The Mediterranean: a cradle of the resurrection plants in Europe*

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Abstract. The fast-growing human population on our planet and the need for improved quality of life leads to a growing demand in food and feed production. This is the main challenge facing the world agriculture. Furthermore, this increase should be gained from the constantly decreasing land areas subject to environmental changes. Since crops are fundamental to the food pyramid, they must be able to realize their potential even under unfavorable environmental conditions and particularly under drought.

Sources of drought tolerance in many important crops are more or less limited or widely exploited. In this respect, the so called 'resurrection plants" represent a very useful model of desiccation tolerance. Their vegetative parts are able to withstand long periods of almost complete water loss and to recover fast upon rewatering.

The Mediterranean region – one of the biodiversity "hot spots" in the world – is the only area where the several species of resurrection plants in Europe have their habitats. All of them – *Haberlea rhodopensis*, *Ramonda serbica*, *R. nathaliae,* and *R. myconi* – belong to one and the same botanical family of *Gesneriaceae*.

The present review is focused on the common and specific traits of these interesting species, with an emphasis on the potential use and potential risk for their biodiversity.

Key words: *Haberlea rhodopensis*, *Ramonda myconi, R. serbica, R. nathaliae,* resurrection plants

Introduction

Unfavorable environmental conditions are the major limiting factor for crops growth and yields (e.g. Cramer & al. 2011). Long-term drought poses a great danger for temperate zones, which are the main areas of crop production. Presently, there are further problems related to "irregular seasoning": change of the seasons order, or of the typical parameters – mild and dry winters are followed immediately by cool and wet summers, or extremely cold winters are followed by very hot and dry periods. Obviously, modern agriculture will be economically relevant and environmentally sustainable only if based on varieties with superior performance under unfavorable conditions. In this respect drought-tolerant crop plants are of crucial importance and have no alternative. World agriculture is on the verge of a Second Green Revolution and along these lines profound and intensive studies into the plants reaction to stress are of paramount importance.

Resurrection plants as a model of desiccation tolerance

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a very useful model of desiccation tolerance. These plants belong to various botanical families and are spread all over the world. The only trait that they have in common is their extreme desiccation tolerance – their vegetative parts are able to withstand long periods (weeks, months, years) of almost complete water loss (about 10 % RWC and less) and to recover fast upon rewatering. The roots of vegetative desiccation tolerance should be traced out deep into the history of Earth's dry surface first primitive plants. The cost of survival appeared to be very high: most, if not all desiccation-tolerant organisms are small and rare (Oliver & al. 2000; Cushman & Oliver 2011).

Discovery of the resurrection plants: a short history

Interest in the resurrection plants has started to grow, especially in the 1970s and 1980s. Considering the fact that most of these plants could be found in regions with predominantly dry conditions, it is reasonable that they were among the most studied species. Good examples are *Craterostigma plantagineum* (Bartels 2005), *Selaginella* spp. (Yobi & al. 2013) and *Myrothamnus flabellifolia* (Moore & al. 2007). The Mediterranean Basin – one of the biodiversity "hot spots" in the world – has characteristically high levels of plant diversity and endemism (Myers & al. 2000). The limited number of resurrection plants in Europe could be found only in this region. Curiously enough, they belong systematically solely to the tropical family of *Gesneriaceae* and are considered to be Tertiary relics (Meyer 1970). One of them is the species *Haberlea rhodopensis* Friv., described in the 1830s both in the Rhodopi Mts and the Balkan Range in Bulgaria (Szelag & Somlyay 2009). The genus *Ramonda* Rich. comprises three species: *R. nathaliae* Panč. et Petrovic. and *R. serbica* Panč., which occur on the Balkan Peninsula and were described in the 1870s, and the earliest documented (at the turn of the 19th century) *R. myconi* (L.) syn. R. *pyrenaica* Rchb. distributed in the Pyrenees (Iberian Peninsula) (Szelag & Somlyay 2011). *R. serbica* has been found in the northwestern areas of Bulgaria, too (Stoyanov & Georgiev 1937). There is another monotypic genus, *Jancaea*, with its only representative *Jancaea heldreichii*, Boiss. discovered in the late 19th century. However, the eventual desiccation tolerance of this species is not documented.

