BRYOPHYTES — МОХООБРАЗНЫЕ

Northernmost mainland record and differentiation of *Metacalypogeia cordifolia* (Calypogeiaceae, Marchantiophyta)

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Abstract. *Metacalypogeia cordifolia* is recorded for the first time for the Republic of Sakha (Yakutia) from the Udokan Range. The species was found in the shaded narrow with nearly vertical walls gorge, about 1.5 m wide and 2–3 m high, that accumulates snow, covering the plants in winter and has a seepage, watering the plants in summer. It is the northernmost mainland record of *M. cordifolia*. The identification is confirmed by obtained complete *trn*L-F cpDNA sequences corresponding to available sequences of *M. cordifolia* from the Russian Far East and Japan. The description of collected plants, their photomicrographs, and data on morphological variation, ecology, and distribution of *M. cordifolia* are provided. The key to distinguish *M. cordifolia* from morphologically similar northern taxa is presented. Differentiation of the genus from morphologically similar representatives of the genera *Bazzania*, *Eocalypogeia*, *Calypogeia*, *Mnioloma*, and *Protocalypogeia* is discussed. A joint analysis of bioclimatic data and habitat conditions, along with the absence of traces of glaciation at the place of gathering the species, indicate that it is a refugium. *Metacalypogeia cordifolia* in the Udokan Range appears to be an Eopleistocene relic.

Keywords: *Metacalypogeia*, distribution, hepatics, liverworts, rare species, Russian Far East, Republic of Sakha (Yakutia), Russia.

Самая северная континентальная находка и отличия *Metacalypogeia cordifolia* (Calypogeiaceae, Marchantiophyta)

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Резюме. *Metacalypogeia cordifolia* впервые выявлен для Республики Саха (Якутия) с хребта Удокан. Вид обнаружен в затененном узком ущелье с почти вертикальными стенками, шириной около 1.5 м шириной и глубиной 2–3 м, в котором зимой скапливается снег, скрывающий печеночники, а летом сочится вода, увлажняющая их местообитание. Это самое северное континентальное местонахождение *M. cordifolia*. Идентификация подтверждается полученной последовательностью *trn*L-F хпДНК, соответствующей доступным последовательностям *M. cordifolia* с российского Дальнего Востока и Японии. Приведено описание образца, микрофотографии и данные о морфологической изменчивости, экологии и распространении *M. cordifolia*. Представлен ключ для отличия *M. cordifolia* от морфологически сходных северных таксонов. Обсуждены отличия рода *Metacalypogeia* от представителей родов *Bazzania*, *Eocalypogeia*, *Calypogeia*, *Mnioloma* и *Protocalypogeia*. Совместный анализ биоклиматических данных и условий местообитания, наряду с отсутствием следов оледенения в месте сбора вида, указывают на то, что оно представляет собой рефугиум. *Metacalypogeia cordifolia* на хребте Удокан является, по-видимому, эоплейстоценовым реликтом.

Ключевые слова: *Metacalypogeia*, печеночники, распространение, редкие виды, Дальний Восток, Республика Саха (Якутия), Россия.

The genus *Metacalypogeia* (S. Hatt.) Inoue was erected from the subgenus *Metacalypogeia* S. Hatt. of the genus *Calypogeia* Raddi (Hattori, 1957; Inoue, 1959). The principal distinctions of *Metacalypogeia* from the related genus *Calypogeia* are: 1) capsule valves moderately elongated, less than 3 times as long as wide, not or slightly twisted (vs. linear, over 3 times as long as wide, twisted);

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2) epidermal cells of capsule having minor nodular thickenings on longitudinal and partly on adjacent latitudinal walls vs. continuous thickenings on some longitudinal walls. Besides those, in the northern part of the range, *Metacalypogeia* is also distinct from *Calypogeia* in: 1) often larger finely granulate oil bodies and chloroplasts (Hattori, 1957; Inoue, 1959); 2) common brown secondary pigmentation.

When describing the subgenus *Metacalypogeia*, it included its type species — *Calypogeia sendaica* Steph., and *C. verruculosa* S. Hatt. (Hattori, 1957). Two years later, H. Inoue discovers mature sporophytes of previously known sterile *Calypogeia cordifolia* Steph. Relying upon the capsule, leaf surface and oil body characters, he attributes *C. cordifolia* to *Metacalypogeia* and recognizes it as a separate genus (Inoue, 1959) with two species, *M. cordifolia* and *M. montana* (Horik.) Inoue that is now included in synonyms of *M. alternifolia*, and was firstly recognized as *Bazzania montana* Horik. (Horikawa, 1932). *Metacalypogeia cordifolia* is designated by Inoue (1959) as the type species of the genus *Metacalypogeia* instead of *C. sendaica* — the type species of the subgenus *Metacalypogeia*. In the above cited article of Inoue (1959), the following species are listed as synonyms of *M. cordifolia*: *Calypogeia sendaica* Steph., *C. stephaniana* Beauverd, and *C. viridis* Steph. In 1963, Inoue (1963) adds to the list of synonyms *C. rigida* Horik. Later, Inoue (1974) for unknown reasons omits the latter species in the list of synonyms. Despite rather numerous synonyms provided below with the species description, they all are heterotypic, and their correctness needs to be carefully tested. Phylogenetically *M. cordifolia* and *M. alternifolia* are sister related and compose a strongly supported clade within Calypogeiaceae (Masuzaki *et al.*, 2010).

