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Eco-anatomical differences between Balkan endemo-relict species of *Gesneriaceae*

Abstract

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A comparative anatomical study of the leaves of *Jancaea heldreichii*, *Ramonda nathaliae*, *Ramonda serbica*, and *Haberlea rhodopensis* reveals that their adaptive features are specific structural responses to environmental constraints of their respective habitats.

Introduction

The species *Jancaea heldreichii* (Boiss.) Boiss., *Ramonda nathaliae* Pančić & Petrović, *Ramonda serbica* Pančić, and *Haberlea rhodopensis* Friv. belong to a group of poikilohydric representatives of the otherwise tropical-subtropical family *Gesneriaceae*. They are all endemo-relict species of the Balkan Peninsula (Košanin 1921), and are unique as the probably only examples of "resurrection plants" among the Holarctic phanerogam flora (Gaff 1989).

In their geographical distribution, the Balkan *Gesneriaceae* are typical relict species. Thus, *Jancaea heldreichii* represents a stenendemic genus of Mt Olympus (Strid 1991), while *Haberlea rhodopensis* (Strid 1991), *Ramonda nathaliae*, and *R. serbica* (V. Stevanović & al. 1986, 1991) have widely scattered, disjunct occurrences on the Balkan Peninsula. All four are typical chasmophytes that inhabit north-facing limestone (rarely serpentine) rocks at altitudes ranging from 100 to 2400 m.

At present these plants are considered as threatened and, as such, they are protected by law. For this very reason they should be intensively studied in order to explore the best ways of protecting them as unique genetic resources.

The aim of the present investigation was to study the morphological and functional responses of the Balkan "resurrection plants" to the environmental conditions of their respective habitats. We see the specific eco-anatomical properties of these poikilohydric plants as one of the essential features of their adaptive strategy, which is primarily based on the genetically determined desiccation tolerance of their protoplasm and its ability to safeguard the essential metabolic systems in the dry state so as to reactivate them rapidly upon rehydration (Gaff 1980, Bewley & Krochko 1982, B. Stevanović & al. 1992).

Material and methods

Fresh and FAA-fixed plant material was used. *Jancaea heldreichii* was collected in Papa Rema (Mt Olympus, Greece), *Ramonda nathaliae* near Lukovo (F.Y.R. Makedonija), *R. serbica* in the Raec gorge (F.Y.R. Makedonija), and *Haberlea rhodopensis* near Bačkovo (Mts Rodope, Bulgaria). Some plants collected in their natural habitats were planted in the botanical garden in Belgrade and used for analysis as fresh material.