The resurrection capacity of the members of *Gesneriaceae* has been discovered relatively earlier than that of the other species with the same behavior outside Europe. Quite accidentally, somewhere in the late 1920s it was observed that *Ramonda nathaliae* plants from the herbariums could recover when rehydrated (Velchev & al. 1975). Probably by analogy, the same was claimed for the other two members of the *Ramonda* genus: *R. myconi* and *R. nathaliae*. In those days, the only well-documented recovery after full desiccation was reported for *Haberlea rhodopensis* (Ganchev 1950), when it was shown that dry plants can recover after up to three years of full desiccation.

Phylogenetic and biodiversity studies of resurrection plants

The intensive studies focused on the resurrection plants from *Gesneriaceae* could be classified as going mainly in three directions: desiccation tolerance, phylogenetic analyses and biological activity of plant extracts.

Since *Ramonda* genus is represented by three species, their taxonomy, biodiversity and potential relationships were of particular interest. The genetic diversity and structure of *R. myconi* has been strongly influenced by several historical factors acting throughout the Pleistocene (Dubreuil & al. 2008). The same is true for the other *Ramonda* species distributed in the Balkans (Siljak-Yakovlev & al. 2008). The three *Ramonda* species show significant genetic diversity and even have various chromosome numbers and ploidy levels. In some areas, the Balkan species *R. nathaliae* and *R. serbica* share habitats and are able to cross. Since polyploidy could be considered as the major evolutionary mechanism in the genus *Ramonda* (Siljak-Yakovlev & al. 2008), examination of the origin and evolution of polyploidy within the complex of *Ramonda* species is of particular interest from a phylogenetic and phylogeographical aspect. It will allow the reconstruction of chorological history and cytogeography of these three paleoendemic species from the Balkan and Iberian Peninsulas.

Until recently, there were almost no studies of the genetic diversity of *Haberlea*, despite the report at the beginning of the 20th century of a second species, *Haberlea ferdinandi-coburgii* Urum. (Urumoff 1902). On the basis of several quantitative trait differences, the species has been distinguished in the northern mountains of Bulgaria, near Lovech. Although the latter report remained unconfirmed by other authors, this species has continued so far to be quoted along with *H. rhodopensis* in literature, botanical gardens and nurseries. To evaluate the genetic diversity of *Haberlea* in Bulgaria, we have collected plant material from the major localities in the country, including the disputable region of Lovech. We have found relatively low levels of genetic diversity among the populations (Petrova & al. 2014). Spatial differentiation and somewhat higher level of diversity among the high-altitude populations in the Balkan Range could be an indication that these areas have served as refugial places for the species. The collected genetic data suggest that the population from Lovech (the putative locality of *H. ferdinandi-coburgii*) is linked both to the Balkan and to the Rhodopean populations. This was further confirmed by the morphological and nuclear DNA levels. Thus, our data could be considered the first sufficiently convincing evidence that *H. ferdinandi-coburgii* is practically a synonym of *H. rhodopensis*.

Further studies have shown that the European *Gesneriaceae* genera have an origin in the early Oligocene (Petrova & al. 2015). In the Late Oligocene (c. 25 million years ago), the *Haberlea* lineage emerged as a separate species from the *Ramonda* spp. The three different *Ramonda* species have evolved some 8.5 million years ago. The present-day populations of *Haberlea* diverged in the Late Pleistocene (about 720 000 years ago) indicating glacial refugial areas for the species in Bulgaria and Greece.

Biotechnological studies

As a result of the biodiversity investigations, it could be assumed that the localities of all resurrection species are more or less well documented (Dubreuil & al. 2008; Siljak-Yakovlev & al. 2008 and the references therein; Petrova & al. 2014, 2015). On the other hand, the interest in *Ramonda* and *Haberlea* as desiccation-tolerant species focused particular attention on the possibilities of growing these plants under controlled conditions. In parallel and as a consequence of the achieved success with other resurrection plant species systems from outside Europe, e.g. *Craterostigma plantagineum* (Furini & al. 1994; Toldi & al. 2002), it became evident that biotechnological approaches are the best way to explore and eventually use the specific mechanisms of desiccation tolerance in the European resurrection plants.

Along these lines, it was of major importance to develop efficient protocols for *in vitro* culture. An efficient *in vitro* culture of *R. myconii* has been reported first (Tóth & al. 2004) and later served as a background for the development of a transformation protocol (Tóth & al. 2006).