Metacalypogeia cordifolia is a temperate Pacific-East Asian species, occurring in oceanic and suboceanic territories with isolated locations in the mainland (Fig. 1), whereas *M. alternifolia* is mostly Sino-Himalayan species that reaches insular parts of East Asia (Bakalin *et al.*, 2020; Klimova *et al.*, 2024) and spreads northwards to Hokkaido I., Japan (Yamada, Iwatsuki, 2006). The former species is known from Russia, whereas the latter is considered as provisional (Potemkin, Sofronova, 2009), but not recorded from Russia yet.

Identification of collection gathered in 2002 in the Udokan Range (Fig. 2A), SW Yakutia, that is located 21 km NNW northwards from the railway station Olekma and about 1000 km westwards from the Sea of Okhotsk (Fig. 1), resulted in the find of *Metacalypogeia cordifolia*. It has cells mostly with decomposed oil bodies and looks like questionable small *Calypogeia*-like hepatic. These facts raised the problem of their differentiation, and initiated the molecular study and comparison of the specimen.

Taking into account that Yakutian plants differ from the southern population of *Metacalypogeia cordifolia*, the goal of our study is to make a comprehensive illustrated description of *Metacalypogeia cordifolia* focused on Yakutian plants and to characterize its variability, ecology, distribution, and differentiation from similar northern species, which important for its further finds, in the mainland, particularly.

Fig. 1. Distribution of *Metacalypogeia cordifolia*. Grey shadow — main range, black circles — disjunctive localities: SW Yakutia, Udokan Range (this report), Ayan Settlement surroundings, Pribrezhnyi Range (Bakalin *et al.*, 2021a), Attu Island in Aleutian Islands (Talbot *et al.*, 2018), Guizhou Province of China (Bakalin *et al.*, 2015).

Material and Methods

Specimens examined. **Russia, Republic of Sakha (Yakutia),** Udokan Range, 21 km north-northwest from the railway station Olekma, gorge, on soil over rocky wall with *Anastrophyllum* sp., *Blepharostoma trichophyllum* (L.) Dumort., *Cephalozia bicuspidata* (L.) Dumort., *Scapania parvifolia* Warnst., *Schistochilopsis incisa* (Schrad.) Konstant., *Sphenolobus minutus* (Schreb.) Berggr., *Trilophozia quinquedentata* (Huds.) Bakalin, [57°09′N, 120°31′E, 1000–1100 m a. s. l.], 30 VII 2002, *Sofronova 02-07-30-01*, LE B-0028867, SASY; **Khabarovsk Territory**, Tardoki-Yani Range, southern spur of Sukhaya Pad' Stream middle course,

Fig. 2. A — Udokan Range near the study area, B — Vertical wall of the gorge near the collecting place of *Metacalypogeia cordifolia*. Photo by L. V. Kuznetsova.

2.5 km upstream of its mouth (48°50′N, 138°06′E), 620 m a. s. l. Mixed forest in the flood plain. Mesic cliffs in partial shade on steep slope to stream. 28 VIII 2013, *V. A. Bakalin Kh-45-40-13*, LE (Hepaticae Rossicae Exsiccatae Fasc. IX, 222); *ibid.,* Baidzalsky Mountain System, Yarap River middle course (50°16′52″N, 134°42′45″E), 570 m a. s. l. Moist coniferous forest. Moist cliffs in part shade. 11 VIII 2016, *V. A. Bakalin Kh-25-25-16* , LE B0020390 (Hepaticae Rossicae Exsiccatae Fasc. XIV, 337); [**Sakhalin Region**], Kuril Is., Shikotan I., between Malaya Tserkovnaya and Voloshina bays, larch and bamboo forest, on trunk of larch. 15 IX 2006, *T. I. Nyushko 034.5–06*, LE; [**Primorye Territory**]... Shkotovskii District, Upper Maykhe River, 15 verst from Novo-Khotunichi Village, 3 VIII 1927, *V. Transchel*, det. A. A. Abramova (translated from Russian).

Molecular methods. DNA was extracted from dried plant tissue with HiPure SF Plant DNA Kit (Magen, China). In course of available DNA markers for the genus *Metacalypogeia* in GenBank and our previous study (Vilnet *et al.*, 2011), the *trn*L-F cpDNA was chosen as an appropriate marker to check the identity of Yakutian specimen. Four *trn*L-F accessions of the genus *Metacalypogeia* and *Mnioloma fuscum* (Lehm.) R. M. Schust. as an outgroup species were downloaded from GenBank (Table 1).

Amplification and sequencing of *trn*L-F were performed using primers suggested by Taberlet *et al.* (1991). PCR was carried out in 20 µl volumes with the following protocol: 3 min at 94 °C, 30 cycles (30 s 94 °C, 40 s 56 °C, 60 s 72 °C), 2 min of final extension at 72 °C. Amplicon was visualized on 1% agarose TAE gels by EthBr staining and purified using the Cleanup Mini (Evrogen, Russia). The sequencing reactions were provided with the ABI Prism BigDye Terminator v. 3.1 Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3730 DNA Analyzer (Applied Biosystems, USA).

