

NOTES ON THE GENUS *CHIONOLOMA* DIXON (POTTIACEAE, BRYOPHYTA)  
IN THE RUSSIAN FAR EAST

ЗАМЕТКИ О РОДЕ *CHIONOLOMA* DIXON (POTTIACEAE, BRYOPHYTA)  
НА РОССИЙСКОМ ДАЛЬНЕМ ВОСТОКЕ

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Abstract

*Chionoloma stenocarpum* is newly recorded from Russia; it was collected in 2024 in three localities in Khasansky District of Primorsky Territory, close to its only known locality in Asia, Mt. Chang Bai in northeastern China. Molecular data confirm its segregation from *C. tenuirostris*; it occupies an orphaned position in a clade where *C. minus*, *C. hibernicum*, *C. cylindrotheca* and *C. tenuirostris* fall; its disjunct distribution in East Asia and East North America is considered as typical for relicts of Arcto-Tertiary flora. Two morphologically identical specimens of *C. cylindrotheca* collected in close sites in southern extremity of Primorsky Territory possessed different ITS sequences, suggesting classification within *C. cylindrotheca* s.l. for one specimen and within *C. tenuirostre* s.l. for another. According to the ITS data, the latter specimen groups with two GenBank accessions of *C. cf. tenuirostre* from Indian Ocean islands; however, according to the plastid data, these three specimens and the second specimen from Primorsky Territory appear in a clade sister to *C. cylindrotheca* s. str.-clade, thus showing a supported conflict of topologies. Therefore ancient reticulation event might have underlie the origin of this lineage, which we consider as a cryptic species within *C. cylindrotheca*. Morphological differentiation of *C. cylindrotheca* from similar *C. tenuirostris* is discussed. Descriptions and illustrations of *C. stenocarpum* and *C. cf. cylindrotheca* based on specimens from Russia are provided; they are supplemented by the key to identification of *Chionoloma* species known in Russia.

Резюме

*Chionoloma stenocarpum* впервые приводится для России; она была собрана в 2024 г. в трех местонахождениях в Хасанском районе на юге Приморского края, недалеко от единственного известного местонахождения этого вида в Азии, на плоскогорье Чанбайшань на северо-востоке Китая. Молекулярные данные подтверждают его выделение из *C. tenuirostris*; вид занимает изолированное положение в кладе, куда также попадают *C. minus*, *C. hibernicum*, *C. cylindrotheca* и *C. tenuirostris*, и его дизъюнктивное распространение в Восточной Азии и восточной части Северной Америки считается типичным для реликтов Аркто-Третичной флоры. Два морфологически идентичных образца *C. cylindrotheca*, собранные в близких местонахождениях на г. Мраморная и г. Приозерная в южной оконечности Приморского края, обладают разными последовательностями ITS: один попадает в кладу *C. cylindrotheca* s.l., а другой – в кладу *C. tenuirostre* s.l. В последней наш образец формирует изолированную кладу с двумя образцами с островов Индийского океана, но по пластидным данным все три эти образца, а также второй Приморский образец формируют кладу, сестринскую *C. cylindrotheca* s.str. Поддержанный конфликт топологий может свидетельствовать о том, что происхождение этой линии, которую мы предлагаем рассматривать как скрытый вид в *C. cylindrotheca*, могло сопровождаться ретикуляцией. В контексте этой находки обсуждаются отличия *C. cylindrotheca* от морфологически похожей *C. tenuirostris*. Приводятся описания и иллюстрации *C. stenocarpum* и *C. cf. cylindrotheca* по образцам из России, а также ключ для определения встречающихся в России видов *Chionoloma*.

KEYWORDS: rare species; Arcto-Tertiary relicts; biogeography; Primorsky Territory; *trnL*-ITS, *trnF*; *atpB-rbcL*; *trnG*; cryptic species; reticulation