On the other hand, establishment of *in vitro* propagation system is very important from the population's conservation viewpoint. This is particularly true of the endemic plants with limited number of individuals and limited areas of distribution. As it might be expected, intensive studies of *in vitro* culture for *R. serbica* and *R. nathaliae* were carried out in the Balkans. Populations of *R. serbica* and *R. nathaliae* from Serbia, Montenegro, Albania, Macedonia, and Bulgaria have been used as sources of explants for the development of *in vitro* protocols (Sabovljevic & al. 2008; Dontcheva & al. 2009; Daskalova & al. 2012; Gashi & al. 2012).

A simple and efficient protocol for *in vitro* regeneration and propagation was developed for *Haberlea rhodopensis* (Djilianov & al. 2005). It allows routine maintenance of *ex situ* collection of the species available for multipurpose use: establishment of suitable stress platforms, *ex situ* collection from the main localities, supply of plant material for various studies on desiccation tolerance, and other parameters of interest (Djilianov & al. 2009; Petrova & al. 2010). Recently, a protocol for genetic transformation was also developed (Petrova & al. 2013). A slightly alternative protocol for *in vitro* propagation of *H. rhodopensis* with conservation purposes has been also reported recently (Daskalova & al. 2010).

Desiccation tolerance

Various aspects of the desiccation tolerance of the European resurrection plant species are of particular interest, since, as already mentioned, they are perennial and thus survive not only dry and hot summers but also cold and snowy winters. Most data are accumulated from investigations performed into *R. serbica*, *R. nathaliae* and *H. rhodopensis,* while data on *R. myconi* appear to be scarce. Earlier parallel studies with these species have shown more or less similar mechanisms of stress reaction (Stefanov & al. 1992; Markovska

& al. 1994, 1995; Műller & al. 1997). These similarities were further confirmed when investigations were performed individually. For example, the importance of sugars as osmoprotectants and the scavenging systems has been well documented (Sgherri & al. 2004; Živković & al. 2005; Yahubyan & al. 2009; Djilianov & al. 2011). Similarities could be found when the photosynthetic systems were examined under stress and recovery (Augusti & al. 2001; Peeva & Maslenkova 2004; Georgieva & al. 2005, 2007, 2008; Degl'Innocenti & al. 2008; Peeva, & Cornic 2009; Strasser & al. 2010). On the other hand, differences in some parameters have been observed (e.g. in the dynamics of phenolic compounds under stress and recovery) (Sgherri & al. 2004; Veljovic-Jovanovic & al, 2008; Djilianov & al. 2011). These and other results once again confirm the idea of the existence of uniform mechanisms shared by most resurrection plant species that are common too for stress-tolerant non-resurrection plants. Along with this, resurrection plants have species-specific particular traits that alone or most probably in complex determine their unique desiccation tolerance (e.g. Toldi & al. 2009). To understand what are the specific traits that make *Ramonda spp.* and *H. rhodopensis* able to withstand both drought and cold, we shall need a system biology approach, which became possible with the recent development of the various "omics" technologies. There are already sginifficant results obtained in other resurrection plant systems (Moore & al. 2009; Suarez Rodriguez & al. 2010; Yobi & al. 2013). The access to sophisticated and up-to-date technologies is crucial for such studies. Along these lines, the studies performed with *H. rhodopensis* appear to be most advanced. Extensive molecular, proteomic, metabolic endogenous hormone analyses at various stages of stress and recovery have been recently performed and gave further insights into the resurrection behavior of this Bulgarian endemic (Berkov & al. 2011; Georgieva & al. 2012; Gechev & al. 2013; Djilianov & al. 2011; Mladenov & al. 2013, 2015 a, b; Moyankova & al. 2014a).

Biological activity of plant extracts

In addition to desiccation tolerance, there is a growing interest in using resurrection plants as unique sources of valuable bioactive compounds. Based on the presumption that such compounds not only contribute or determine the stress tolerance of the plant per sé, but could be useful in various areas, intensive studies are in progress into the extracts of *H. rhodopensis*. It has been already shown that extracts of this plant could be an important ingredient in human skin protective cosmetics (Dell'Acqua & Schweikert 2012). There are also encouraging results obtained in model animal systems treated with *Haberlea* extracts against various stress factors (e.g. Popov & al. 2010, 2011, 2012). Using our own plant material, routinelly propagated and grown under controlled conditions, we were able to show recently that extracts of *H. rhodopensis* could bring biological modalities in human anticancer therapy (Hayrabedyan & al. 2013). Various effects on plant pathogens growth have been shown, too, after treatment with *Haberlea* extracts (Moyankova & al. 2013, 2014a). Total methanol extracts showed inhibitory effects against the *Herpes simplex* viruses (Moyankova & al. 2014b). We have demonstrated that extracts from *Haberlea* revitalized and ameliorated cellular growth of chronologically ageing *Saccharomyces cerevisiae* (Georgieva & al. 2015).