Obtained sequence was assembled and aligned with downloaded accessions in BioEdit 7.0.1 (Hall, 1999). The variability of *trn*L-F was evaluated as *p*-distances in Mega 11 (Tamura *et al.*, 2021) using the pairwise deletion option for counting gaps. Phylogeny was tested by maximum likelihood method with program IQTree (Nguyen *et al.*, 2015) with the HKY+F as the best-fit evolutionary model of nucleotide substitutions selected in Modelfinder (Kalyaanamoorthy *et al.*, 2017) and ultrafast bootstrapping procedure with 1000 iterations (Hoang *et al.*, 2018).

Table 1

The list of specimens included in phylogenetic estimation

The sequence obtained in this study is in bold

Taxon	Specimen voucher	GenBank accession number, *trn*L-F cpDNA
Metacalypogeia cordifolia	Russia: Republic of Sakha (Yakutia), *E. V. Sofronova, 02-07-30-01* (LE B-0028867)	**PV261148**
M. cordifolia	Russia: Primorye Territory, *V. A. Bakalin, P-66-18a-06* (KPABG)	JF421597
M. cordifolia	Japan: Aomori, Mt. Iwaki, *M. Ota, 9200* (CBM)	LC732102
M. alternifolia	Bhutan, *D. G. Long, 28712* (E)	KJ802068
M. alternifolia	Japan: Nagano, Mts. Yatsugatake, *T. Furuki, 25335* (CBM)	LC732098
Mnioloma fuscum	Fiji: *J. E. Braggins et al.* 16 Apr. 2008 (NSW)	KJ802100

Climate data. For comparison of the climate conditions through the species range, we obtained data on 19 Bioclimates (Worldclim, 2020–2022) of nine species locations from North to South (Electronic Supplement[1]). Bioclimatic data from the location in the Primorye Territory, Oblachnaya Mt., were taken from Klimova *et al.* (2024). The other data, obtained from Worldclim (2020–2022), are for the following collecting site locations: Udokan Range (this report); Pribrezhnyi Range, Khabarovsk Territory (Bakalin *et al.*, 2021a); Murder Point, Attu Island, Alaska, USA (Talbot *et al.*, 2018); Mt. Mantou, Heilongjiang Province, NE China[2] (Piippo, 1990); Japanese Minami-Alps, Honshu Island, Japan (Melechin *et al.*, 2021a); Mt. ?Deokgyu [spelled as Dyukyu], Deokgyusan National Park, Republic of Korea (Melechin *et al.*, 2021b); Doupeng Mts., Guizhou Prov., and Mt. Yù Shān, Nantou Co., Island of Taiwan, SE China (Bakalin *et al.*, 2015; Yao, Yang, 2023, respectively); Mt. Pulog, Luzon Island, Philippines (Del Rosario, 1975).

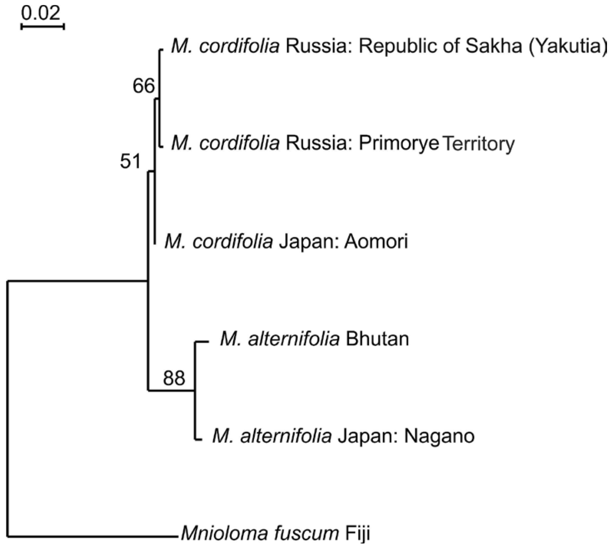

Fig. 3. The phylogram for the genus *Metacalypogeia* obtained from the maximum likelihood method based on *trn*L-F cpDNA sequence data. Bootstrap support values are indicated.

Results

Molecular study. The *trn*L-F alignment includes 450 positions. The arithmetic mean of log likelihood in ML analysis was -1445.961. Obtained tree topology is shown in Fig. 3. Yakutian specimen of *Metacalypogeia cordifolia* was located in a clade with two specimens from the Primorye Territory, Russia, and from Japan. Two specimens of *M. alternifolia* from Bhutan and Japan composed a clade that is sister related to clade with three *M. cordifolia* specimens.

The variability of *trn*L-F sequences among three *M. cordifolia* specimens is 0.4%, among *M. alternifolia* — 0.9%, interspecific variability counts 2.1–2.8% (Table 2). Phylogenetic position and level of sequence similarity achieved from *trn*L-F sequence data clearly suggested Yakutian specimen as *M. cordifolia*.

Morphological study. The description below is based on the Yakutian impoverished specimen. Characters in square brackets are known from the descriptions of more southern Japanese populations of *Metacalypogeia cordifolia* mainly and not developed in our material.

[1] Electronic supplement is available at the end of the article page on the journal website (https://doi.org/10.31111/nsnr/2025.59.2.B1).

[2] Having no certain data on the collecting localities in NE China and relying upon not always congruent published data on the occurrence of *Metacalypogeia cordifolia* in NE China (cf.: Gao, Chang, 1981; Inoue, 1981; Piippo, 1990), we selected a location for the bioclimatic comparison with similar conditions that located south-southeast of our collecting place in the Udokan Range.

