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A REDISCOVERY OF *CRYPTOLEPTODON REMOTIFOLIUS* (NECKERACEAE, BRYOPHYTA) IN THE CAUCASUS, WITH COMMENTS ON ITS GENERIC PLACEMENT

CRYPTOLEPTODON REMOTIFOLIUS (NECKERACEAE, BRYOPHYTA) ВНОВЬ НАЙДЕН НА КАВКАЗЕ И УТОЧНЕНА ЕГО РОДОВАЯ ПРИНАДЛЕЖНОСТЬ

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Abstract

Leskea catenulata subsp. *remotifolia* was described in 1877 based on specimens from Georgia (Caucasus) and later never reported from this country. It was recently found that this taxon is identical with the Hyrcanian species traditionally called *Pseudoleskeella laxiramea*. It was recently placed into *Forsstroemia* or *Leptodon*. In 2022 the species was again collected in Georgia, in a locality 15 km from the *locus classicus*. It appeared to be identical to the Iranian specimens in its ITS sequences. However, in the molecular phylogenetic tree based on ITS it is resolved in a clade with *Cryptoleptodon pluvinii,* whereas *Leptodon smithii, L. longisetus,* and *L. corsicus* form a clade sister to *Cryptoleptodon*. Since the representatives of these two clades possess considerable morphological distinctions, we suggest to consider *Cryptoleptodon* as a separate genus. This conclusion is also supported by the statistical support of each clade (*Leptodon* and *Cryptoleptodon*) which higher than the support of their common clade, both from Bayesian and maximum parsimony analyses.

Резюме

Описанную из Грузии по сборам 1877 года *Leskea catenulata* subsp. *remotifolia* с тех пор более в стране на находили. Недавние исследования выявили ее таксономическую идентичность с ирано-гирканским видом, традиционно называвшимся *Pseudoleskeella laxiramea*. Последние работы относили его к другим родам, а именно или к *Forsstroemia*, или к *Leptodon*. В 2022 году вид был повторно собран в Грузии, к 15 км от *locus classicus*. По последовательностям ITS он оказался полностью идентичным иранским растениям. Вместе с тем, в молекулярно-филогенетическом дереве по последовательностям ITS он оказывается в кладе с *Cryptoleptodon pluvinii*, тогда как *Leptodon smithii, L. longisetus* и *L. corsicus* образуют сестринскую кладу. Ввиду того, что виды этих клад значительно отличаются морфологически, мы предлагаем считать *Cryptoleptodon* отдельным родом. Этот вывод поддерживается и тем, что статистические поддержки обеих клад, *Leptodon* и *Cryptoleptodon,* значительно выше, чем поддержка их совместной клады и в Байесовом анализе, и в анализе методом максимальной парсимонии.

KEYWORDS: mosses, rare species, ITS, taxonomy

INTRODUCTION

The moss flora of the Caucasus was first comprehensively described by Brotherus (1892). He introduced a number of new taxa from this region, and these were later restudied and discussed in numerous publications. Some of them, however, remained enigmatic and variously treated until the recent time, partly because of the lack of recent collections. The species discussed in the present paper is one such taxon. *Leskea catenulata* subsp. *remotifolia* Lindb. ex Broth. was originally collected by Brotherus in 1877 from the valley of the Rioni River and then described by him in Musci Caucasici (Brotherus, 1892). No collection of it was reported from the Caucasus since then.

Later *Leskea catenulata* subsp. *remotifolia* was mentioned by Schiffner (1908) in the publication with the description of *Leskea laxifolia* from Iran, which, according to him, was very similar to the former taxon. Schiffner hesitated to synonymise these taxa because of lack of any material of *Leskea catenulata* subsp. *remotifolia* for study.

