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ON THE GENUS *DICRANOWEISIA* (RHABDOWEISIACEAE, BRYOPHYTA) IN RUSSIA

РОД *DICRANOWEISIA* (RHABDOWEISIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus *Dicranowesia* includes in Russia one species, *D. cirrata*, with a limited distribution in its most western regions: in Kaliningrad Province and the Black Sea coastal area in the Caucasus. Despite of quite few known populations of the species in Russia, they comprise two clearly differentiated phenotypes, which also differ in the nuclear ITS sequences. The first ribotype is widespread in the world: it includes plants from the western North America, West Europe eastwards to the Baltic Sea region, some parts of the Caucasus, and East Africa. The second ribotype is known in Russia from a restricted area in the North Caucasus, with rather dry Mediterranean vegetation dominated by *Juniperus* & *Pistacea.* This second ribotype has a limited Old World Mediterranean distribution in Turkey, Greece, Tunisia, Morocco, and Canary Islands. The widespread ribotype is rare in Russia but potentially may expand its range, since it occurs sometimes in man-made habitats, while the population of the 'Old World Mediterranean' ribotype requires a conservation concern. Plants of the latter are morphologically distinct: they have short capsules and poorly differentiated costa, usually lacking stereids. The same two traits were used as diagnostic for *D. africana*, described from Rwanda, however one sequenced collection of this species from Tanzania belongs to the widespread ribotype.

Резюме

Род *Dicranowesia* представлен в России одним видом, *D. cirrata,* который имеет ограниченное распространение только в западных регионах: в Калининградской области и на Черноморском побережье Кавказа. Несмотря на то, что в России известны немногочисленные популяции вида, они представляют два хорошо дифференцированных фенотипа, которые отличаются также по последовательностям ядерного ITS. Один их этих риботипов широко распространен в мире: к нему относятся растения из Северной Америки, Европы (на восток до стран Балтии), из некоторых районов Кавказа и Восточной Африки. Второй риботип известен в России с очень ограниченной по площади территории на Северном Кавказе, где в растительном покрове имеются можжевелово-фисташковые редколесья Средиземноморского типа. Этот риботип имеет более ограниченное распространение, он встречается только в регионах Старого Света со средиземноморским климатом (в Турции, Греции, Тунисе, Марокко и на Канарских островах). Широко распространенный риботип представлен в России единичными популяциями, но расширение его ареала возможно, поскольку он растет в антропогенных местообитаниях, тогда как более редкий второй риботип, вероятно, нуждается в охране. Относящиеся к нему растения имеют морфологические отличия, а именно более короткие коробочки и слабо дифференцированную жилку, часто не имеющую стереид. Эти же самые признаки приводились как диагностические для *D. africana*, вида, описанного из Руанды, однако оказалось, что один отсеквенированный образец из Танзании принадлежит к широко распространенному риботипу.

KEYWORDS: mosses, molecular phylogeny, ITS, phylogeography, conservation

INTRODUCTION

The genus *Dicranowesia* Lindb. ex Milde for a long time included two widespead species, temperate *D. cirrata* (Hedw.) Lindb. and arctic-alpine *D. crispula* (Hedw.) Milde, until the molecular phylogenetic data showed that the latter belongs to a distinct lineage. Thus it was segregated into its own family (Fedosov *et al*., 2016) and then even order Hymenolomatales (Bechteler *et al*., 2023). Currently *Dicranowesia* is accepted with four species (Brinda & Atwood, 2025), but only one of them is widely used in recent literature and represented by DNA sequences in GenBank (https://www.ncbi.nlm.nih.gov/genbank/, accessed

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on 15 May 2025). Among other species there are East African *D. africana* Dixon, obviously a close relative of *D. cirrata*, and two species from Subantarctic and Tasmania, which placement in the genus *Dicranoweisia* s. str. has to be proved.

Dicranowesia cirrata is a generally western species in Europe, known in Russia from a few localities in its westernmost part. The species was reported from Kaliningrad (former Königsberg) by Klingraeff (1893), and also recently collected in the area (coll. Christian Wolfram, 9.VI.2001, MHA). Brotherus (1892) did not mention any localities of this species within Russia in his Moss flora of the Caucasus, and it has been reported in this region for the first time only by Ignatov *et al*. (2002) from Khosta (the Sochi area), and then from the Utrish Reserve, Novorossijsk District (Ignatova *et al.*, 2005).