Conclusion

In conclusion, the resurrection plants from the Balkans and Iberian regions could be a very usefull model not only for understanding better the phenomena of desiccation tolerance. There is a growing body of data showing the potential of *Ramonda spp.* and *H. rhodopensis* as sources of valuable multipurpose compounds. Many questions remain open and only further joint efforts and systemic approaches could ensure successful results. It would be best, if the groups working in the area, especially in all Balkan countries, would develop a systematic program with the final goal: conservation of biodiversity and, along with this, efficient exploitation of these rare and ancient endemic plants.

References

Augusti, A., Scartazza, A., Navari-Izzo, F., Sgherri, C., Stevanovic, B. & Brugnoli, B. 2001. Photosystem II photochemical efficiency, zeaxanthin and antioxidant contents in the poikilohydric *Ramonda serbica* during dehydration and rehydration. – Photosynth. Res., **67**(1-2): 79-88.

Bartels, D. 2005. Desiccation tolerance studied in the resurrection plant *Craterostigma plantagineum*. – Integr. Compar. Biol., **45**: 696-701.

Berkov, S., Nikolova, M., Hristozova, N., Momekov, G., Ionkova, I. & Djilianov, D. 2011. GC-MS profiling of bioactive extracts from *Haberlea rhodopensis*: an endemic resurrection plant. – J. Serb. Chem. Soc., **76**(2): 211-220.

Cramer, G.R., **Urano, K.**, **Delrot, S.**, **Pezzotti, M.** & **Shinozaki, K.** 2011. Effects of abiotic stress on plants: a systems biology perspective. – BMC Plant Biol, **11**: 163.

Cushman, J. & Oliver, M. 2011. Understanding vegetative desiccation tolerance using integrated functional genomics approaches within a comparative evolutionary framework. – In: **Ulrich Luttge, E.B. & Bartels, D.** (eds), Ecological Studies: Desiccation Tolerance in Plants, pp. 307-338. Heidelberg-Springer.

Daskalova, E., Dontcheva, S., Yahubyan, G., Minkov, I. & Toneva, V. 2010. Ecological characteristics and conservation of the protected resurrection species *Haberlea rhodopensis* Friv. as *in vitro* plants through a modified micropropagation system. – Biotechnol. Biotech. Eq., **24**: 213-217.

Daskalova, E., Dontcheva, S., Zekaj, Z., Bacu, A., Sota, V., Abdullai, K., Gashi, B., Minkov, I., Toneva, V. & Kongjika, E. 2012. Initial determination of polymorphism and *in vitro* conservation of some *Ramonda serbica* and *Ramonda nathaliae* populations from Albania, Macedonia and Bulgaria. – Biotechnol. Biotech. Eq., **26**: 16-25.

Degl'Innocenti, E., Guidi, L., Stevanovic, B. & Navari, F. 2008. CO_2 fixation and chlorophyll *a* fluorescence in leaves of *Ramonda serbica* during a dehydration–rehydration cycle. – J. Plant Phys., **16**(7): 723-733.

Dell'Acqua, G. & Schweikert, K. 2012. Skin benefits of a myconoside-rich extract from resurrection plant *Haberlea rhodopensis* Int. – J. Cosm. Sci., **34**(2): 132-139.

Djilianov, D., Genova, G., Parvanova, D., Zapryanova, N., Konstantinova, T., & Atanassov, A. 2005. *In vitro* culture of the resurrection plant *Haberlea rhodopensis*. – Plant Cell Tissue Org. Cult., **80**: 115-118.

Djilianov, D., Dobrev, P., Moyankova, D., Vankova, R., Georgieva, D., Gajdošová, S. & Motyka, V. 2013. Dynamics of endogenous phytohormones during desiccation and recovery of the resurrection plant species *Haberlea rhodopensis*. – J. Plant Growth Reg., **32**: 564-574.