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## INTRODUCTION

The genus *Chionoloma* Dixon was established in 1922 to accommodate several species from SE Asia. Its relationships with such genera as *Trichostomum* Hedw., *Oxystegus* (Limpr.) Hilp. and *Pseudosymblypharis* Broth. remained unclear until molecular-phylogenetic and morphological studies by Alonso *et al.* (2016, 2019) demonstrated that the latter two genera have to be combined with *Chionoloma*. They provided a worldwide revision of this genus, which resulted in recognizing within it 22 species and one variety. Most these species are distributed in tropics and southern hemisphere, with few exceptions, including a cosmopolitan *Chionoloma tenuirostre* (Hook. & Taylor) M. Alonso, M. J. Cano & J. A. Jiménez, which is widespread in boreal areas of Holarctic. Until recently, only the latter species was known in Russia, named as *Oxystegus cylindricus* (Bruch) Hilp. (Abramova *et al.*, 1961; Bardunov, 1969; Savicz-Lyubitskaya & Smirnova, 1970; Bardunov & Cherdantseva, 1982) or *Oxystegus tenuirostris* (Hook. & Taylor) A.J.E. Smith (Ignatov & Ignatova, 2003; Ignatov *et al.*, 2006). Two other species which are now referred to *Chionoloma* were added to the moss flora of Russia by Ignatova *et al.* (2012), both found in the Russian Caucasus. First of them was *Oxystegus daldinianus* (De Not.) Köckinger, O. Werner & Ros (= *Chionoloma cylindrotheca* (Mitt.) M. Alonso, M. J. Cano & J. A. Jiménez); it was collected in the Black Sea coastal area, near Lazarevskoe Settlement (Sochi District of Krasnodar Territory). The second species, from Gunib District in Dagestan, was tentatively identified as *Pseudosymblypharis bombayensis* (Müll. Hal.) P. Sollman, with a note that the Caucasian plants deviate considerably from typical morphotype of this species. The latter specimen was revisited by Alonso *et al.* (2019) and referred to *Chionoloma orthodontum* (Müll. Hal.) M. Alonso, M.J. Cano & J. A. Jiménez. The second record of this species from the Caucasus, Ingushetia, was published by Kuznetsova *et al.* (2024). Since then, several attempts to identify *Oxystegus daldinianus* in the Russian Far East and Transbaikalia were made, but these specimens were confirmed to belong to *C. tenuirostre* by molecular markers.

In September of 2024, during a short field trip to the southern extremity of Primorsky Territory, VF and OP collected several puzzling specimens of a pottiaceous moss with oblong-obovate, crisped in dry condition leaves, which did not belong to any species known in Russia; these collections contained mature sporophytes with long, yellowish setae, long cylindrical capsules and comparatively short, straight peristome without basal membrane. Morphologically these plants agreed the description and illustrations of the poorly known *C. stenocarpum*, provided by Alonso *et al.* (2019). Also in the southernmost extremity of the Primorsky Territory, in Mramornaya and Priozernaya Mts, several specimens of large *Tortella*-like plants of *Chionoloma*, which did not

resemble widespread in the area *C. tenuirostre*, were collected. We decided to apply a combined morpho-molecular approach in order to test the identity of the aforementioned specimens.

## MATERIAL AND METHODS

Phylogenetic part of study is based on the nuclear ITS region and plastid markers *atpB*, *trnG* and *trnL-F*, earlier studied for many species of the genus by Alonso *et al.* (2016). The laboratory protocols of DNA extraction, PCR, and sequences for ITS were essentially the same as in previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005), PCR protocol for *trnG* followed Bakalin & Vilnet (2014) and for *atpB* & *trnL-F* Alonso *et al.* (2016). Newly obtained sequences of nr ITS were added in the dataset used by Ignatova *et al.* (2012), and additional sequences representing other species of *Chionoloma* were downloaded from GenBank to assess the affinity of *Chionoloma stenocarpum* in a broader phylogenetic context. Plastid data were concatenated and added in the alignment with a selection of the other species of *Chionoloma* presented in GenBank. Voucher data of the originally studied specimens and GenBank accession numbers for the newly generated sequences are provided in the Table 1. For Genbank accessions involved in the plastid dataset, GenBank accession numbers of the all-four markers are also provided in the Table 1. Datasets were realigned manually using BioEdit (Hall, 1999), and six accessions of *Tortella* were added for rooting the ITS tree, so the final dataset included 92 terminals and 969 positions; for rooting the plastid tree, originally obtained sequence of *Tortella fragilis* was used; plastid dataset included 31 terminals and 1645 positions. Indel data were scored using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005) and added to the datasets prepared to Bayesian inferences. Bayesian analyses in MrBayes 3.2.7. (Ronquist *et al.*, 2012) were set for 5 million generations and sampling frequency one tree each 1000 generations, average standard deviations of split frequencies were checked to have decreased below 0.01 after first 1.5 million of generations for ITS tree and after 0.2 million generations for plastid dataset. The chain temperature was set at 0.02 in all analyses, and GTR model with sampling throughout the model space (setting nst = mixed) was used in all analyses. Convergence of the analyses was assessed via ESS values, checked using Tracer v.1.7.2. (Rambaut *et al.*, 2018) to be higher than 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. 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, GTR+G+I model of nucleotide substitutions and otherwise standard settings. Due to conflicts of topologies in the ingroup, the nuclear and plastid data were not concatenated, and we present trees inferred from these two datasets separately.