Despite of so limited distribution, we encountered a considerable variation between Russian populations of *D. cirrata*. The plants from the Northern Caucasus, Utrish area appeared to be distinct from the description of the species in European literature. The poorly differentiated costa in the transverse leaf section and short ovate capsules were the most distinct characters. Moreover, both these distinctions were mentioned by Dixon (1920) in the original description of *D. africana* from East Africa, Kenya. Therefore, we undertook a molecular phylogenetic study checking if the Utrish plants belong to the latter species. Such analysis was facilitated due to the copiose sequence data from the previous study of Shaw *et al*. (2003). *Dicranoweisia cirrata* was one of three model species used by these authors to test if the intercontinental genetic variation may support the ancient age of the Madrean-Tethyan disjunction in mosses.

The observations on morphology were also in the focus of the present study.

MATERIALS AND METHODS

Molecular analysis: sampling and laboratory work

For assessing the affinities of the *Dicranoweisia cirrata*-like plants from the xeric Black Sea coastal area, nr ITS sequences were obtained from the selection of Russian specimens according to the protocol described by Gardiner *et al*. (2005). This marker appeared to be informative in the previous study of *D. cirrata* infraspecific diversity in a worldwide scope (Shaw *et al.*, 2003). Our dataset comprised 40 accessions, including 8 originally studied specimens: two from xeric areas in the vicinities of Anapa Town, three from humid Black Sea coastal areas (Khosta, Abkhasia), one from Kaliningrad Province, one from Spain, vicinity of Madrid, and one from Tanzania, originally referred to *D. africana* (see Appendix); 32 ITS sequences used in the study by Shaw *et al*. (2003) were downloaded from GenBank. *Rhabdoweisia crispata* was added in the alignment as an outgroup according to the topology obtained by Fedosov *et al*. (2021), and *Brideliella wahlenbergii* was also included for rooting the tree.

In addition to nuclear ITS, we sequenced plastid *trn*L–F and *rps*4, since some (few) sequences in GenBank for *Dicranoweisia* samples had some variation. However, in all eight samples we found no variable positions in both these plastid markers, and therefore did not include them in further analysis.

Phylogenetic analysis

Sequences were aligned manually using BioEdit (Hall, 1999). Indel data were scored using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005). ML trees were computed in iQ-tree (Trifinopoulos *et al*., 2016) via the web server http://iqtree.cibiv.univie.ac.at/ with 1000 generations of ultrafast bootstrap and otherwise default parameters. Optimal models of nucleotide substitutions were identified by the program as K2P for ITS1 and 5.8S, and TPM2u+F+I for ITS2. Also to visualize infraspecific molecular affinities that could not be assessed within the dichotomous tree, we prepared a Splitstree based on the same matrix with the indels taken into account via SplitsTree 4.12.6 (Huson & Bryant, 2006).

RESULTS

Molecular phylogenetic analysis

Molecular phylogenetic tree resolved *Dicranoweisia* monopyletic, with BS=100 (Fig. 1D). The clade of 9 Californian specimens of *D. cirrata* form a clade (BS=77) sister to all other studied samples of this genus. These samples comprise a grade, where at first one Mexican specimen splits off, leaving the polytomy of specimens from Old World Mediterranean region (green in Fig. 1D) and nested within them the relatively high supported (BS 90) terminal clade (red in Fig. 1D). The terminal clade includes specimens from Western North America, from California to British Columbia and eastwards to Idaho, European plants from Spain to Baltic Sea area, from the Caucasus, and Kilimanjaro area in East Africa.

The split trees were prepared with outgroups and without outgroups, but as the *Dicranoweisia* part of split tree was subidentical in them, only the latter split-tree is shown here. Its topology comprises three larger groups already described for the ML tree, and one Mexican specimen in between ‘purely Californian’ and ‘Old World Mediterranean’ group. The ‘widespread group’ includes 24 samples, 60% of all studied samples. Being most widespread, it has the minimal genetic variation, as seen from a relatively shorter branch length in the split-tree graph.

Morphological observations

Finding of the specific position of plants from the Northern Caucasus, Utrish, in the obtained phylogenetic tree led us to the re-study of all collections from that area (Fig. 2) and comparing them with West European specimens and the plants from Kaliningrad Province (Fig. 3). *Dicranoweisia africana* (Fig. 4) was also compared with various groups of *D. cirrata*. The differences between them were found to be as follow:

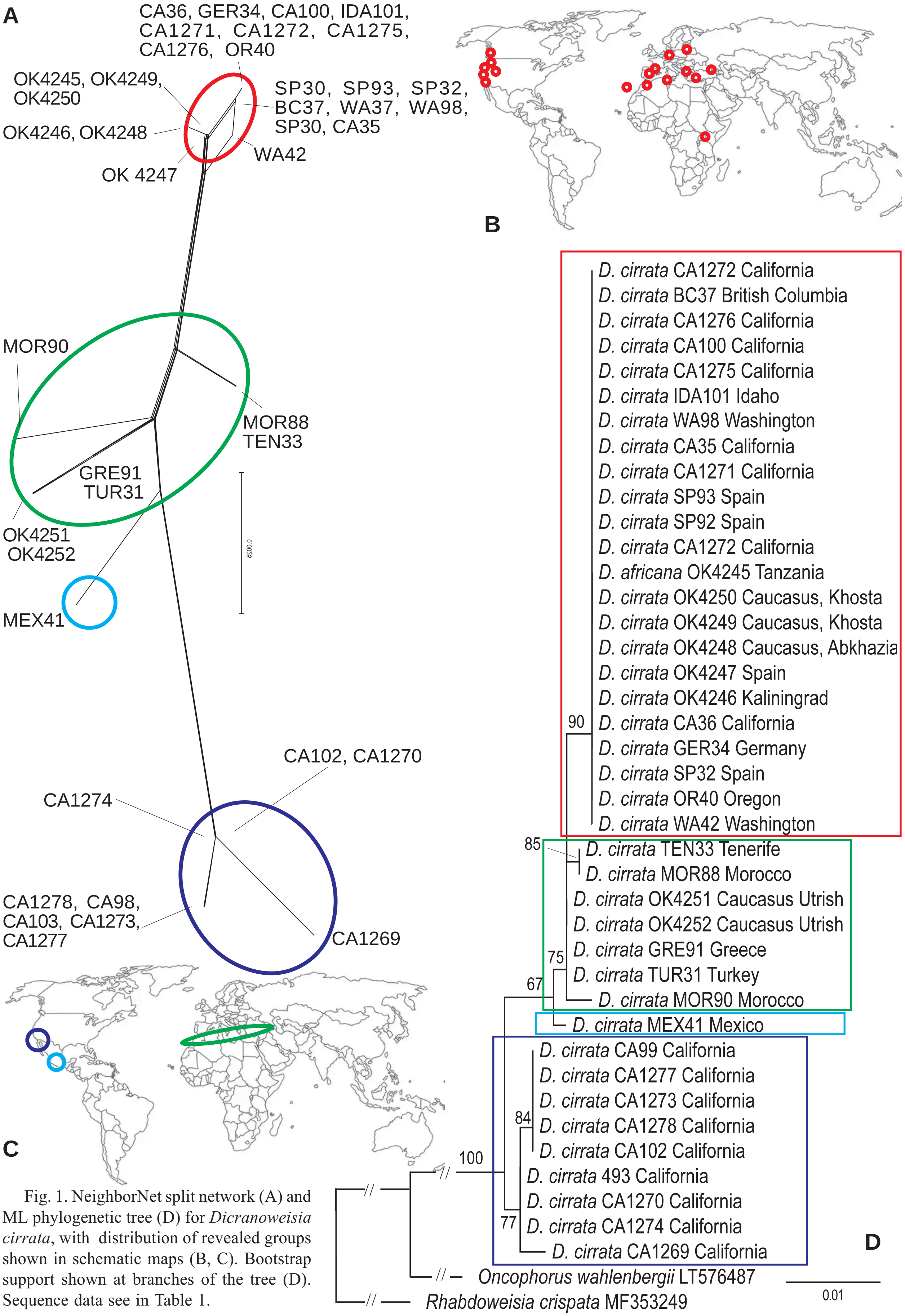

Fig. 1. NeighborNet split network (A) and ML phylogenetic tree (D) for *Dicranoweisia cirrata*, with distribution of revealed groups shown in schematic maps (B, C). Bootstrap support shown at branches of the tree (D). Sequence data see in Table 1.