Djilianov, D., Ivanov, S., Georgieva, T., Moyankova, D., Berkov, S., Petrova, G., Mladenov, P., Christov, N., Hristozova, N., Peshev, D., Tchorbadjieva, M., Alexieva, V., Tosheva, A., Nikolova, M., Ionkova, I. & Van den Ende, W. 2009. A holistic approach to resurrection plants. *Haberlea rhodopensis* – a case study. – Biotechnol. Biotech. Eq., **23**: 1414-1416.

Djilianov, D., Ivanov, S., Moyankova, D., Miteva, L., Kirova, E., Alexieva, V., Joudi, M., Peshev, D., & Van den Ende, W. 2011. Sugar ratios, glutathione redox status and phenols in the resurrection species *Haberlea rhodopensis* and the closely related non-resurrection species *Chirita eberhardtii*. – Plant Biology, **13**: 767-776.

Dontcheva, S., Daskalova, E., Yahubyan, G., Denev, I., Minkov, I. & Toneva, V. 2009. Conservation of the protected resurrection species *Ramonda serbica* Panč-habitat Montana distict, Bulgaria as *in vitro* plants through a modified micropropagation system. – Biotechnol. Biotetech. Eq., **23**: 369-372.

Dubreuil, M., Riba, M. & Mayo, M. 2008 Genetic structure and diversity in *Ramonda myconi* (Gesneriaceae): effects of historical climate change on a preglacial relict species. – Amer. J. Bot., **95**: 577-587.

Furini, A., Koncz, C., Salamini, F. & Bartels, D. 1994. *Agrobacterium*-mediated transformation of the desiccation-tolerant plant *Craterostigma plantagineum*. –Plant Cell Rep., **14**: 102-106.

Ganchev, I. 1950. Anabiotic desiccation resistance and other biological traits of *Haberlea rhodopensis* Friv. – Izv. Bot. Inst. (Sofia), **1**: 191-214 (in Bulgarian).

Gashi, B., Abdullai, K., Mata, V. & Kongjika, E. 2012. Effect of gibberellic acid and potassium nitrate on seed germination of the resurrection plants *Ramonda serbica* and *Ramonda nathaliae*. – African J. Biotech., **11**: 4537-4542.

Gechev, T., Benina, M., Obata, T., Tohge, T., Sujeeth, N., Minkov, I., Hille, J., Temanni, M.R., Marriott, A., Bergström, E., Thomas-Oates, J., Antonio, C., Mueller-Roeber, B., Schippers, J., Fernie, A. & Toneva, V. 2013 Molecular mechanisms of desiccation tolerance in the resurrection glacial relic *Haberlea rhodopensis*. – Cell Mol. Life Sci., **70**(4): 689-709.

Georgieva, K., Lenk, S. & Buschmann, C. 2008. Responses of the resurrection plant *Haberlea rhodopensis* to high irradiance. – Photosynthesis, **46**: 208-215.

Georgieva, K., Maslenkova, L., Peeva, V., Markovska, Y., Stefanov, D. & Tuba, Z. 2005. Comparative study on the changes in photosynthetic activity of the homoiochlorophyllous desiccation-tolerant *Haberlea rhodopensis* and desiccation-sensitive spinach leaves during desiccation and rehydration. – Photosynth Res., **85**(2): 191-203.

Georgieva, K., Szigeti, Z., Sarvari, E., Gaspar, L., Maslenkova, L., Peeva, V., Peli, E. & Tuba, Z. 2007. Photosynthetic activity of homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and rehydration. – Planta, **225**(4): 955-964.

Georgieva, M., Moyankova, D., Djilianov, D., Uzunova, K., Miloshev, G. (2015). Methanol extracts from the resurrection plant *Haberlea rhodopensis* ameliorate cellular vitality in chronologically ageing *Saccharomyces cerevisiae* cells. – Biogerontology, **16**(4): 461-472.

Georgieva, T., Christov, N. & Djilianov, D. 2012. Identification of desiccation-regulated genes by cDNA-AFLP in *Haberlea rhodopensis* – a resurrection plant. – Acta Phys. Plant, **34**(3): 1055-1066

Hayrabedyan, S., Todorova, K., Zasheva, D., Moyankova, D., Georgieva, D., Todorova, J. & Djilianov, D. 2013. *Haberlea rhodopensis* has potential as a new drug source based on its broad biological modalities. – Biotech. Biotech. Eq., **27**(1): 3553-3560.