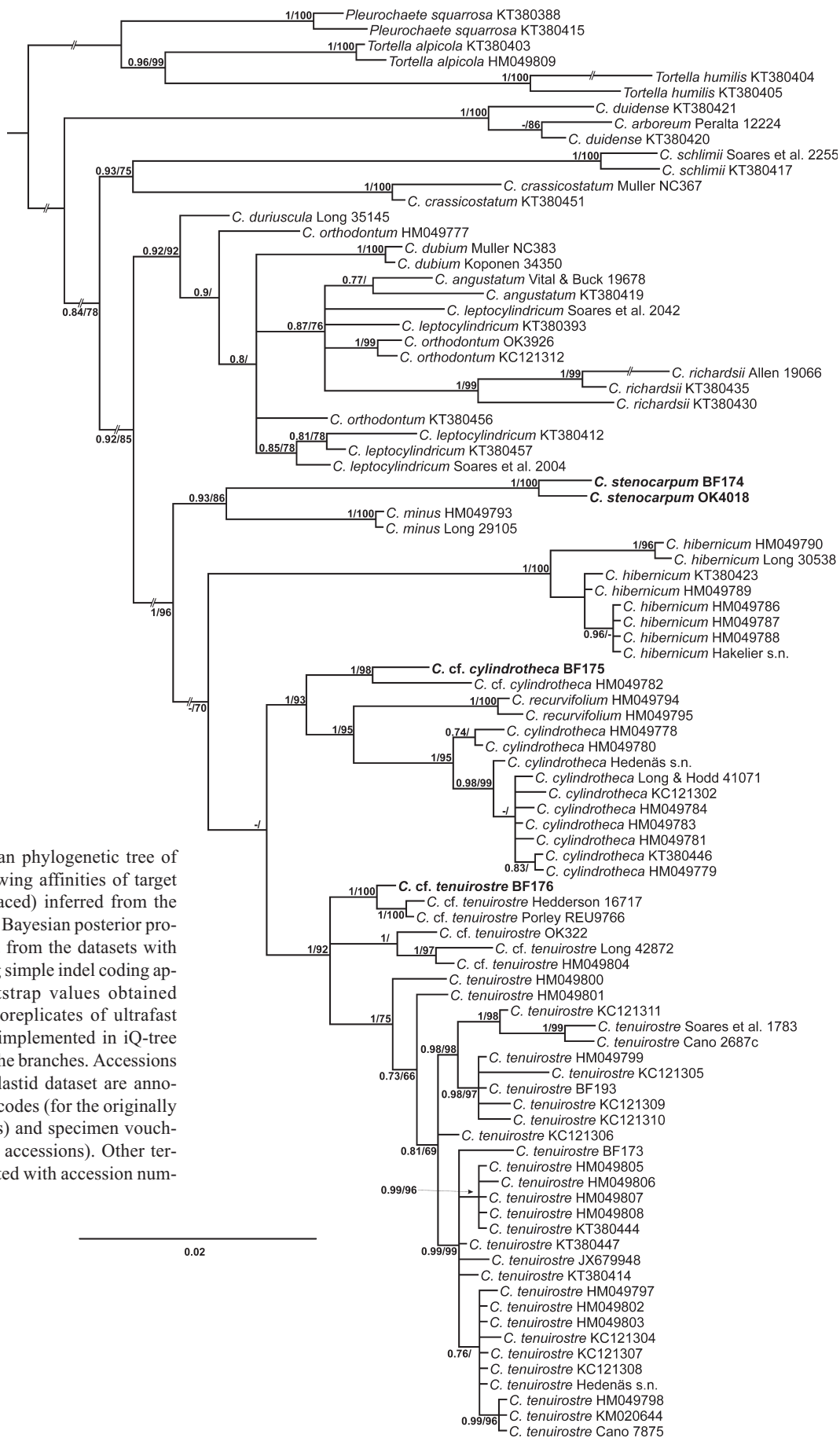


Fig. 1. Bayesian phylogenetic tree of *Chionoloma*, showing affinities of target specimens (boldfaced) inferred from the nr ITS sequences. Bayesian posterior probabilities inferred from the datasets with indels coded using simple indel coding approach and Bootstrap values obtained from 1000 pseudoreplicates of ultrafast bootstrapping as implemented in iQ-tree are shown above the branches. Accessions included in the plastid dataset are annotated with isolate codes (for the originally studied specimens) and specimen vouchers (for GenBank accessions). Other terminals are annotated with accession number of sequence.