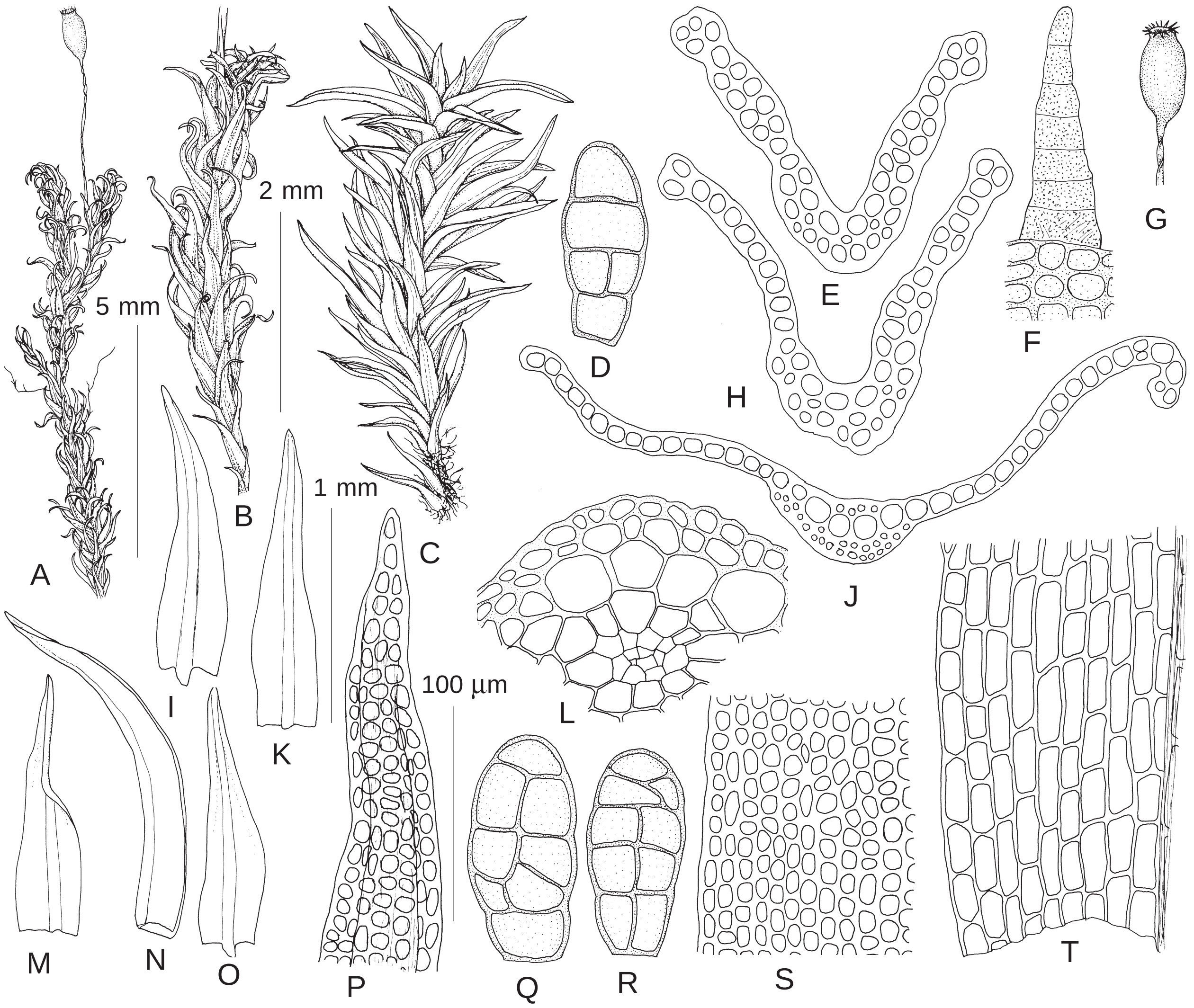

Fig. 2. *Dicranoweisia cirrata* (from: Krasnodar Territory, Utrish Reserve, *Ignatov & Ignatova 05-368*, MHA9049743). A–B: habit, dry; C: habit, wet; D, Q–R: gemmae; E, H, J: leaf transverse sections; F: peristome; G: capsule; I–K, M–O: leaves; L: stem transverse section; P: upper leaf cells; S: median leaf cells; T: basal leaf cells. Scale bars: 5 mm for A; 2 mm for B–C, G; 1 mm for I–K. M–O; 100 µm for D–F, H, J, L, P–T.

1) Leaf transverse sections

Utrish' *Dicranoweisia* has leaves bi- or occasionally partly tristratose distally, in mid-leaf bistratose at margins and sometimes in between costa and leaf margin; in lower part leaf unistratose, occasionally with bistratose margins.

Widespread *Dicranoweisia* has leaves in upper part bistratose at margins and sometimes in between costa and leaf margin; in mid-leaf leaves are unistratose except bistratose margin and very rarely with bistratose patches 1–2 cells wide in between costa and leaf margin; in lower part leaf lamina unistratose.

2) Costa transverse sections

Utrish' *Dicranoweisia* has costae in upper and middle parts 2–3-stratose, with inapparent differentiation and lacking stereids; only at leaf base in the better developed leaves dosral and ventral stereid bands are present; dorsal epidermis lacking.

Widespread *Dicranoweisia* has costae in upper and middle parts 3–6-stratose, with singular dorsal stereids near leaf apex but with clear dorsal and also clear albeit small ventral stereid band in mid-leaf; near the leaf base stereid bands are also clearly differentiated; dorsal epidermis is usually differentiated throughout the costa length or absent in the basalmost leaf part.