Table 2

The values of *p*-distances of *trn*L-F cpDNA for the genera *Metacalypogeia* and *Mnioloma*, %

	Taxon	1	2	3	4	5
1	*Metacalypogeia cordifolia* Yakutia					
2	*M. cordifolia* Primorye Territory	0.4				
3	*M. cordifolia* Japan	0.4	0.4			
4	*M. alternifolia* Bhutan	2.4	2.2	2.2		
5	*M. alternifolia* Japan	2.1	2.1	2.8	0.9	
6	*Mnioloma fuscum* Fiji	13.6	13.3	13.3	14.8	14.0

Metacalypogeia cordifolia (Steph.) Inoue, 1963, J. Hattori Bot. Lab. 21: 233. (Fig. 4)

≡ *Calypogeia cordifolia* Steph., 1908, Bull. Herb. Bois., ser. 2, 8(9): 661 [= Species Hepaticarum 3: 393].

= *Calypogeia heterophylla* Steph., 1924, Species Hepaticarum 6: 448, nom illeg., homonym of *Calypogeia heterophylla* (Steph.) Steph., 1908, Species Hepaticarum 3: 407.

= *Calypogeia sendaica* Steph., 1924, Species Hepaticarum 6: 451.

= *Calypogeia viridis* Steph., 1924, Species Hepaticarum 6: 452.

= *Calypogeia stephaniana* Beauverd, 1924, Species Hepaticarum 6: 572 (species epithet for *C. heterophylla* Steph., nom. illeg.)

= *Calypogeia rigida* Horik., 1934, J. Sci. Hiroshima Univ., Series B, Division 2 (Botany) 2: 185.

Plants green, yellowish-green, yellowish to brownish-dark green, brown and fuscous in older shoot sectors, 0.7–1.2[2–3] mm wide and (0.3)0.5[1–3] cm long. Stem ± fleshy, 0.15–0.3 mm wide, 7–10 cells high, not pigmented or brown, cortical cells yellowish to brownish, with not thickened to slightly thickened walls, slightly smaller or larger than the medullary cells, and indistinctly delimited from them. Branching rare [postical-intercalary, without ventral flagellae], not seen. Leaves closely to loosely imbricate, slightly convex, obliquely spreading with sometimes *upturned antical margin near the base of upper leaves* and incurved distal parts of leaves, ovate-triangular, not decurrent, usually with rounded apices, sometimes shortly pointed, shallowly bilobed [or deeply incised to ca. 0.2 the length (Stephani, 1924: 448, description of *Calypogeia heterophylla* Steph.; Horikawa, 1934, Pl. 16: 2)]. Underleaves distant, 1.1–1.6 [2.5[3]] as wide as stem, appressed, [nearly orbicular (a little wider than long)] to reniform, apex truncate, not decurrent, emarginate or occasionally notched or shortly incised. Rhizoid initial zone compact, oval. Cells usually with distinct small to medium, acute to slightly bulging trigones and ± brown cell walls. Apical cells subisodiameric or slightly elongated, 20–30(37) × 20–25 µm. Marginal cells (12)16–27 × (20)24–32(45) µm. Median cells (19)22–32 × (19)24–32(40) µm [23–30 × 30–40 µm]. Basal cells (19)20–30(37) × (24)27–37(45–62) µm [26–36 × 41–54 µm]. Leaf surface delicately, distinctly to indistinctly punctate-verruculose (Figs. 4E, F, J — surface view; Inoue,1959: Fig. 1: h — leaf cross section view). [Oil bodies preserved longer than in *Calypogeia* (Bakalin, pers. com.), however, also disintegrated, occasionally preserving in some cells for decades, like in the Yakutian specimen collected in 2002 (Fig. 4J), gray brown and opaque, ± granulate, sometimes biconcentric, often occlude over half of the cell lumen, variable in size, number, (4)6–20(30) per cell, 3–7 or 5–8 µm in diam., oblong 4–8 × 3–5 µm or larger 6–10 × 5–7 µm (Hattori, 1953: 65, 1957: 83; Inoue, 1959, Schuster, 1969, Bakalin *et al.*, 2021b)]. Gemmae lacking. [Dioicous. Androecia small, from axis of underleaves. Bracts in 2–7 pairs. Marsupium appearing sessile laterally on leading stem. Capsule 2.5– 3 times as long as in diam., the valves weakly twisted. Capsule wall bistratose. Outer layer 2–3 times thicker than inner layer, with thickenings on alternating longitudinal walls: minute nodular, and short delicate incomplete and complete semiannular thickenings on adjacent walls. Inner layer with solid complete semiannular thickenings on longitudinal walls. Spores punctate. Elaters 2-spiral

[3] The different types of the genus *Metacalypogeia* and its precursor, the subgenus *Metacalypogeia*, are described with different underleaf width. According to the protologues of the type of the genus, *Calypogeia cordifolia*, "Amphigastria caulina majuscula subtriplo latiora reniformia transverse inserta" and of the subgenus type *C. sendaica* "amphigastria caulina majuscula, caule triplo latiora" (Stephani, 1924), i. e., less than three times as wide as the stem or three times as wide as stem. Inoue (1963) describes underleaves up to 2.5 as wide as the stem that corresponds results of our study but not corresponds the protologue of *C. sendaica*.