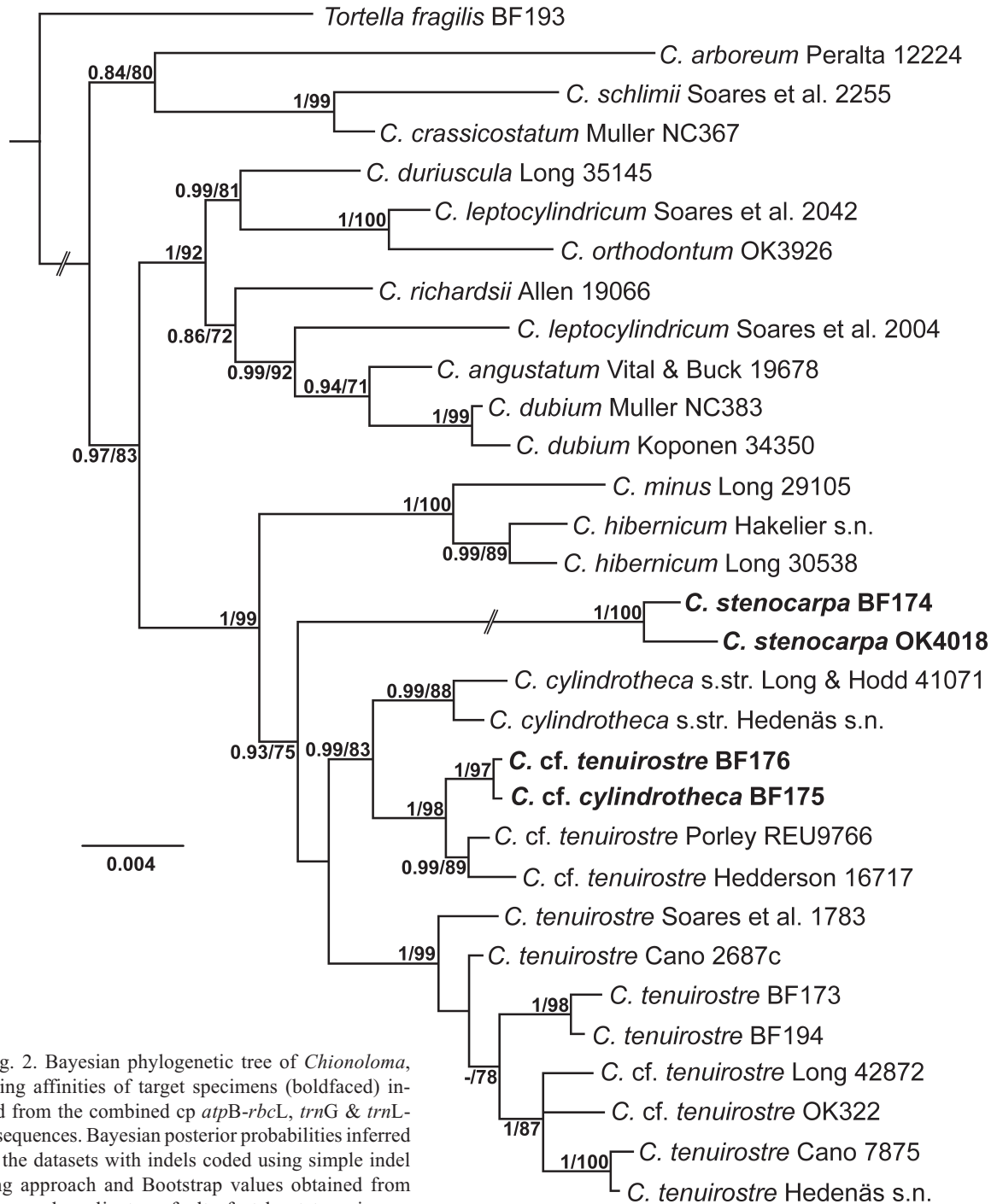


Fig. 2. Bayesian phylogenetic tree of *Chionoloma*, showing affinities of target specimens (boldfaced) inferred from the combined cp *atpB-rbcL*, *trnG* & *trnL-trnF* sequences. Bayesian posterior probabilities inferred from the datasets with indels coded using simple indel coding approach and Bootstrap values obtained from 1000 pseudoreplicates of ultrafast bootstrapping as implemented in iQ-tree are shown above the branches.