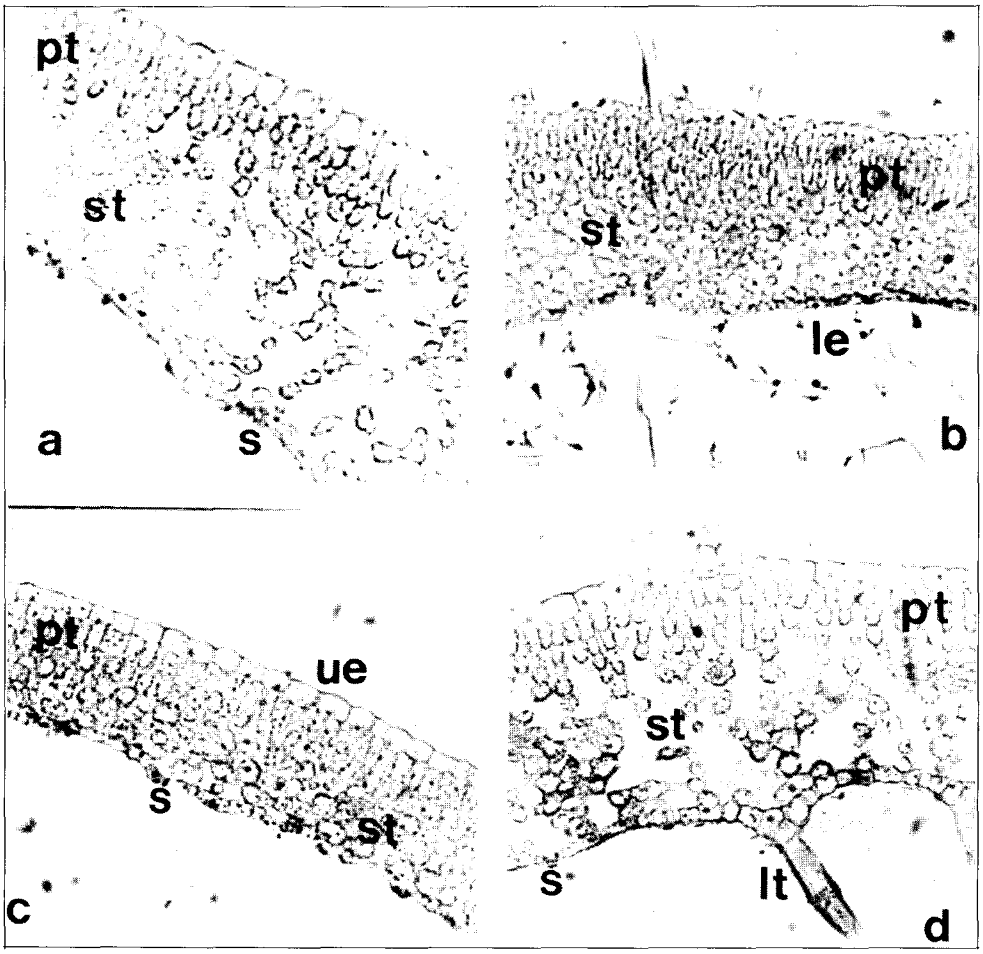

Fig. 1. Leaf cross-sections. – **a,** *Jancaea heldreichii;* **b,** *Ramonda nathaliae;* **c,** *R. serbica;* **d,** *Haberlea rhodopensis.* – le = lower epidermis, lt = linear trichome, pt = palisade tissue, s = stomata, st = spongy tissue, up = upper epidermis.

Permanent microscope slides were made by the standard paraffin method (Chamberlain 1931, Prozina 1960, Jensen 1962). Trichomes, epidermal cells and stomata were examined on permanent slides by light microscopy, and on leaf samples from herbarium specimens, sputter-coated with gold, by scanning electron microscopy (Jeol JSM-35). Quantitative data were computed by applying StatGraf 4.2.