Subsequently Townsend (1966) studied the original material of *Leskea catenulata* subsp. *remotifolia* and came to the conclusion of its identity with a rather widespread Iranian species, *Leskea laxifolia*. Hedenäs & Zare (2010) additionally studied the Iranian material and argued for a generic position in the genus *Forsstroemia* Lindb. as *F. remotifolia* (Lindb. ex Broth.) Hedenäs & Zare, placed

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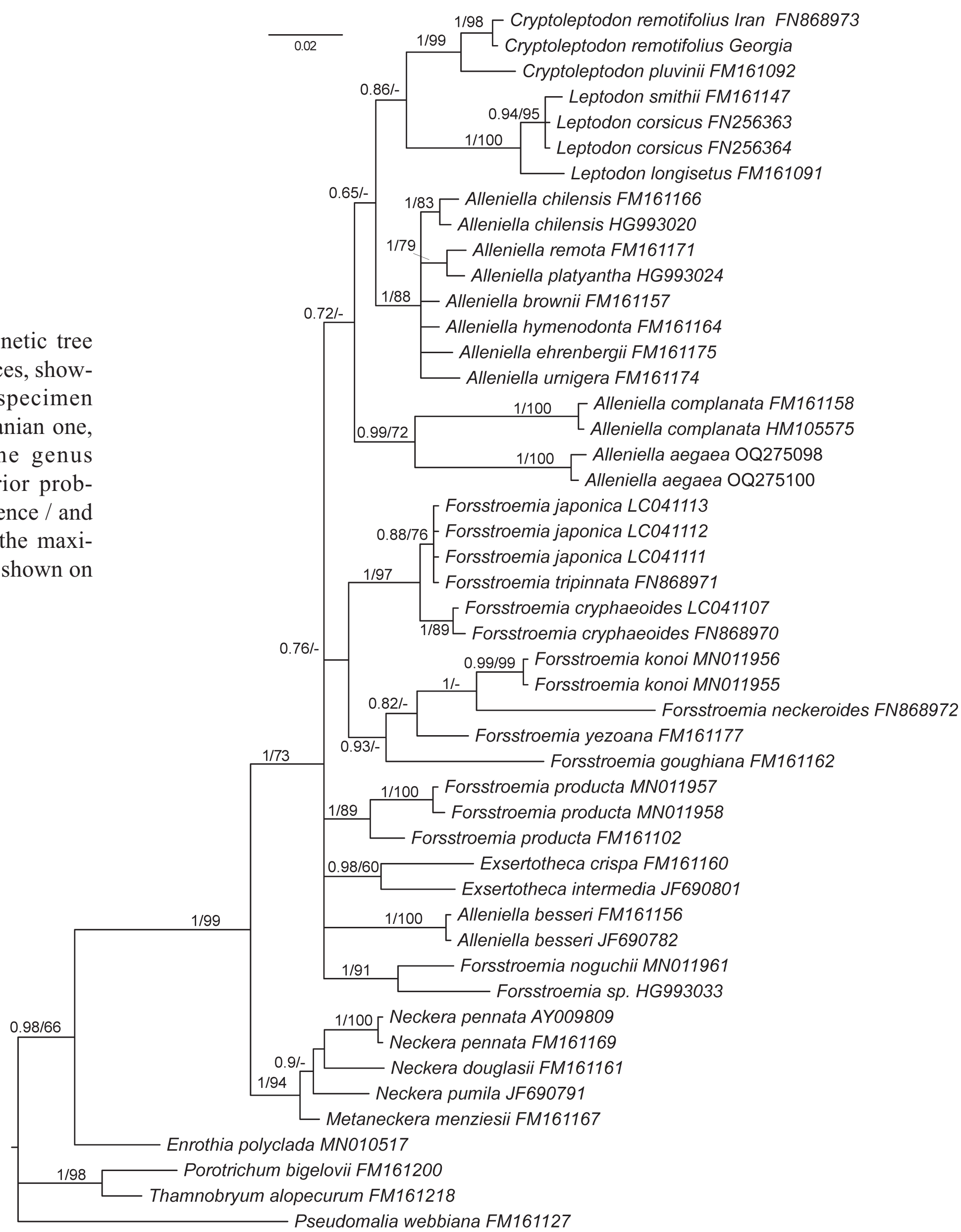

Fig. 1. Bayesian phylogenetic tree based on nuclear ITS sequences, showing position of Georgian specimen (Nosova #22-01) sister to Iranian one, and their placement in the genus *Cryptolentodon*. The posterior probabilities from Bayesian inference / and the Bootstrap support from the maximum parsimony analysis are shown on the branches.