3) Capsules

Utrish' *Dicranoweisia* has ovate capsules, with the length to width ratio 2:1, while in widespread *Dicranoweisia* capsules are cylindric, ca. 3:1; in both cases, capsules have constriction below mouth, so ovate capsules are widest in the middle when open, while the longer capsules are widest well below the middle (unless the capsules are not cylindric).

4) Gemmae in Utrish' *Dicranoweisia* are rare, not found in the majority of specimens; they are relatively short and two cell wide (Fig. 2Q); in the widespread ribotype of *D. cirrata* they are found rather regularly and are relatively longer, sometimes spindle-shaped, one or

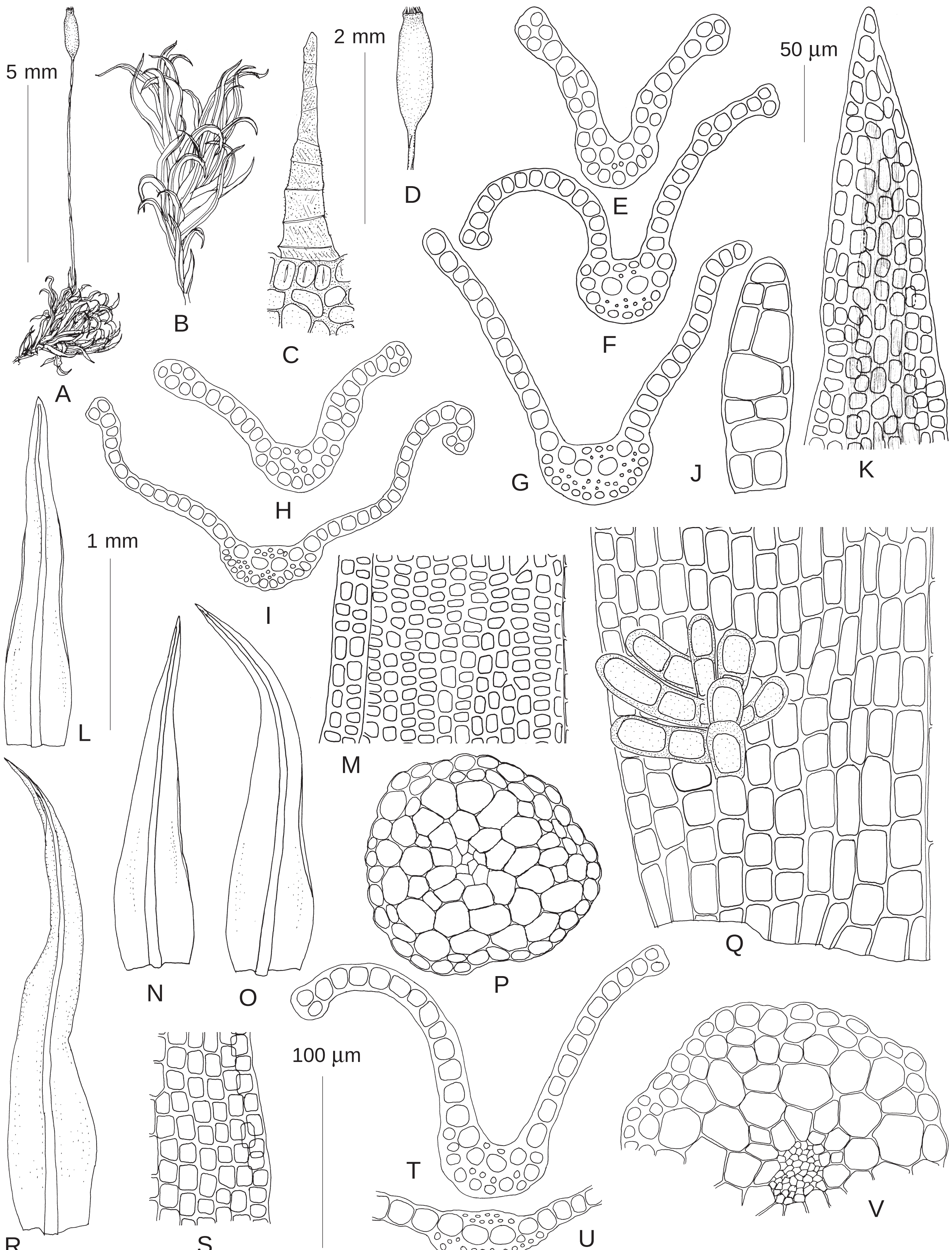

Fig. 3. *Dicranoweisia cirrata*: (A–G, J–K, M–Q: from Kaliningrad Province, 3.VI.2001 *Wolfram s.n.*, MHA9049746; H–I, L: from Krasnodar Territory, Khosta, 1.VIII.2002 *Ignatov & Ignatova s.n.*, MHA9047209; R–W: from Germany, 14.VI.2008 *Shanzer s.n.*, MHA9057477). A–B: habit, dry; C: peristome; D: capsule; E–I, N–U: leaf transverse sections; J: gemma; K: upper leaf cells; L, N–O, R: leaves; M, S: mid-leaf cells; P, V: stem transverse sections; Q: basal leaf cells. Scale bars: 5 mm for A; 2 mm for B, D; 1 mm for L, N–O, R; 50 µm for E–G, P, T–V; 100 µm for R, M, Q, S.