## RESULTS

In the tree inferred from nuclear ITS sequences (Fig. 1), accessions of *Chionoloma* group in several not supported or weakly supported clades. The clade composed of *C. arboreum* (Mitt.) M. Alonso, M.J. Cano & J.A. Jiménez and *C. duidense* (E.B. Bartram) M. Alonso, M.J. Cano & J.A. Jiménez splits first, followed by the clade consisting of *C. schlimii* (Müll. Hal.) M. Alonso, M.J. Cano & J.A. Jiménez and *C. crassicostatum* (D.H. Norris & T.J. Kop.) M. Alonso, M.J. Cano & J.A. Jiménez,

leaving remaining accessions of *Chionoloma* in two large groupings. First of them (PP 0.92, BS 92) includes accessions of the predominantly tropical species, *C. angustatum* (Mitt.) M. Menzel, *C. dubium* (Thér.) M. Alonso, M.J. Cano & J.A. Jiménez, *C. leptocylindricum* (Müll. Hal.) M. Alonso, *C. orthodontum*, and *C. richardsii* (E.B. Bartram) M. Alonso, M.J. Cano & J.A. Jiménez downloaded from GenBank. The second grouping (PP1, BS96) includes four major clades composed largely of species distributed in temperate climates of northern Hemisphere,



affinities among which, as assessed by supports of the backbone nodes, got no support. Sequences obtained from specimens referred to *C. stenocarpum* appeared in the not supported grouping with those of European *C. minus* (Köckinger, O. Werner & Ros) M. Alonso, M.J. Cano & J.A. Jiménez, which splits first within this large clade, followed by the maximally supported clade of *C. hibernicum* (Mitt.) M. Alonso, M.J. Cano & J.A. Jiménez. Remaining accessions form two moderately supported clades; one of them (PP1, BS93) contains accessions of *C. cylindrotheca* including those of *C. recurvifolium* (Taylor) M. Alonso, M.J. Cano & J.A. Jiménez, which form a nested clade within it; the second clade corresponds to *C. tenuirostre* s.l. The first of the latter two clades comprises three clades. One of them, composed of two accessions of *C. cf. cylindrotheca* (PP1, BS98), including the specimen from the southernmost part of Primorsky Territory BF175 and GenBank accession HM049782 (Holoak 14-176), splits first, leaving maximally supported clade of *C. recurvifolium* sister to the highly supported (PP1, BS95) *C. cylindrotheca*-clade. Finally, within the *C. tenuirostre* s.l. clade, three clades appear. One of the two minor clades, which includes the second “problematic” specimen from the southern extremity of Primorsky Territory (BF176), gets maximal support, while most other accessions land within the major clade (PP1, BS75) corresponding to *C. tenuirostre*, which has complex inner phylogenetic structure and includes specimens from Europe, Russian Caucasus, Siberia, and Russian Far East.

In the tree inferred from the concatenated dataset of three plastid markers (Fig. 2), strongly supported clade of *C. schlimii* and *C. crassicosata* forms not supported clade with the single involved accession of *C. arboreum*, leaving remaining members of *Chionoloma* in not supported clade. It includes the same two supported major clades, as in the tree inferred from the nuclear data: one clade (PP1, BS92) includes “southern”, predominantly tropical species *C. angustatum*, *C. dubium*, *C. duriuscula*, *C. leptocylindricum*, *C. orhtodontium* and *C. richardsii*, and the second clade (PP1, BS99) is composed of temperate and widespread species *C. minus*, *C. hibernicum*, *C. cylindrotheca*, *C. tenuirostre* and *C. stenocarpum*. The topology within the second clade differs from that inferred from the nuclear data. Maximally supported clade of two European species, *C. hibernicum* and *C. minus* is sister to the not supported clade where accessions of the three other species appear. Maximally supported *C. stenocarpum* is sister to not supported clade composed of the highly supported (PP1, BS98) clade of *C. tenuirostre* and weakly supported (PP0.99, BS83) clade of *C. cylindrotheca* s.l. Within the later clade, three specimens from the clade “*C. cf. tenuirostre*”, i.e., BF176 from Russian Far East, REU9766 from Reunion and Hedderon 16717, form a highly supported clade where another specimen from Primorsky Territory, BF175 appear, and this clade is sister to the weakly supported “*C. cylindrotheca* s.str.” clade. Two representatives of the second

small “*C. cf. tenuirostre*” clade, Ignatov & Ignatova 05-3381 and Long 42872, appeared deep nested within the *C. tenuirostre* s.str. clade, while two newly studied specimens of *C. tenuirostre* from the Russian Far East (BF173) and Yakutia (BF194) form a highly supported clade.