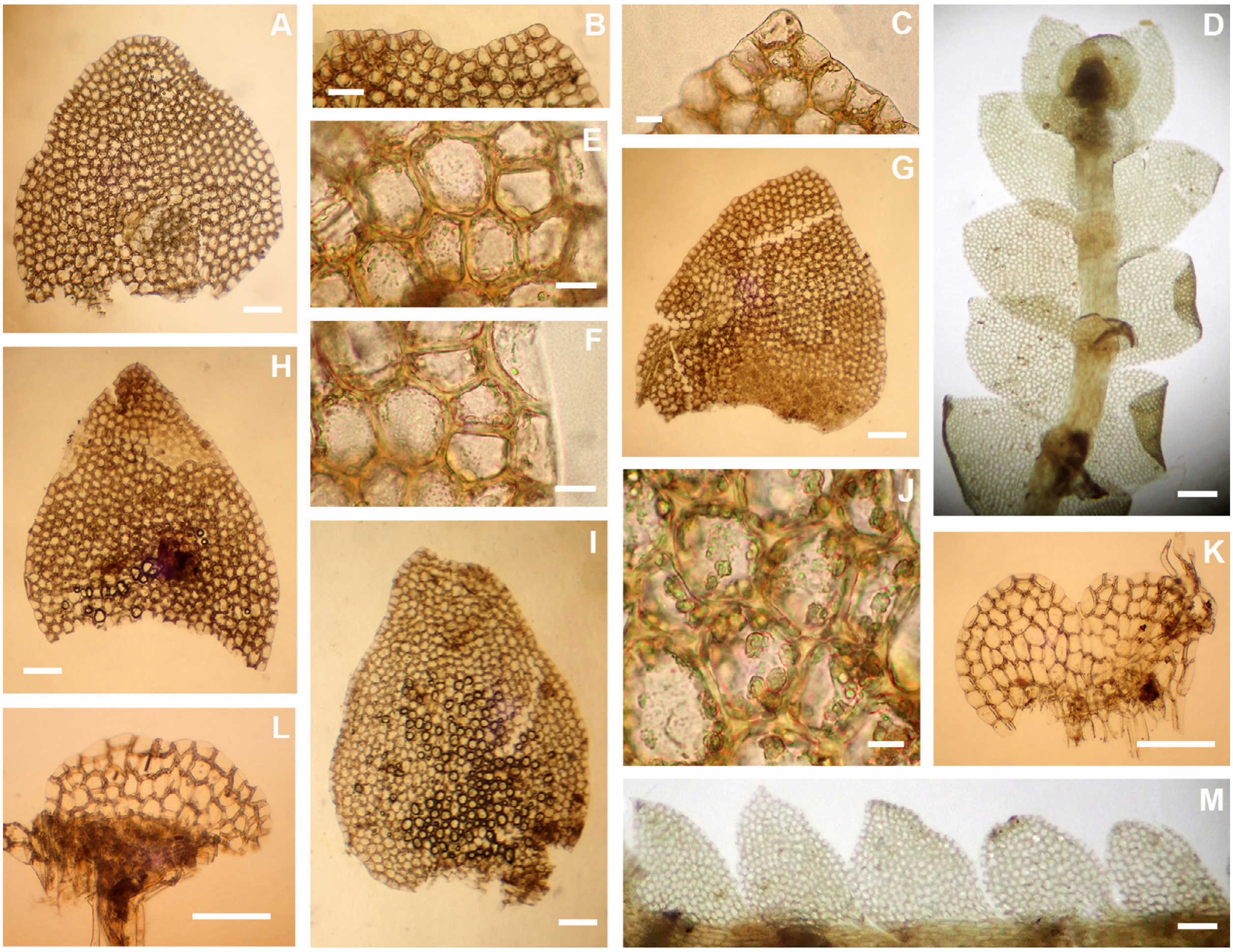

Fig. 4. *Metacalypogeia cordifolia* (LE B-0028867).
A, H, G, I — leaves; B, C — leaf apices; D — shoot sector, postical view; E, F, J — submarginal (E, F) and median leaf cells (J) with distinct punctate-verruculose surface and in J with strongly modified remnants of oil bodies; K, L — underleaves; M — shoot sector, antical view. Scale bars: A, G, H, I, K, L — 100 μm; B — 50 μm; D, M — 200 μm; C, E, F, J — 15 μm.

(Inoue, 1959: Fig. 1, 1974: Pl. 19; Schuster, 1969: 102, 105)].

Illustrations: Horikawa, 1934, Pl. 16: 1–6 (as *Calypogeia rigida*); Hattori, 1953, Pl. I: 10–12 — (oil bodies of *C. sendaica*); Inoue, 1959: Fig. 1, 1974: Pl. 19; Zerov, 1965: Fig. 1; Del Rosario, 1975: Fig. 91; Gao, Chang, 1981: Fig. 6: 1–12; Bakalin *et al.*, 2021b: 314, Figs. 791, 792 (oil bodies); this treatment, Fig. 4.