in the Neckeraceae, not Leskeaceae, where this species was attributed by previous authors. Shortly after that, a molecular phylogenetic studies of Olsson *et al*. (2012) suggested another generic placement of the species in question: their analysis of ITS and two plastid markers put it into the genus *Leptodon* D. Mohr, as *L. remotifolius* (Lindb. ex Broth.) S.Olsson, Enroth, Huttunen & D. Quandt. This genus also belongs to the Neckeraceae, but *L. remotifolius* is looking very different from *Leptodon smithii* (Dicks. ex Hedw.) F. Weber & D. Mohr, the type of the genus and a widespread species in the Caucasus, southern Europe and many other parts of the world.

In the course of random collecting in 2022, Nosova collected a specimen of the species in question in Georgia, in the vicinity of Kutaisi Town, about 15 km from the locus classicus of *Leskea catenulata* subsp. *remotifolia.* The aim of this paper is to check the identidy of this taxon with the Iranian population using molecular markers, and to elucidate, as much as possible, its generic position.

Material and Methods

We sequenced two regions: the nuclear internal transcribed spacer region, including ITS1, gene 5.8S RNA and ITS2, and a plastid region including rps4 gene (partial), tRNA-Thr gene, tRNA-Leu gene and tRNA-Phe gene, partial. Both of them proved to be informative in previous studies of pleurocarpous mosses as a whole (Huttunen *et al*., 2012), and the Neckeraceae in particular (Olsson *et al*., 2009a,b,c, 2011, 2012; Ignatov *et al*., 2019; Blockeel *et al*., 2023).

The laboratory protocol for DNA extraction, amplification and sequencing was the same as described in, e.g., Gardiner *et al*. (2005), and in Olsson *et al*. (2009a) for *trn*S-F.