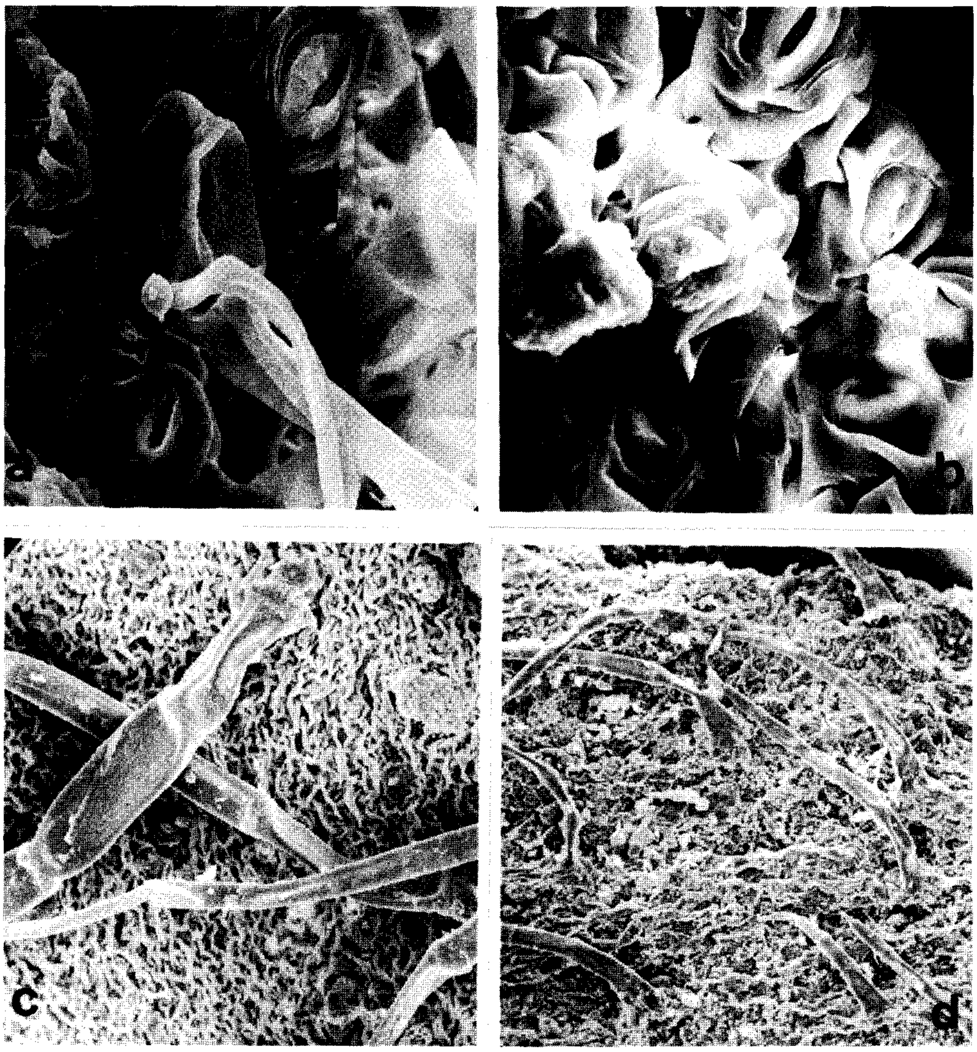

Fig. 2. Scanning electron micrographs of leaf surfaces. – **a,** *Jancaea heldreichii,* stomata and stalked capitate glandular trichomes of the abaxial epidermis (x 1230); **b,** *Ramonda nathaliae,* stomata of the abaxial epidermis (x 1230); **c,** *R. serbica,* stomata and trichomes of the adaxial epidermis (x 160); **d,** *Haberlea rhodopensis,* indumentum of the abaxial epidermis (x 89).

Results

Among the species examined, *Jancaea heldreichii* has the smallest and thickest leaves (722.48-116.68 µm thick; Fig. 1a), covered on both sides with dense, long, multicellular, unbranched, multiply intertwined trichomes. The indumentum, which also includes a small number of capitate, stalked glandular trichomes (Fig. 2a), is 2-3 times as thick as the leaf blade, which appears silvery grey adaxially and pale brown abaxially. The ratio of palisade tissue to spongy tissue is 1 : 3 (Fig. 3). The palisade parenchyma consists of three tiers of tightly packed cells, whereas the spongy tissue is composed of 5-7 layers of roundish cells separated by very large intercellular spaces (Fig. 1a). The leaves are amphistomatic, and the stomata are slightly raised above the surface (Fig. 2a).

The leaves of *Haberlea rhodopensis* are largest, and also quite thick (Fig. 1d). Trichomes are scattered on the upper (adaxial) face of the leaf (Fig. 2d), whereas the abaxial face is covered with a dense, pale brown indumentum of multicellular trichomes. The ratio of palisade tissue to spongy tissue is 1 : 2.5 (Fig. 3), and the mesophyll structure (Fig. 1d) is similar to that of *Jancaea heldreichii*. The leaves are hypostomatic, the stomata being level with the epidermal cells.