Ecology. Mountain species restricted to forest belts, growing on soil or/and among mosses on rocks, on moist cliffs in partly shaded places, in Central Japan and NE China also on decaying logs and once on tree base (Inoue, 1962, 1981; Gao, Chang, 1981): in mountain *Larix* forest, i. e., light coniferous forest, in SW Yakutia; in dark coniferous forests in the Russian Far East and Japan; in deciduous, mountain deciduous-coniferous, dark coniferous forests, and elfin wood belt in oceanic and suboceanic territories; 15–2527 m a. s. l. Known associated species according to Inoue (1962), Bakalin *et al.* (2021b) and our data are *Anastrophyllum* sp., *Bazzania denudata* (Lindenb. et Gottsche) Trevis., *Bazzania tricrenata* (Wahlenb.) Lindb., *Blepharostoma* sp., *Blepharostoma trichophyllum*, *Cephalozia bicuspidata*, *Cephaloziella* sp., *Diplophyllum taxifolium* (Wahlenb.) Dumort., *Douinia plicata* (Lindb.) Konstant. et Vilnet, *Herbertus* aff. *buchii* Juslén, *Lepidozia reptans* (L.) Dumort., *Marsupella emarginata* (Ehrh.) Dumort., *Plagiochila porelloides* (Torr. ex Nees) Lindenb., *Scapania stephanii* Müll. Frib., *S. parvifolia*, *Schistochilopsis incisa*, *Solenostoma rossicum* Bakalin et Vilnet, *Sphenolobus minutus*, *Trilophozia quinquedentata*, and *Tritomaria exsecta* (Schmidel) Schiffn. ex Loeske.

Distribution. Mostly temperate East Asian — **Russia**, SW Yakutia, Udokan Range (this report), Khabarovsk Region (Ayan, Khekhtsir, Sikhote-Alin, etc.) (Gambaryan, 2001; Konstantinova *et al.*, 2009; Bakalin, 2015, Bakalin *et al.*, 2021a, Klimova *et al.*, 2024, etc.), Sakhalin Region (Southern Sakhalin and Kuril Is.), Primorye Territory (Zerov, 1965; Bakalin, 2010, etc.); **USA**, Alaska, Attu

I. in Aleutian Is. (Talbot *et al*., 2018); **China**, Heilongjiang, Jilin (Gao, Chang, 1981; Piippo, 1990, etc.), Guizhou (Bakalin *et al*., 2015), Taiwan (Inoue, 1963, etc.); **Republic of Korea** (Choi *et al*., 2021, etc.); **Japan** (Inoue, 1962; Yamada, Iwatsuki, 2006, etc.); **Philippines**, Luzon (Del Rosario, 1975: 202–204; Tan, Engel, 1986). The records from Maui I., Hawaii, based on collections of H. A. Miller made in 1953 (University of Tennessee Herbarium, 2024a, b), are not confirmed by the checklist of Hawaiian hornworts and liverworts (Staplers, Imada, 2006), where only *Metacalypogeia alternifolia* listed.

Variation and differentiation. Description above demonstrates much variability of *Metacalypogeia cordifolia* in size of plants and leaf shape. Despite much smaller size of the Yakutian plants in comparison with the plants described from the Far East, Japan, Taiwan, and Philippines, their variability in cell size, leaf and underleaf shape are in the same range. Noteworthy that in the Yakutian plants underleaves are narrower, 1.1–1.6 as wide as the stem, whereas Inoue (1959) described them as up to 2.5 as wide as stem. The leaf shape in studied and compared plants from the Russian Far East has considerable variability. The leaf surface is variable as well. The plants of mod. *viridis* may develop slightly punctate surface in the lower part of leaves. The remarkable feature of *Metacalypogeia* species is numerous large chloroplasts, which mostly occlude cell lumen together with oil bodies, making the plants opaque and chlorophyllose that is not characteristic of the related genus *Calypogeia*. Oil bodies in *M. cordifolia* may be partly preserved for decades, particularly in carefully dried and not moistened repeatedly specimens.

Because of the leaf and underleaf shape *Metacalypogeia cordifolia* might be confused with the following regionally known taxa: *M. alternifolia*, *Calypogeia integristipula* Steph., *C. neesiana* (C. Massal. et Carestia) Müll. Frib., *C. pseudointegristipula* Bakalin et al., *Eocalypogeia schusteriana* (S. Hatt. et Mizut.) R. M. Schust., and some species of *Bazzania* Gray. Its distinctions from the North Holarctic taxa are key out below.

Taking into account that *Metacalypogeia* was first described as *Bazzania montana*, its differences from *Bazzania* should be mentioned: rhizoids from the underleaf bases only, lack of ventral flagella, chiefly entire in apices leaves, and ± flattened vs. usually rounded stem with inner cells thin-walled or somewhat evenly thickened rather than unevenly thickened walls. Recently described from Yunnan and Sichuan provinces, South China, *Bazzania calypogeioides* (Bakalin *et al*., 2024) have much in common with *Metacalypogeia cordifolia* but differs in lack of rhizoids, common shortly bidentate in apices leaves, sparse ventral flagellae, smooth leaf surface, and pale green color.