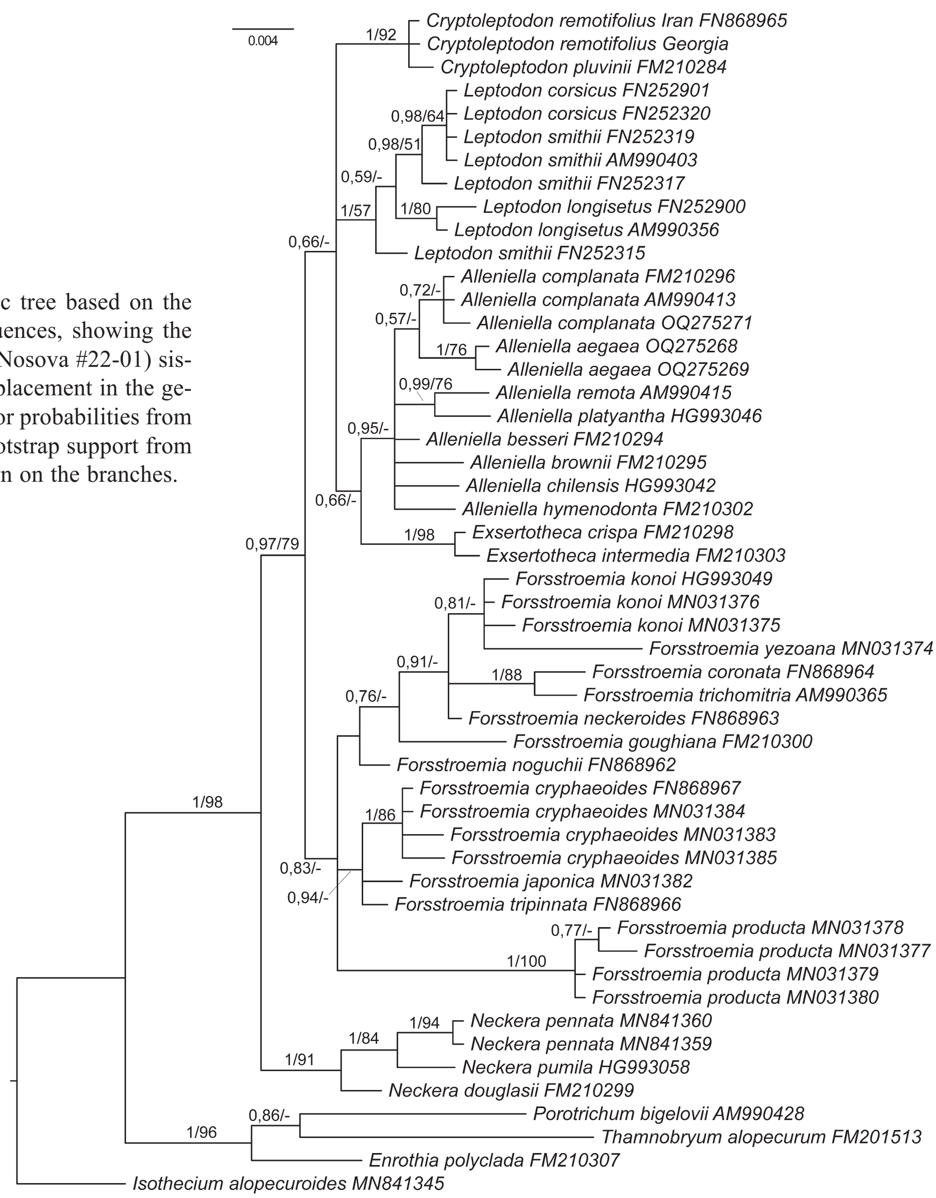

Fig. 2. Bayesian phylogenetic tree based on the plastid rps4-*trn*T-*trn*L-*trn*F sequences, showing the position of Georgian specimen (Nosova #22-01) sister to the Iranian one, and their placement in the genus *Cryptoleptodon*. The posterior probabilities from Bayesian inference / and the Bootstrap support from the parsimony analysis are shown on the branches.

Nuclear and plastid sequences were analysed separately. They were aligned using MAFFT v. 7.505 (2022/Apr/10) with the E-INS-i aligning strategy with otherwise default options, and after that checked for obvious inconsistencies manually. Aligned ITS sequences (798 positions) were complemented by coded indels, and indels of any length were coded manually (C deletion, T insertion) as single mutational events (72 positions).

The plastid alignment has fewer gaps, which were not coded, and the 3-bp fast inversed region in the trnL was deleted following Quandt & Stech (2004).

The Bayesian analysis was performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012) with the GRT+G model, and run with 10 000 000 generations (reached all PSRF equal to 1.000, and ESS>1000) for ITS, and for plastid region 5000000 generations were used, as they already gave the same result. Partitioning follows initially suggested partitions, nruns=4, nchain=6, temp=0.02. Maximum parsimony analyses were performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculations for 1000 replications (using the following parameters: N search reps 100, starting trees per rep 100, max trees 100, 'do max').

Results

The molecular phylogenetic tree based on ITS resolved the Georgian plant in a mutual clade with the Iranian one (Fig. 1) with high support (PP=1, BS=98).

The general tree topology has a basal grade of three early divergent groups: *Enrothia, Thamnobryum + Porotrichum, Metaneckera + Neckera* and a terminal clade comprised by a broad polytomy formed by species currently referred to the genera *Forsstroemia, Exsertotheca, Alleniella, Leptodon* and *Cryptoleptodon*. Among the latter group, *Forsstroemia, Exsertotheca,* and *Alleniella besseri* are spread in polytomy in small clades of which only clades with one or two species obtain maximal Bayesian support (PP=1).

Fig. 3. Georgian locality of *Cryptoleptodon remotifolius* (A), and the plant habit (B, C, photos of the herbarium specimen).

The biggest clade in this polytomy includes nine species of *Alleniella* and five species of the former *Leptodon* s.l. (including *Cryptoleptodon*). The mainly European *A. complanata* + *A. aegaea* form a clade (P=0.99, BS=0.72) sister to all other species that form two subclades. One combines tropical and South American *Alleniella* (PP=1, BS=100). Another clade includes *Leptodon* s.l., with low support (PP=0.86, BS<60), whereas its two subclades are well supported. The first subclade comprises *Leptodon* s.str., including *L. smithii, L. corsicus* and *L. longisetus*, while the second includes *Cryptoleptodon pluvinii* and '*Leptododon remotifolius*' from Iran and Georgia (PP=1, BS=98).