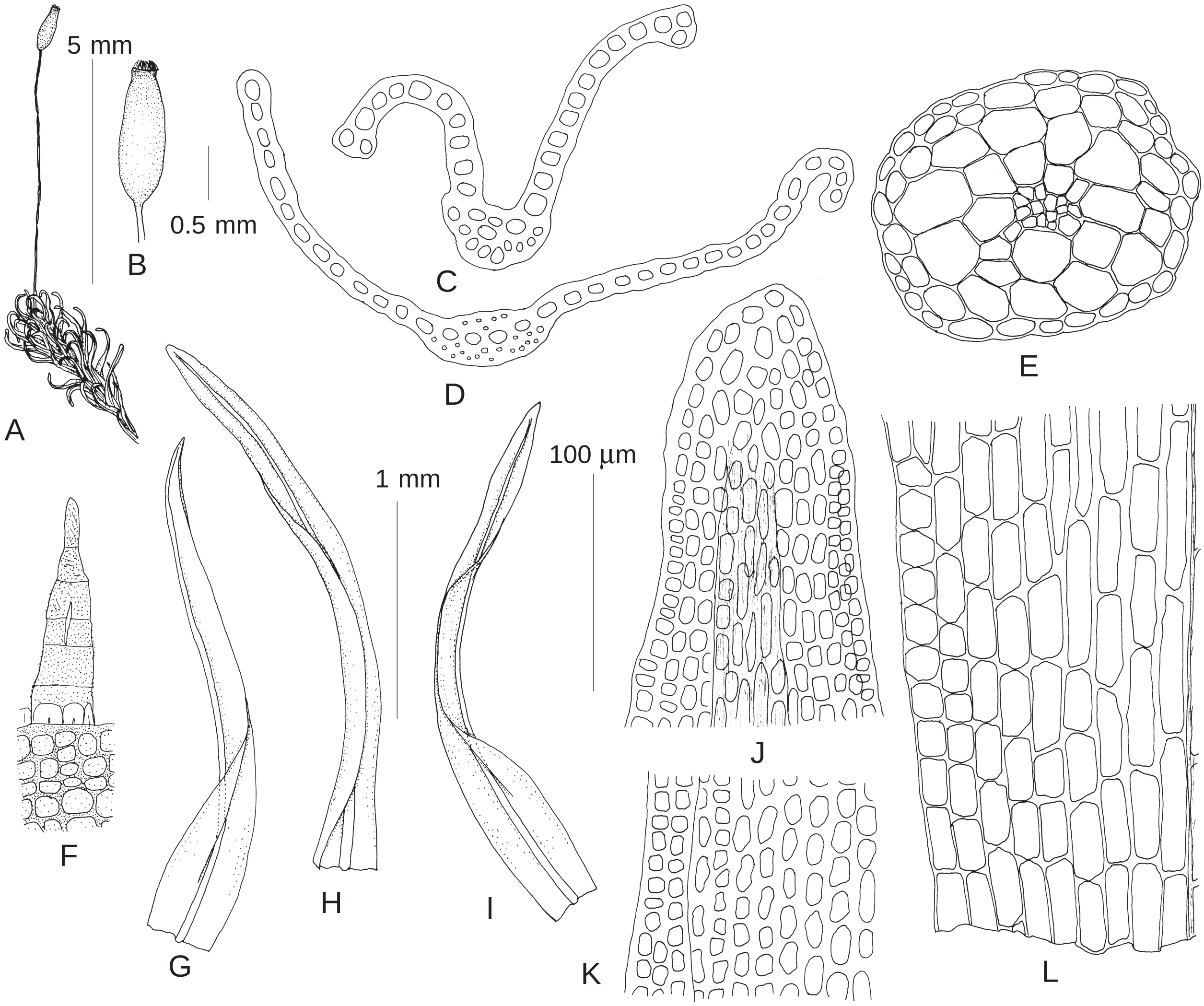

Fig. 4. *Dicranoweisia africana*: (from: Africa, Tanzania, Kilimanjaro Mts., *Pócs et al. 88130/A*, MHA9057479). A: habit, dry; B: capsule; C–D: leaf transverse sections; E: stem transverse section; F: peristome; G–I: leaves; J: upper leaf cells; K: mid-leaf cells; L: basal leaf cells. Scale bars: 5 mm for A; 1 mm for G–I; 0.5 mm for b; 100 µm for C–F, J–L.

two cells wide, often being one cell wide in their middle (Fig. 3J).