Besides *Calypogeia* and *Bazzania, Metacalypogeia cordifolia* can be confused with *Mnioloma fuscum* (Lehm.) R. M. Schust. and *Protocalypogeia asakawana* (S. Hatt. ex Inoue) Y. Inoue et Furuki (≡ *Calypogeia asakawana*. S. Hatt. ex Inoue). For description of the former species, see Gao *et al.* (2002), for the latter — Inoue (1964, 1974) and Inoue, Furuki (2024). *Metacalypogeia cordifolia* is distinct: from *Mnioloma fuscum* in finely verruculose leaf surface (vs. coarsely verruculose) and in rhizoids from the underleaf bases (vs. from the stem); from *Protocalypogeia asakawana*, having also verruculose leaf surface, in usual ± brownish color of plants (vs. pale green); lack of rhizomatous caulids, giving origin to leafy shoots (vs. presence); ± transversely inserted and non decurrent bilobed underleaves with rather broad V-like or crescentic sinus (vs. arcuately inserted and decurrent entire, truncate or notched underleaves with narrow sinus); leaf cells with distinct trigones (vs. without trigones).

Key to differentiate *Metacalypogeia cordifolia* from morphologically similar North Holarctic taxa

1. Leaves ± convex. Plants opaque, green to ± brown, chlorophyllose 2
— Leaves plane. Plants ± translucent, pale, greyish and bluish green, rare brownish, not chlorophyllose .... *Calypogeia* species 5
2. Rhizoids common, from underleaf bases only. Postical small-leaved flagellae never developed. Inner stem cells thin-walled or slightly evenly thickened 3
— Rhizoids lacking or rare, mostly on flagellae. Postical small-leaved flagellae common. Inner stem cells with unevenly thickened walls, in angles particularly .... *Bazzania* species
3. Underleaves nearly orbicular to reniform, emarginate or occasionally notched or shortly incised. Leaf surface ± punctate-verruculose 4
— Underleaves mostly deeply (2/5–3/5 the length) bilobed. Leaf surface smooth .... *Eocalypogeia schusteriana*
4. Underleaves × 1.1–2.5 as wide as stem, often retuse to occasionally notched and shortly incised, usually appressed to the stem, with plane marginal parts. Leaf apices often rounded, not acuminate .... *Metacalypogeia cordifolia*
— Underleaves mostly over × 2.5 as wide as stem, usually broadly rounded, ± deflected from the stem, often with recurved marginal parts. Leaf apices often acuminate .... *M. alternifolia*

5(1). Undreleaves entire or shallowly notched 6
— Underleaves ± bilobed ..... Regional *Calypogeia* species not resembling *Metacalypogeia* species
6. Plants greyish green, in herbarium occasionally brownish, 1.5–3 mm wide. Apical leaf cells not forming distinct continuous border. Rhizoid initial zone remarkable, oval to suborbicular 7
— Plants pale or yellowish green, 0.7–1.8 mm wide. Apical leaf cells elongated, forming continuous border. Rhizoid initial zone narrow, linear ...... *Calypogeia neesiana*
7. Underleaves not or hardly decurrent, usually undivided or slightly immarginate. Leaf surface smooth. Leaf cell trigones usually lacking. Widespread .... *C. integristipula*
— Underleaves distinctly decurrent for 1/3–1/2 the stem width, shortly emarginate to distinctly divided by semicrescentic sinus into two obtuse lobes. Leaf surface finely verruculose. Leaf cell trigones distinct in marginal leaf cells. Southern Russian Far East .... *C. pseudointegristipula*[4]

Discussion

The main range of *Metacalypogeia cordifolia* is within temperate zone of the Pacific and East Asia, in oceanic and suboceanic often elevated territories (see Fig. 1; Electronic supplement) with not very hot summer and quite significant precipitation, besides Yakutian and NE Chines locations.

The locality in the Udokan Range is about 1000 km from the Sea of Okhotsk (Fig. 1), and within a territory with a harsher climatic condition: a continental climate with hot summers and cold, low-snow winters (Nauchno-prikladnoi..., 1989). The comparison of the bioclimatic data (Electronic supplement[1]) shows that the Udokan Range locality has the lowest Annual Mean Temperature (BIO1) and Minimal Temperature of Coldest Month (BIO6) as well as maximal Temperature Annual Range (BIO7), which, however, not much differ from obtained data on the conditionally selected location in the Heilongjiang Prov., NE China, where the species may occur. Precipitation amount in the selected location in NE China even somewhat less than in the Udokan Range (compare BIO12–BIO19).