The plastid sequence tree (Fig. 2) is similar to the ITS one. However, the species of *Forsstroemia* and *Alleniella* in this case are not mixed, and both found in their own monogeneric clades, albeit with low support.

Cryptoleptodon and *Leptododon* do not form sister clades, being resolved in a tritomy with the clade of *Alleniella*+*Exsertotheca*. The clade of *Leptodon* is maximally supported in the Bayesian analysis (PP=1), while in MP it is not supported (BS=57). The *Cryptoleptodon* clade has support in both the Bayesian (PP=1) and MP analyses (BS=92); note that the latter value exceeds support of many monospecific clades, e.g. *Leptodon longisetus* (80), *Forsstroemia cryphaeoides* (86), *Alleniella aegaea* (76).

Discussion

The almost total identity of sequences of the Georgian and Iranian plants, and the statistical proof of their close relationship supports the previously made conclusions of their conspecifity, achieved by morphological studies (Townsend, 1966; Hedenäs & Zare, 2010).

The Caucasian plants are somewhat smaller than the Iranian ones, for which the plant size was reported up to 25 cm (Hedenäs & Zare, 2010; Frey & Probst, 1974). It can, however, be explained by the fact, that in Iran the species is rather frequent in humid forests, meaning that the best developed individuals are available for study