Stems and leaves in Utrish specimens are shorter than in many West European plants, but high variation of European specimens and a limited number of Utrish samples hamper their quantitative comparison. However, both Utrish and West European *D. cirrata* are obviously smaller than some Californian plants, though other collections from California hardly differ from the West European ones. Among features of Californian plants never seen in Old World, the deeply cleft peristome teeth were observed in some specimens, while in others they were identical to those in European plants (Fig. 3C).

Dicranoweisia africana represented by sequenced specimen from Tanzania agrees with the species original description in having poorly differentiated stereids in costa, more or less developed only shortly above the leaf base and not covered by the differentiated dorsal epidermis, like in Utrish plants. We found in the studied specimen capsules being longer than in Utrish plants, although in West European plants capsules are occasionally still longer, thus not contradicting the diagnosis of Dixon (1920). At least three traits of *D. africana* distinguish it from other specimens of *Dicranoweisia* studied by us: (1) leaves are linear, with parallel sides at a considerable distance vs. more or less gradually tapering in *D. cirrata*; (2) leaf apices are rounded vs. acute or occasionally blunt; (3) laminal cells are thick-walled, which is especially well seen in transverse leaf section (Fig. 4C, D).

DISCUSSION

A considerable part of the analyzed data were obtained by Shaw *et al*. (2003), who concluded that the age of Madrean-Tethyan disjunction in mosses can unlikely be explained by the vicariant hypothesis. The identical sequences of variable DNA region in European and western North America plants are obviously against it. Our additional data and rooted phylogenetic tree allow delimiting three lineages within the genus (Fig. 1). It shows that the plants of the 'purely Californian clade' are the most isolated in the genus, while plants from the 'wide-

Fig. 5. Utrish area, where the ‘Old World Mediterranean’ ribotype of *Dicranoweisia cirrata* occurs. A: slope with *Juniperus*+*Pistacea*+*Pinus* vegetation; B, C: habitats of *Dicranoweisia cirrata* in more open places; D: *Dicranoweisia cirrata* on exserted roots of *Juniperus* (insets with close-ups of capsules).

spread clade’ are also fairly common in California. Similarly, our original search of the common traits for the all-Caucasian *Dicranoweisia* led us to the conclusion of the total mixture in morphology, until molecular data revealed that the Utrish plants and all others samples belong to a more or less well separated groups, differing also in a number of morphological features.

Interestingly, the ancient groups, i.e. the ‘purely Californian’ clade and the ‘Old World Mediterranean’ group are more variable genetically compared to the ‘widespread clade’ (Fig. 1A). This can be tentatively interpreted as the latter has an outstanding ability to a rapid dispersal, whereas the ancient groups are more strictly confined, at least as far as the present sampling indicates.

Phylogeographic consideration

The results of the phylogenetic analysis (Figs 1A, D) can be interpreted in favour of New World origin of the genus *Dicranoweisia*, with subsequent migration to the Old World, where their most ancient genotypes retained in Mediterranean region. The later diversification happened probably in the Old World, where the most recently evolved group of haplotypes appeared and spread throughout western part of Eurasia, North Amercia and East Africa.

Such scenario, based on 40 sequences of one multicopy DNA marker, is certainly not a properly proved one, and more data is required for solid confirmation. However its similarity with the history of some other moss genera having the ‘Mediterranan’ distribution is noteworthy.

For example, the evolution of the genus *Homalothecium* (Huttunen *et al*., 2008; Hedenäs *et al*., 2009), excluding its most ancient clades, shows that the genus was diversified in North America, then crossed the Atlantic and produced in the Old World a clade that includes of *H. philippeanum*, *H. lutescens*, *H. sericeum,* and the most recent split from the latter, *H. mandonii. Homalothecium sericeum* spread well beyond the Mediterranean region, becoming common almost throughout Europe, reaching eastwards Central Asian mountains, westwards crossing Atlantic and reaching Newfoundland and Labrador. Though *H. sericeum* itself does not extend much far to the south, its most closely related species, *H. mandonii,* occurs in Madeira, Canary Islands, and tropical Cape Verde Islands, having very small differences in ITS sequences, but stable morphological distinction.

Conservation issues

The presented morphological and molecular variation of *Dicranoweisia cirrata* in Russia and some other areas is not enough to provide the basis for any taxonomic recognition, at least until the much broader molecular and morphological sampling is conducted. At the same time, the belonging to the group of an ‘Old World Mediterranean’ ribotype raised the status of the Utrish’ *D. cirrata* against other populations of the species which grow on trees in town streets.