The bioclimatic data, however, do not permit properly evaluate conditions in each particular collecting site. The case of the Udokan Range locality supports this statement. In the Udokan Range, the species was gathered in narrow gorge, about 1.5 m wide and 2–3 m high, with nearly vertical rocky walls wet in the summer time due to melting permafrost (Fig. 2B). Despite scant winter precipitation, the strong winds should accumulate in the gorge much snow that should shelter the liverwort collection site near the bottom, providing favorable conditions for the species survival in such an extreme climate. Besides that, the gorge is located in a forest belt, composed of *Larix cajanderi* Mayr, from which the canopy, unlike the black taiga, does not create a special shade. Probably because of this the species survived in a narrow gorge oriented to the northeast, which preserved the habitat from the scorching sun in summer and covered with snow in winter. The gorge is also a shelter for extremely rare in Yakutia *Bazzania tricrenata* (Wahlenb.) Lindb., *Gymnomitrion commutatum* (Limpr.) Schiffn., *Herbertus aduncus* (Dicks.) Gray, *Lejeunea alaskana* (R. M. Schust. et Steere) Inoue et Steere, *Scapania glaucocephala* (Taylor) Austin, *S. verrucosa* Heeg, *Tetralophozia sibirica* Vilnet et Bakalin. [as *T. filiformis* (Steph.) Urmi] (Sofronova, 2021). The gorge possesses a humid microclimate and forms an exceptional habitat for species of different distribution patterns, i. e., arctoboreomontane, arctomontane, montane, and boreal. Among them, *Gymnomitrion commutatum*, *Herbertus aduncus*, *Lejeunea alaskana* are arctomontane. The arctomontane liverworts, occurring in Yakutia in the forest belt, usually indicate a lowering of the high-mountain belt to a modern forest belt level during the time of the former cooling of the climate. The montane species *Bazzania tricrenata, Scapania verrucosa, Tetralophozia sibirica* are also probably avoid the zone of permafrost, and, in this particular longitudinal sector, their locations appear to be the northernmost. The boreal *Scapania glaucocephala* was gathered in untypical habitat, on soil in fissure of wet rock together with *Diplophyllum taxifolium* (Wahlenb.) Dumort., *Gymnomitrion commutatum* (Limpr.) Schiffn., *Scapania crassiretis* Bryhn, and *Schistochilopsis incisa* (Schrad.) Konstant. (Sofronova, 2021). *Scapania glaucocephala* was represented by a few gemmiparous plants of typical morphology. Previously, this species was recorded on the northern macroslope of the Udokan Range also from untypical habitat — the base of alive *Chosenia* Nakai (Bakalin, 2004).

The find of the temperate *Metacalypogeia cordifolia* in this location together with the abovementioned species might be explained also from geochronological point of view. The studied territory since the end of the first half of the Proterozoic era and during the further geological development, was not an arena for either geosynclinal

[4] The distinctive characters of *Calypogeia pseudointegristipula* follow Bakalin *et al.* (2022).

sediment accumulation, or intensive folding deformations, nor metamorphic transformations. A long period of mountain-valley glaciation took place in the Quaternary period (Prirodnye..., 1962). However, despite the fact that less than 3 km from this place there are numerous traces of the exaration, the place itself was not hit by glaciers in the ice age. This is also indirectly confirmed by the probing carried out by L. V. Kuznetsova and D. J. Gnutov near this location in 2001, where no permafrost was found: up to 83 cm depth there were soil horizonts and below them the large-scale debris rock material (pers. com. L. V Kuznetsova).

In the study area, in Eopleistocene, climate cooling has begun. The Neogen vegetation communities gradually disappeared, and phytocoenoses of Anthropogene began to form. This resulted in the impoverishment of the generic and species composition. The tropical and subtropical genera almost completely disappeared from the composition of plant coenoses of North Asia. Only in the forests of Sakhalin and the Far East, *Magnolia* L., *Liquidambar* L., *Podocarpus* L'Hér. ex Pers., *Taxus* L., and some others still preserved. In the Upper Eopleistocene in South Yakutia, a dark coniferous taiga with a slight admixture of broad-leaved species and *Tsuga* (Endl.) Carrière was still widespread. However, already in Samarovsky glaciation there were already widely developed tundra and forest-tundra landscapes. During the maximal glaciation, the participation of moisture-loving plants in the vegetation cover significantly reduced, whereas the role of xerophytes increased (Giterman *et al*., 1968).

Because of that, we consider that *Metacalypogeia cordifolia* in the Udokan Range migth be an Eopleistocene relic.

No other temperate species among liverworts and mosses known from the Udokan Range. However, *Taraxacum pseudonivale* Malyschev and *Paraquilegia microphylla* (Royle) J. Drumm. et Hutch. were found near collecting place of *Metacalypogeia cordifolia*. They have similar more southern mountain distribution. *Taraxacum pseudonivale* has main range in the Baikal Hemiboreal Province, in Stanovoye Upland, and recorded from the Amur Region (Krasnaya..., 2017), whereas *Paraquilegia microphylla* is recorded also in the south-east of the republic from the Tokinsky Stanovik Range (Krasnaya..., 2017) and widespread in the southern Siberian mountains (Flora..., 1993). In the Far East, it is known from the Amur and Khabarovsk regions. Outside Russia, it is reported from Kazakhstan, Central Asia, Mongolia, and China (Luferov, 2022).

Conclusions

Our find of *Metacalypogeia cordifolia* in the Udokan Range demonstrates a case of an isolated location of a temperate species previously known mainly from the ocean and suboceanic regions. The harsh climatic conditions of the collecting place cause impoverished morphology of plants but do not modify their main distinctive characters. Taking into account a superficial similarity of *M. cordifolia* with abovementioned *Calypogeia*-like taxa, we do not exclude its possible overlook. Its further careful search in the similar wet shaded narrow gorges in Siberia is desirable.

The joint analysis of the bioclimatic data, habitat conditions along with the absence of traces of glaciation in the locality point that it is a refugium. *Metacalypogeia cordifolia* in the Udokan Range appears to be an Eopleistocene relic.

The find of temperate *Metacalypogeia cordifolia* in very narrow northeast stretched and slightly shaded by light coniferous forest gorge, covering the plants in winter and has a seepage, watering the plants in summer, shows how habitat conditions may offset bioclimatic conditions of an area. This points at the importance of analysis of the habitat conditions for elucidation of the origin of isolated species localities.

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