#### DISCUSSION

Our molecular results based both on the nuclear ITS and plastid data are not suggestive regarding the affinities of the East Asian specimens referred on the morphological ground to *C. stenocarpum*. In general, fast evolving nr ITS often fails to provide reasonable resolution of the backbone phylogeny in large genera, but, at the same time, it is useful for identifying closely related species and infraspecific segregates (Álvarez & Wendel, 2003). Probably this is a reason, why the topology inferred from the nuclear ITS does not reveal close affinity of *C. minor* and *C. hibernicum*, which appears in the tree inferred from the plastid dataset and also in the tree published by Alonso *et al.* (2016); otherwise, absence of this grouping in the ITS-based tree might have originated from the artifact of the alignment. At the same time, regarding taxonomic position and affinities of *C. stenocarpum*, two datasets largely agree, confirming its orphaned position. Nevertheless, the results obtained for *C. stenocarpum* show that this poorly known species (1) belongs to *Chionoloma*, as was concluded by Alonso *et al.* (2019) based on morphology; (2) is well distinct from all the previously sampled taxa of *Chionoloma*, including *C. tenuirostre*, where it was placed by Zander (1982); (3) represents one of the lineages within the clade of *Chionoloma*, which underwent radiation in temperate North Hemisphere. Thus, we confirm the taxonomic solution made by Alonso *et al.* (2019) by considering *C. stenocarpum* as a separate species, which was followed by Brinda & Atwood (2023). Moreover, Alonso *et al.* (2019) mentioned morphological similarity of *C. stenocarpum* and *C. minus*, which got partial support in the obtained topology. At the same time, these two species differ in morphology and distribution: *C. minus* is known so far exclusively from Central Europe and Scotland (Köckinger *et al.*, 2010; Alonso *et al.*, 2019), while *C. stenocarpum* was recorded for East Asia, East North America and Central America (see below). Such distribution occurs in bryophytes which are supposed to represent relicts of Arcto-Tertiary flora (Kryshtofovich, 1929; Iwatsuki, 1958; Schofield, 1980).

With few records in the southernmost part of the Primorsky Territory and isolated localities in Northern China, North America and Mexico, it appears to be one of the rarest species in this group. However, distribution of this species, at least in East Asia, likely was strongly underestimated. First, it represents a complex and, until recently, weakly understood group, being rather close to the extremely morphologically polymorphic *C. tenuirostre* and also resembling insufficiently understood East Asian species of *Weissia*, recently considered by Ignato-

va *et al.* (2024). On the other hand, broad-leaved forest and forest-steppe biomes in the southernmost part of Russian Far East remain weakly covered by bryological studies (Bardunov & Cherdantseva, 1982; Cherdantseva, 1989; Pisarenko & Bakalin, 2017), and just a miserable amount of specimens from this area is represented in herbaria. The degree of bryological exploration of Northern China is probably also quite low.

At the same time, in the southern extremity of the Primorsky Territory many thermophilous plants that do not occur further north are concentrated (Komarov, 1923; Kolesnikov, 1963; Valova, 1963; Chubarj, 2000; Kozhevnikov *et al.*, 2019). The schemes of botanical zoning highlight the phenomenon of the peculiarity of the flora and vegetation of the Russian Far East southwest. The territory located south of latitude 44°N is distinguished at high hierarchical level (Kolesnikov, 1955, 1969; Nikolskaja *et al.*, 1969; Kurenzova, 1968; Kozhevnikov & Kozhevnikova, 2014). At the next level of division, the southwest tip of the area is again designated as a particular district; the border is drawn along the watershed of the rivers Riazanovka and Gladkaya, ~42.44°–42.52°N (Vorobiev, 1949; Kolesnikov, 1961; Kurenzova, 1968). This phenomenon takes place largely due to the unique characteristics of the climate (Krestov & Nakamura, 2007; Krestov *et al.*, 2009). The proximity to the warm Sea of Japan and the terrain features of the district contribute to the formation of a warm and humid climate (Valova, 1963; Climate Data, 2024). The sum of positive temperatures, average annual air temperature, and average annual soil surface temperature also are the highest for Primorsky Territory. Winters are almost snowless, and soil is often almost completely exposed during the winter months. As the results of our field trip show, a unique climatic conditions support populations of many thermophilous species of mosses, and further processing of the collection may increase the number of such interesting findings.