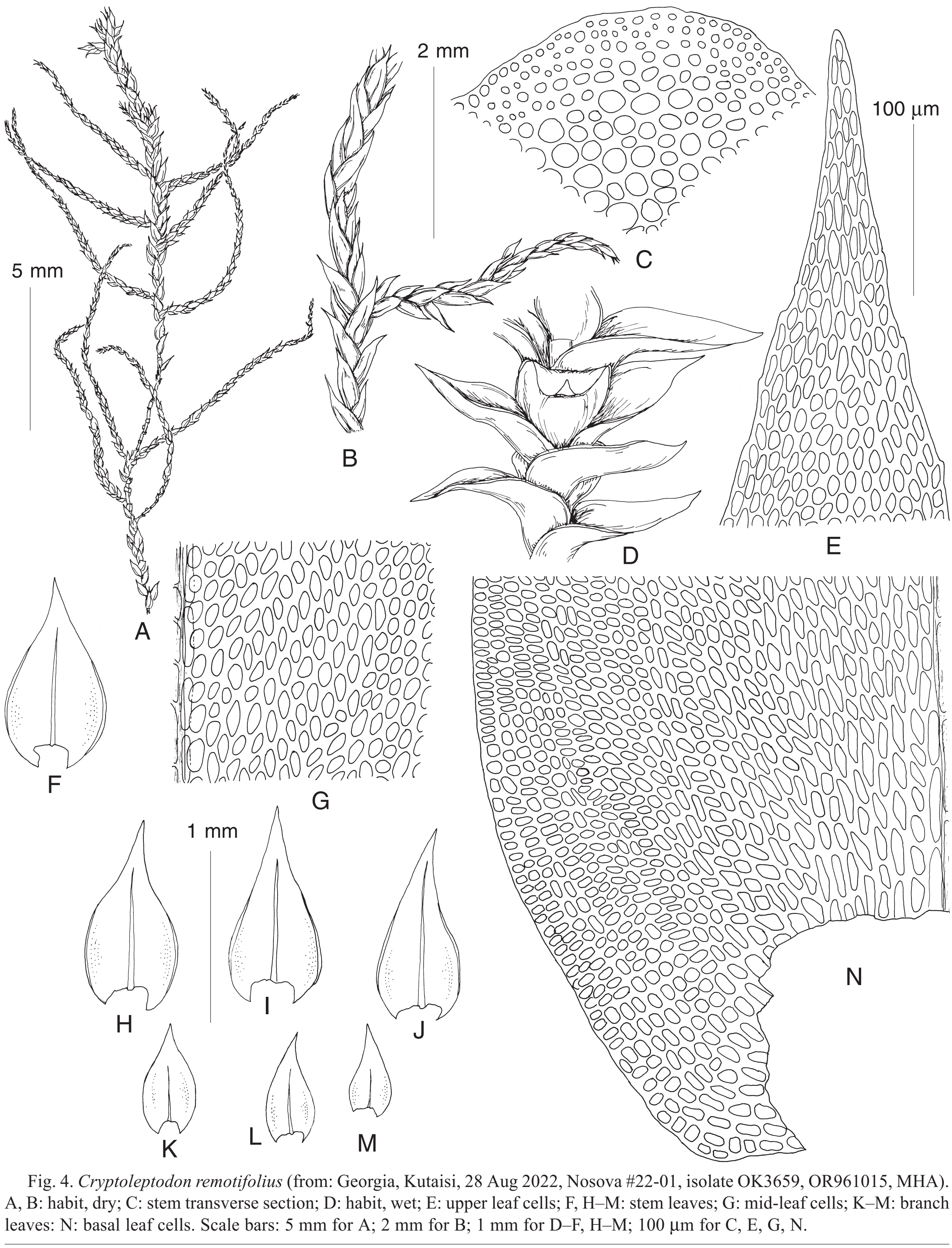

Fig. 4. *Cryptoleptodon remotifolius* (from: Georgia, Kutaisi, 28 Aug 2022, Nosova #22-01, isolate OK3659, OR961015, MHA). A, B: habit, dry; C: stem transverse section; D: habit, wet; E: upper leaf cells; F, H–M: stem leaves; G: mid-leaf cells; K–M: branch leaves: N: basal leaf cells. Scale bars: 5 mm for A; 2 mm for B; 1 mm for D–F, H–M; 100 µm for C, E, G, N.

while we saw only a limited number of shoots from a dry rock outcrop (Fig. 3).

The generic placement is more intriguing. The complicated history of the generic placement of this species is seen already from the nomeclatural citations (below). The slender habit and short laminal cells indicate similarity with *Leskea* (especially in a broad circumscription of this genus, used in the 19th century), *Pseudoleskea* and *Pseudoleskeella*, which were referred to the Leskeaceae during the 20th century. Hedenäs & Zare (2010) not-