Markovska, Y., Tsonev, T., Kimenov, G. & Tutekova, A. 1994. Physiological changes in higher poikilohydric plants – *Haberlea rhodopensis* Friv. and *Ramonda serbica* Panc. during drought and rewatering at different light regimes. – J. Plant Phys., **144**: 100-108.

Markovska, Y., Tutekova, A. & Kimenov, G. 1995. Ultrastructure of chloroplasts of poikilohydric plants *Haberlea rhodopensis* Friv. and *Ramonda serbica* Panc. during recovery from desiccation. – Photosynthesis, **31**: 613-620.

Meyer, F.K. 1970. *Gesneriaceae* as link of the flora of the Tertiary in Europe. – Wiss. Z. Friedrich-Schiller-Univ, Jena, Math-Naturwiss, Reihe, **19**: 401-411 (in German).

Mladenov, P., Zasheva, D., Christov, N., Peshev, D., Rolland, N., Tchorbadjieva, M. & Djilianov, D. 2013. Sub-cellular fractionation and gel-based proteomics of *Haberlea rhodopensis*: a promising approach to open the black box of resurrection plants. – Bulg. J. Agric. Sci., **19**(2): 22-25.

Mladenov, P., Zasheva, D., Djilianov, D. & Tchorbadjieva, M. 2015a. Towards proteomics of desiccation tolerance in the resurrection plant *Haberlea rhodopensis*. – Dokl. Bulg. Akad. Nauk., **68**(1): 59-64.

Mladenov, P., Finazzi, G., Bligny, R., Moyankova, D., Zasheva, D., Boisson, A-M., Brugière, S., Krasteva, V., Alipieva, K., Simova, S., Tchorbadjieva, M., Goltsev, V., Ferro, M., Rolland, N. & Djilianov, D. 2015b. *In vivo* spectroscopy and NMR metabolite fingerprinting approaches to connect the dynamics of photosynthetic and metabolic phenotypes in resurrection plant *Haberlea rhodopensis* during desiccation and recovery. – Front. Plant Sci., **6**: 564.

Moore, J., Lindsey, G., Farrant, J. & Brandt, W. 2007. An overview of the biology of the desiccation-tolerant resurrection plant *Myrothamnus flabellifolia*. – Ann. Bot., **99**: 211-217.

Moore, J., Le, N., Brandt, W., Driouich, A. & Farrant, J. 2009. Towards a systems-based understanding of plant desiccation tolerance. – Trends Plant Sci., **14**(2): 110-117.

Moyankova, D., Georgieva, D., Batchvarova, R., Slavov, S. & Djiljanov, D. 2013. Effect of extracts from the resurrection plant *Haberlea rhodopensis* on *in vitro* growth of plant pathogens. – Dokl. Bulg. Akad. Nauk., **66 (9):** 1269-1272.

Moyankova, D., Lyubenova, A., Slavov, S. & Djiljanov, D. 2014a. Extracts of the endemic resurrection plant *Haberlea rhodopensis* stimulate *in vitro* growth of various *Phytophthora* spp. pathogens. – Eur. J. Plant Path., **138**(1): 149-155.

Moyankova, D., Hinkov, A., Georgieva, D., Shishkov, S., Djilianov, D. 2014b. Inhibitory effect of extracts from *Haberlea rhodopensis* Friv. against *Herpes simplex* virus. – Dokl. Bulg. Akad. Nauk., 67 (10): 1369-1376.

Müller, J., Sprenger, N., Bortlik, K., Boller, T. & Wiemken, A. 1997. Desiccation increases sucrose levels in *Rhamonda* and *Haberlea*, two genera of resurrection plants in the *Gesneriaceae*. – Phys. Plant., **100**: 153-158.

Myer, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. – Nature, **403**: 853-858.

Oliver, M., Tuba, Z. & Mishler, B.D. 2000. The evolution of vegetative desiccation tolerance in land plants. – Plant Ecol., **151**: 85-100.

Peeva, V., & Maslenkova, L. 2004. Thermoluminescence study of Photosystem II activity in *Haberlea rhodopensis* and spinach leaves during desiccation. – Plant Biol., **61 (3):** 319-324.

Peeva, V. & Cornic, G. 2009. Leaf photosynthesis of *Haberlea rhodopensis* before and during drought. – Env. Exp. Bot., **65**: 310-318.