Utrish is one of the few places in Russia where Mediterranean type of vegetation occurs at 10–200 m elev.,

Table 1. Data of de novo sequenced *Dicranoweisia* specimens.

Species	Isolate	Country & Vaucher	ITS
D. africana	OK4245	Tanzania, Kilimanjaro Mt., *Pocs et al. 88130/A*, Bryophyta Africana Selecta Series 5 #113, MHA9057479	PV768814
D. cirrata	OK4246	Kaliningrad Province, Curonian Spit, *Wolfram s.n.*, MHA9049746	PV768815
D. cirrata	OK4247	Spain, La Pedzira, *Ignatov & Spirina 19-1039*, MHA9062566	PV768816
D. cirrata	OK4248	Caucasus, Abkhazia, *Doroshina s.n.*, Bryophyta Rossica et Civ. Coll. Exs. Fasc. XII #507, MHA9062143	PV768817
D. cirrata	OK4249	Krasnodar Territory, Khosta, *Ignatov & Ignatova s.n.*, MHA9047210	PV768818
D. cirrata	OK4250	Krasnodar Territory, Khosta, *Ignatov & Ignatova s.n.*, MHA9047209	PV768819
D. cirrata	OK4251	Krasnodar Territory, Utrish, *Ignatov & Ignatova 05-368*, MHA9049743	PV768820
D. cirrata	OK4252	Krasnodar Territory, Utrish, *Ignatov & Ignatova 05-386*, MHA9049738	PV768821

dominated by *Juniperus oxycedrus*, *J. excelsa*, *J. foetidissima*, *Pistacia mutica*, *Quercus pubescens*, *Carpinus orientalis*, *Paliurus spina-christi,* and *Cotinus coggygria* (Fig. 5A), with many gravely openings (Fig. 5B, C) where *Dicranoweisia cirrata* is abundant on the exposed roots and creeping trunks of *Juniperus* (Fig. 5D). *Nogopterium gracile* is known in the Russian Caucasus only in the Utrish area; there were also found rare in Russia *Zygodon rupestris, Syntrichia virescens, S. laevipila, Habrodon perpusillus,* and *Antitrichia curtipendula.*

Some Mediterranean species that occur in Utrish are common in the neighboring areas of the Black Sea area of Caucasus and Crimea: *Leptodon smithii, Rhynchostegium confertum, Rhynchostegiella tenella, Scorpiurium circinatum, Sciuro-hypnum flotovianum,* and *Cirriphyllum crassinervium.* However, a strinkg boundary in composition of the bryophyte flora exists between the Utrish Area and coastal area only 50 km southwards from Utrish and then extending for at least four hundred kilometers along the Russian and Georgian parts of the Black Sea coast where climate is more humid. Some species that are very common and abundant in the latter region, e.g. *Thamnobryum alopecuroides, Exsertotheca crispa, Ctenidium molluscum,* and *Homalothecium phillipeanum* were collected in Utrish in a single locality each, while *Leucodon immersus, Homalia trichomanoides,* and *Metzgeria conjugata* were not recorded there (Ignatova *et al*., 2005). These features of the Utrish area highlight its biogeographic peculiarity, explaining the presence of the 'Old World Mediterranean' ribotype of *D. cirrata*. Its conservation value has to be evaluated as higher, following the approach demonstrated different risk of extinction of different genetic races in mosses (Hedenäs, 2019; Hedenäs *et al.,* 2020).

Fortunately, the Utrish area received a status of the strict Nature Reserve, which excludes clear-cuttings and over population by tourists in summer time. However, the danger for the Utrish *D. cirrata* exists from another side. The widespread ribotype of this species started to expand in more humid regions of the Black Sea coastal area, albeit so far to a moderate extent. However, the climate warming and wetting may favor such expansion further, which might cause genetic swamping of Utrish' *D. cirrata* due to introgressive hybridization and even lead to its silent genetic extinction (Gómez *et al*., 2015; Ghosh *et al*., 2012; Rhymer & Simberloff, 1996).

The shuttle life strategy (During, 1979) of *D. cirrata* and autoicous sexual condition may speed up such introgression, raising the risk of a very rapid extinction of the 'Old World Mediterranean' ribotype. The pointing out this problem might look an over-speculative and over-alarmous, however the fact that the 'Old World Mediterranean' ribotype has never been detected in e.g. such country as Spain, where all four sequenced specimens belong to the widespread ribotype, may be not a simply occasional. Further study of this small moss genus in various aspect will undoubtely bring better understanding of its hidden diversity and allow optimizing efforts towards its conservation.

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