In the course of this account preparation, we managed to uncover the identity of another mysterious inhabitant of this area, represented by specimens BF175 and BF176. Although formally they fit morphological circumscription of *C. cylindrotheca*, they represent phylogenetically isolated lineage, possessing ITS sequences closer to *C. tenuirostre*, albeit also remarkably diverged from the latter. Thus, at the moment we see no better option than considering them as representatives of a cryptic species within *C. cylindrotheca*. Due to a supported conflict of topologies between nuclear and plastid data regarding affinities of this lineage, its hybridogeneous origin might be proposed. At the same time, the divergence from both potentially parental species indicates that the supposed reticulation took place when ancestors of *C. tenuirostre* and *C. cylindrotheca* had diverged less than they have at the moment, and original ITS haplotype also persisted as exemplified by the specimen BF175. Nevertheless, the occurrence of this third entity does not

simplify the already difficult delimitation of these species and may suggest a possibility of their further hybridization.

#### TAXONOMY

**Chionoloma stenocarpum** (Thér.) M. Alonso, M. J. Cano & J. A. Jiménez, *Ann. Missouri Bot. Gard.* 194: 616. 2019. — *Weisiopsis stenocarpa* Thér., *Smithsonian Misc. Collect.* 85: 14, fig. 8. 1931. — *Oxystegus tenuirostris* (Hook. & Taylor) A. J. E. Sm. var. *stenocarpus* (Thér.) R.H. Zander, *Misc. Bryol. Lichenol.* 9: 73. 1982. Fig. 3.

*Plants* small to medium-sized, in low, loose patches, green or light-green. *Stems* to 1 cm long, simple, without hyalodermis, with weak or well-developed central strand. *Leaves* contorted and crisped when dry, erect-spreading to spreading when wet, not fragile, linear-lanceolate or oblong-lingulate, slightly widened distally, (1.8–) 2.2–3.3×0.3–0.45 mm, rounded at apices, with weakly differentiated bases, often constricted above base; margins plane, entire or finely papillose-crenulate; *costa* strong, excurrent into short, smooth mucro, 50–85 µm wide at leaf base, smooth on dorsal surface, papillose from above leaf base on ventral surface, in transverse section with one layer of guide cells, dorsal stereid band larger than ventral one or equal to it in size, with differentiated ventral epidermis and without dorsal epidermis; upper and median laminal *cells* quadrate and short transverse rectangular, 9–10(–12) µm wide, with moderately dense, simple and bifid papillae, 3–7 per cell; basal laminal cells rectangular, 25–65×11–17 µm, smooth, hyaline; transition from hyaline basal cells to chlorophyllose median cells gradual (hyaline cells change into smooth chlorophyllose cells and then into papillose cells), with straight, not V-shaped boundary. *Autoicous*, specimens from Russia with sporophytes. *Setae* 0.5–1.0 cm, yellowish. *Capsules* cylindrical, 1.0–1.5(–2.3) mm long, straight, occasionally slightly asymmetrical. *Peristome* with very low basal membrane, teeth straight, 145–170 µm long, obliquely striolate. *Opercula* 0.5–0.6 mm long. *Spores* 11–14 µm.

**Distribution and ecology.** This species was described from Mexico; it is considered to be rare worldwide, known from Wisconsin in eastern North America (holotype of *Trichostomum spirale* Grout, referred to synonymy of *Oxystegus tenuirostris* var. *stenocarpus* by Zander, 1982) and one locality in NE China (Mt. Chang Bai in Jilin Province, Koponen *et al.*, 1983). Alonso *et al.* (2019) did not see the specimens from China and thus considered the presence of *C. stenocarpum* in Asia as unconfirmed. However, our findings provide an additional evidence that this rare species has a disjunctive distribution between East Asia and Atlantic North America and therefore likely indeed could have been found in Chang Bai Mt. In Russia this species was collected in three localities. In the vicinity of Kravtsovka Village this species occurs on rocks near Kravtsovskie waterfalls along with