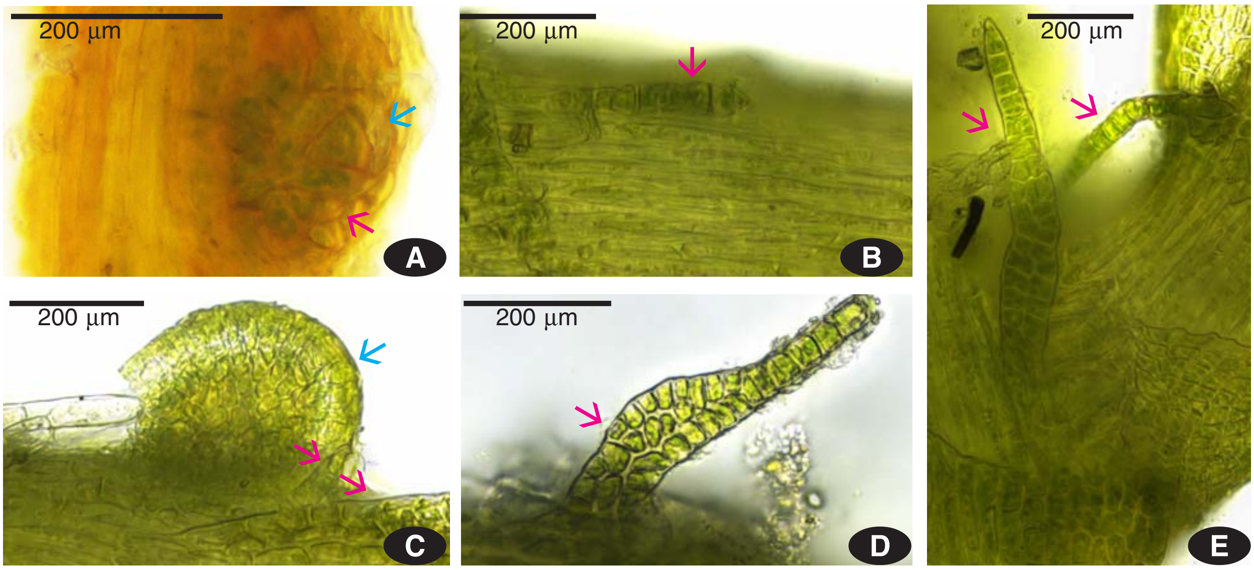

Fig. 5. Branch primordia of *Cryptoleptodon remotifolius* (from: Georgia, Kutaisi, 28 Aug 2022, Nosova s.n., MHA), surrounded by linear outer proximal branch leaves (red arrow) and inner contrasingly different broadly triangular leaves (blue arrows). A similar differentiation between outer and inner proximal branch leaves occurs in *Alleniella* (Ignatov et al., 2021) and *Leptodontium* (Spirina et al., 2020). Broad and narrow proximal leaves are discernible already around branch apical cell (A). Linear leaves may be developed near very poorly delevoped buds (B, D), but may be short near well-developed oes (e.g. C); they are usually retain at base of branches (E).

ed that the the plant size, leaf lamina areolation and conspicuous perichaetial branches are more similar to the genus *Forsstroemia*, especially to *F. indica*, and therefore placed the species in the latter genus, with a detailed comparison between Iranian plants and *F. indica,* showing a number of important distinctions.

Shortly after that, Olsson et al. (2012) referred this species to the genus *Leptodon* based on results of molecular phylogenetic data. This genus, as well as *Forsstroemia*, belongs in the family Neckeraceae, where the generic limits have been drastically changed in the course of recent studies. Worth noting, however, is that before the placement in the Neckeraceae, *Leptodon* and *Forsstroemia* were refered to the Leptodontaceae (Stark, 1987; Enroth, 1992). Also worth noting is that the circumscription of the genus *Leptodon* is not fully identical in different molecular phylogenetic trees: in some of them, the genus *Cryptoleptodon* is accepted along with *Leptodon* (Olsson et al., 2009a)*,* whereas in some others the species sometimes treated in *Cryptoleptodon* are included in *Leptodon* (Olsson et al., 2009b, 2011; Sotiaux et al., 2009)*.* The latter approach has been applied also in the publication of Olsson et al. (2012), where the discussed species has been transferred to the genus *Leptodon*, despite striking morphological dissimilarity.

A similar drastic morphological heterogenity appeared in several genera of the Neckeraceae after molecular phylogenetic studies. Especially surprising were the transfers: (1) of *Alsia californica*, a moss with julaceous foliage and ovate-lanceolate and long acuminate leaves to *Neckera*, where the foliage is complanate and the leaves mostly lingulate, often undulate and apicaly rounded to acute, or at best shortly acuminate; (2) of combining in *Forsstroemia* plants with similarly different leaf shapes, referred previously to the Cryphaeaceae and Neckeraceae (e.g. Noguchi & Iwatsuki, 1989). Therefore the broadening the circumcription of the *Leptodon* is at least not totally exceptional. However, the present analysis suggets a retaining of *Leptodon* as a more homogeneous entity, including only plants with apically rounded leaves.

The type species of the genus *Cryptoleptodon* is *Neckera flexuosa* Harv.*,* currently treated as a synonym of *Cryptoleptodon pluvinii* (Brid.) Broth. This is a large plant with broadly ovate concave leaves and julaceous tumid foliage. It seems that it is quite variable, as e.g. and Chopra (1975) described the branches of *C. pluvinii* as straight, while Enroth (1992) disagreed and provided a photo of the holotype of *C. pluvinii* with somewhat circinate branches. The illustrations of *Neckera flexuosa* in Hooker (1836) shows apiculate or shortly acute leaves, while Gangulee (1976) illustrated its leaves as rounded. In addition, Fleischer (1917) described *Cryptoleptodon acuminatus* M. Fleisch. as a species similar to *C. pluvinii*, but with more robust plants and acuminate leaves. Therefore, the Georgian plants disagrees with *Cryptoleptodon* less than with *Leptodon*. Summing up, all the above mentioned evidence is in favor of the placement of Caucasian and Iranian species in the genus *Cryptoleptodon.*

