive xeromorphic trends which must be seen in connection with its development within an arid region (WENDELBO 1961: 24 seq.). RECHINGER (1953: 448) coined the term palaeoxeromorphs for the autochthonous element of genera that had evolved in the dry inner regions of the Iranian highlands. *Dionysia* is not a true palaeoxeromorphic genus in RECHINGER's sense but just as the characteristic genera *Acanthophyllum*, *Acantholimon*, *Cousinia*, *Eremurus* and *Eremostachys* — endemic to the Irano-Turanian floristic region — it is a genus which has its whole evolutionary history closely connected with the geological and climatological development of the Irano-Turanian area during the Tertiary.

It is a great pleasure for me to dedicate this small study of a typical Iranian genus to my friend KARL-HEINZ RECHINGER on the occasion of his 65th birthday. He has himself through many valuable finds, including two new species, contributed much to the knowledge of the genus *Dionysia*. His generous help and stimulating advice during work with this genus and with other S. W. Asian genera have been much appreciated.

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