Ramonda nathaliae and *R. serbica* are characterized by leaves that are relatively large (Fig. 1b-c, 3), yet smaller than those of *Haberlea rhodopensis*. Ecologically relevant anatomical differences between these sibling species are as follows:

- *Ramonda nathaliae* has thicker leaves (376.2-284.6 µm), a 3-4-tiered palisade tissue, and a compact mesophyll (Fig. 1b);

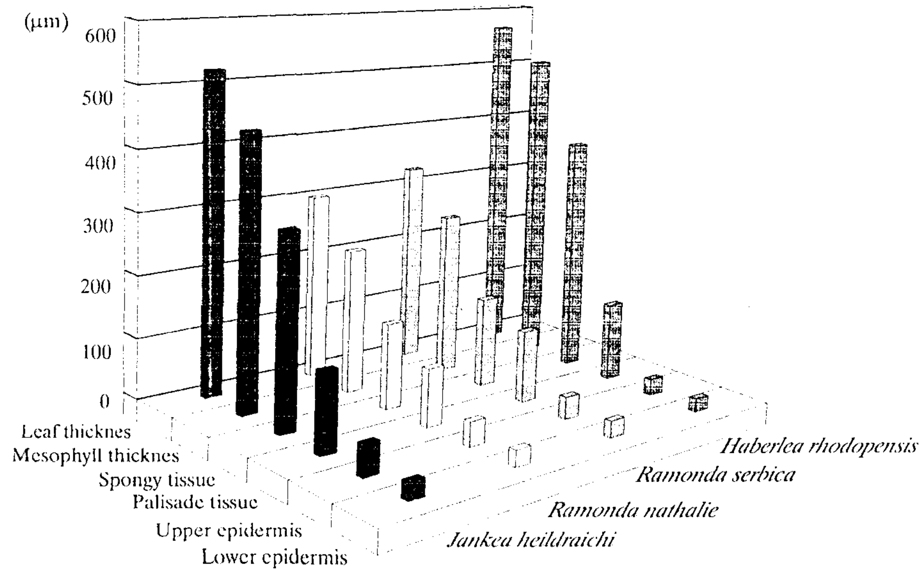

Fig. 3. Relations between the thickness of the leaves and leaf tissues in the four *Gesneriaceae* species studied.

- *Ramonda serbica* has thinner leaves (362-273.3 µm), the palisade tissue is composed of 2-3 cell tiers, and the mesophyll is looser, especially the spongy tissue that exhibits conspicuous intercellular spaces (Fig. 1c).

Ramonda nathaliae and *R. serbica* have the same type of leaf indumentum, composed of multicellular, unbranched hairs that are denser abaxially than adaxially and of scattered glandular hairs, and both have faintly raised stomata on either face of the leaf lamina (Fig. 2b-c).

Discussion and conclusions

The poikilohydric *Gesneriaceae* of the Balkan Peninsula are characterized by a hemicryptophytic life form with rosettes of evergreen leaves as well as by shared morphological features of these leaves and their surface structures. The differences in indumentum thickness, stomata distribution, mesophyll compactness, and the number of cell tiers in the palisade tissue correspond to a lower or higher degree of xeromorphic adaptation. The varying degree of xeromorphism of these plants is a direct adaptive response to the specific conditions of their respective habitats.

The structural differences between these desiccation tolerant "resurrection plants", that we regard as a "secondary" set of adaptations, reflect small-scale ecological and chorological divergences: the least xeromorphic, or rather, the most mesomorphic of them, *Haberlea rhodopensis,* inhabits moist, shaded chasmophytic habitats, chiefly in forest, at altitudes of up to 2000 m; the meso-xeromorphic *Ramonda serbica* is frequent on similarly protected rocky ground in thermophilous forests and on north-facing slopes in gorges, but does not exceed an altitude of 1800 m. *R. nathaliae* and *Jancaea heldreichii* are more markedly xerophytic. *R. nathaliae* is characterized by a xeromorphic mesophyll and a dense hair cover on the abaxial leaf face, which enables its survival under environmental stress conditions (water deficit on shallow, rocky soil, both limestone and serpentine, at altitudes up to 2250 m). The xeromorphism of *J. heldreichii,* expressed in its small and thickly velvety leaves, enables this stenendemic orophyte to survive under the Mediterranean climate conditions of Mt Olympus, in habitats that are more xeric than those of the other Balkan *Gesneriaceae,* as also mentioned by Strid (1991).

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