Taxonomy

Cryptoleptodon remotifolius (Lindb. ex Broth.) Ignatov, comb. nov. — BASIONYM: *Leskea catenulata* subsp. *remotifolia* Lindb. ex Broth., Acta Soc. Sci. Fenn. 19(12): 96. 1892. — *Pseudoleskea remotifolia* (Lindb.

ex Broth.) Paris, Index Bryol. 1037. 1898. — *Leskea remotifolia* Lindb. ex Paris, Index Bryol. 1037. 1898, nom. inval. —*Pseudoleskeella catenulata* subsp. *remotifolia* (Lindb. ex Broth.) Podp., Consp. Musc. Eur. 528. 1954. — *Forsstroemia remotifolia* (Lindb. ex Broth.) Hedenäs & Zare, Nova Hedwigia, Beiheft 138: 62. 2010. — *Leptodon remotifolius* (Lindb. ex Broth.) S.Olsson, Enroth, Huttunen & D. Quandt, J. Bryol. 34: 120, 2012.

TYPE: *Pseudoleskeella catenulata* **P. remotifolia* (Lindb.) [Georgia] Bryotheca Caucasica. Imeretia, Mekvena ad fl. Rion, ad moles umbr. calcar., 6/6 1877, leg. V. F. Brotherus (by Hedenäs & Zare, 2010, isotypes in S, reg. no. B169789, BM; holoype in H (not seen)).

SYNONYMS: *Leskea laxiramea* Schiffn., Österr. Bot. Z. 58: 344. 9 f. 55–60. 1908. *Pseudoleskeella laxiramea* (Schiffn.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 304. 1925. TYPE: Iran, FH, reg. no. 286647 (see Hedenäs & Zare, 2010).

Description (based on the new Georgian specimen): *Plants* in extensive, more or less loose mats, green to olive-green, with oily luster, readily turning to brownish with age. *Stem* creeping, to 5(10) cm long, with alternation of small-leaved and more large-leaved parts, distantly and somewhat irregularly pinnate, branches deviating at about right angle, often attenuate, 6–10 mm, without central strand; outer proximal branch leaves linear, next ones are broadly triangular; axillary hairs 3–5-celled, to 50 µm long. *Stem leaves* erect to appressed when dry, spreading from erectopatent base (large leaves) to erect to patent (smaller leaves), straight to slightly homomallous, 0.9–1.2×0.4–0.6 mm, ovate, gradually rounded to insertion and broadly decurrent, shortly acuminate above, concave, not plicate; costa to 0.5–0.8 the leaf length, 40–50 µm wide near base; margins entire or slightly crenulate, recurved in lower half on one or both sides; median leaf laminal cells 10–20×6–12 µm, ovate to ovate-rhomboidal, thick-walled, smooth, shorter towards margins; basal juxtacostal cells large, to 45 µm long; in alar region numerous cells small, isodiametric to transversely elongate, 5–10 µm long, transversely elongate. *Branch leaves* smaller and longer acuminate. The rest unknown in new specimen [description of perigonia, perichaetia, gametangia and young sporophyte is provided by Hedenäs & Zare, 2010].

Specimen: Georgia, ca. 10 km north of Kutaisi, ca. 42.19 N, 42.41E, 450 m elev., on limestone rock outcrop on a hill slope, Coll. M. Nosova #22-01, 28 Aug 2022, MHA9135059, MW9092494).

The hills where the new find was made (Fig. 3) are composed of Cretaceous limestones, Paleogene limestones, Quaternary sand and gravel deposits (Kralik *et al*., 2014). The climate in Tskhaltubo (ca. 6 km W from the locality of *C. remotifolius*) is characterized by mean temperatures of 5.3°C in January and 23.3°C in July, and the mean annual precipitation 1800 mm (Elizbarashvili & Gongladze, 1980). The vegetation is represented here by temperate rainforest of Colchic type (Nakhutsrishvili, 2012; Nakhutsrishvili *et al*., 2015), providing a refugium for the Caucasian Tertiary flora and is one of the Mediterranean biodiversity hotspots. It is located on the slopes of barrier-mountains of the Great Caucasus Range, a trap of the humid air masses from the Black Sea.

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