Petrova, G. & Djilianov, D. 2013. *In vitro* regeneration and *Agrobacterium*-mediated genetic transformation of the resurrection plant *Haberlea rhodopensis* Friv. – Bulg. J. Agric. Sci., **19 (2):** 10-14.

Petrova G., Moyankova, D., Nishii, K., Forrest, L., Tsiripidis, I., Drouzas, A.D., Djilianov, D. & Möller, M. 2015. The European paleoendemic *Haberlea rhodopensis* (*Gesneriaceae*) has an Oligocene origin, Pleistocene diversifation and occures in a long persisting refugial area in South-Eeastern Europe. – Int. J. Plant Sci., **176 (6):** 499-514.

Petrova, G., Dzhambazova, T., Moyankova, D., Georgieva, D., Michova, A., Djilianov, D. & Möller, M. 2014. Morphological variation, genetic diversity and genome size of critically endangered *Haberlea* (*Gesneriaceae*) populations in Bulgaria do not support the recognition of two different species. – Plant Syst. Evol., **300**: 29-41.

Petrova, G., Tosheva, A., Mladenov, P., Moyankova D. & Djilianov, D. 2010. *Ex situ* collection of model resurrection plant *Haberlea rhodopensis* as a prerequisite for biodiversity and conservation studies. – Biotechnol. Biotech. Eq., **24**: 1955-1960.

Petrova G., Moyankova, D., Nishii, K., Forrest, L., Tsiripidis, I., Drouzas, A.D., Djilianov, D. & Möller M. 2015. The European paleoendemic *Haberlea rhodopensis* (*Gesneriaceae*) has an Oligocene origin, Pleistocene diversifation and occures in a long persisting refugial area in South-Eeastern Europe. – Int. J. Plant Sci., **176 (6):** 499-514.

Petrova, G., Tosheva, A., Mladenov, P., Moyankova D. & Djilianov, D. 2010. *Ex situ* collection of model resurrection plant *Haberlea rhodopensis* as a prerequisite for biodiversity and conservation studies. – Biotechnol. Biotech. Eq., **24**: 1955-1960.

Petrova, G. & Djilianov, D. 2013. *In vitro* regeneration and *Agrobacterium*-mediated genetic transformation of the resurrection plant *Haberlea rhodopensis* Friv. –Bulg. J. Agric. Sci., **19 (2):** 10-14.

Petrova, G., Dzhambazova, T., Moyankova, D., Georgieva, D., Michova, A., Djilianov, D. & Möller, M. 2014. Morphological variation, genetic diversity and genome size of critically endangered *Haberlea* (Gesneriaceae) populations in Bulgaria do not support the recognition of two different species. – Plant Syst. Evol., **300**: 29-41.

Popov, B., Georgieva, S. & Gadjeva, V. 2011. Modulatory effects of total extracts of *Haberlea rhodopensis* against the cyclophosphamide induced genotoxicity in rabbit lymphocytes *in vitro*. – Trakia J. Sci., **9 (1):** 51-57.

Popov, B., Georgieva, S. & Lalchev, S. 2012. Radioprotection from genetic damages by resurrection plant *Haberlea rhodopensis – in vivo/ in vitro* study with rabbits. – Trakia J. Sci., **10(3):** 41-47.

Popov, B., Radev, R. & Georgieva, S. 2010. *In vitro* incidence of chromosome aberrations in gamma-irradiated rabbit lymphocytes, treated with *Haberlea rhodopensis* extracts and vitamin C. – Bulg. J. Vet. Med., **13(3):** 148-153.

Sabovljevic, A., Sabovljevic, M., Rakic, T. & Stevanovic, B. 2008. Establishment of procedures for *in vitro* maintenance, plant regeneration, and protoplast transfection of the resurrection plant *Ramonda serbica*. – Belg. J. Bot., **141**: 178-184.

Sgherri, C., Stevanovic, B. & Navari-Izzo, F. 2004. Role of phenolics in the antioxidative status of the resurrection plant *Ramonda serbica* during dehydration and rehydration. – Phys. Plant., **22:** 478-485.

Siljak-Yakovlev, S., Stevanovic, V., Tomasevic, M., Brown, S.C. & Stevanovic, B. 2008. Genome size variation and polyploidy in the resurrection plant genus *Ramonda*: cytogeography of living fossils. – Envir. Exp. Bot., **62**: 101-112

Stefanov, K., Markovska, Y., Kimenov, G. & Popov, S. 1992. Lipid and sterol changes in leaves of *Haberlea rhodopensis* and *Ramonda serbica* at transition from biosis into anabiosis and vice versa caused by water stress. – Phytochem., **31**: 2309-2314.

Stoyanov, B. & Georgiev, T. 1937. *Ramonda serbica* Panc. in Bulgaria. – God. Sofiisk. Univ. "Kliment Okhridski" Agronom. Lesov. Fac., Kn. **2**, Lesov.: 42-53 (in Bulgarian).

Strasser, R., Tsimilli-Michael, M., Qiang, S. & Goltsev, V. 2010. Simultaneous *in vivo* recording of prompt and delayed fluorescence and 820-nm reflection changes during drying and after rehydration of the resurrection plant *Haberlea rhodopensis*. – Biochem. Biophys. Acta, **176**: 1313-1326.

Suarez Rodriguez, M., Edsgärd, D., Hussain, S., Alquezar, D., Rasmussen, M., Gilbert, T., Nielsen, B., Bartels, D. & Mundy, J. 2010. Transcriptomes of the desiccation-tolerant resurrection plant *Craterostigma plantagineum*. – Plant J., **63** (2): 212-228.

Szelag, Z. & Somlyay, L. 2009. History of discovery and typiffication of *Haberlea rhodopensis* (Friv.) (*Gesneriaceae*). – Ann. Bot. Fenn., **46**: 555-558.

Szelag, Z. & Somlyay, L. 2011. Lectotypiffication of *Ramonda serbica* Panc. (*Gesneriaceae*). – Acta Soc. Bot. Poloniae, **80:** 77-78.

Toldi, O., Tuba, Z. & Scott, P. 2009. Vegetative desiccation tolerance: Is it a goldmine for bioengineering crops? – Plant Sci., **176:** 187-199.

Toldi, O., Tóth, S., Ponyi, T. & Scott, P. 2002. An efficient and reproducible genetic transformation protocol for the model resurrection plant *Craterostigma plantagineum* Hoscht. – Plant Cell Rep., **21:** 63-69.

Tóth, S., Scott, P., Sorvari, S. & Toldi, O. 2004. Effective and reproducible protocols for *in vitro* culturing and plant regeneration of the physiological model plant *Ramonda myconi* (L.) Rchb. – Plant Sci., **166**: 1027-1034.

Tóth, S., Kiss, C., Scott, P., Kovacs, G., Sorvari, S. & Toldi, O. 2006. *Agrobacterium*-mediated genetic transformation of the desiccation tolerant resurrection plant *Ramonda myconi* (L.) Rchb. – Plant Cell Rep., **25**: 442-449.

Urumoff, I. 1902. Plantae novae bulgaricae. Period. Spis. Bulg. Knizh. Druzh., **63**: 573 (in Latin).

Velchev, V., Ganchev, S. & Vassilev, P. 1975. Ecological and biological studies on *Ramonda serbica* Panč. and *Haberlea rhodopensis* Friv. – In: In Honour of Acad. Daki Yordanov, Bulg. Acad. Sci., pp. 174-184 (in Bulgarian).

Veljovic-Jovanovic, S., Kukavica, B. & Navari-Izzo, F. 2008. Characterization of polyphenol oxidase changes induced by desiccation of *Ramonda serbica* leaves – Phys. Plant., **132**: 407-416.

Yahubyan, G., Gozmanova, M., Denev, I., Toneva, V. & Minkov, I. 2009. Prompt response of superoxide dismutase and peroxidase to dehydration and rehydration of the resurrection plant *Haberlea rhodopensis*. – Plant Growth Reg., **57:** 49-56.

Yobi A., Wone, B., Xu, W., Alexander, D., Guo, L., Ryals, J., Olier, M. & Cushman, J. 2013. Metabolomic profiling in *Selaginella lepidophylla* at various hydration states provides new insights into the mechanistic basis of desiccation tolerance. – Molec. Plant, **6:** 369-85.

Živković, T., Quartacci, M., Stevanović, B., Marinone, F. & Navari-Izzo, F. 2005: Low-molecular weight substances in the poikilohydric plant *Ramonda serbica* during dehydration and rehydration. – Plant Sci., **168(1):** 105-111.