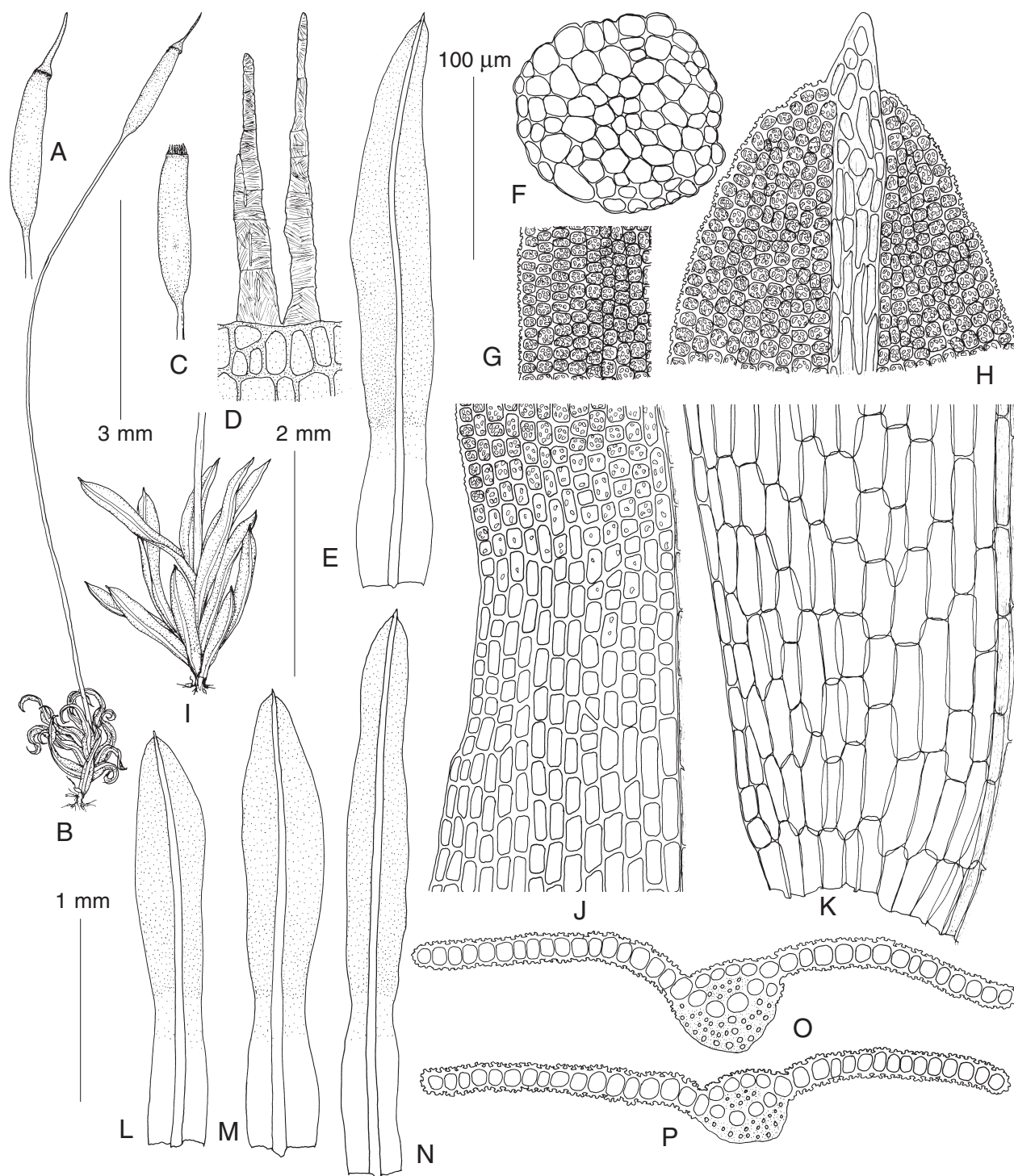


Fig. 3. *Chionoloma stenocarpum* (from: Russia, Primorsky Territory, Khasansky District, Fedosov & Pisarenko, MW9133380). A, C: capsules; B: habit, dry; D: peristome; E, L–N: leaves; F: stem transverse section; G: mid-leaf laminal cells; H: upper laminal cells; I: habit, wet; J: cells at transition from base to acumen; K: basal laminal cells; O–P: leaf transverse sections. Scale bars: 3 mm for B; 2 mm for A, C, I; 1 mm for E, L–N; 100  $\mu\text{m}$  for D, F–K, O–P.

*Timmiella anomala*. In the vicinities of Andreevka Town it grows in the disturbed oak (*Quercus mongolica*, *Q. dentata*) forest with *Aralia continentalis*, *Coryllus heterophylla*, *Lespedeza bicolor* and admixture of herbs (*Aster scaber*, *Hieracium umbellatum*, *Melampyrum roseum*, *Micranthes manchuriensis*, *Saussurea grandiflora*,

*Syneilesis aconitifolia*, etc.) on oak trunks. In the latter locality this species probably is not rare: three collections were made along the single path rising up the hill in quite typical for this area ecotope, which covers hills around Andreevka and settlements nearby on the altitudinal range 30–250 m. Koponen *et al.* (1983) mentioned that Chinese



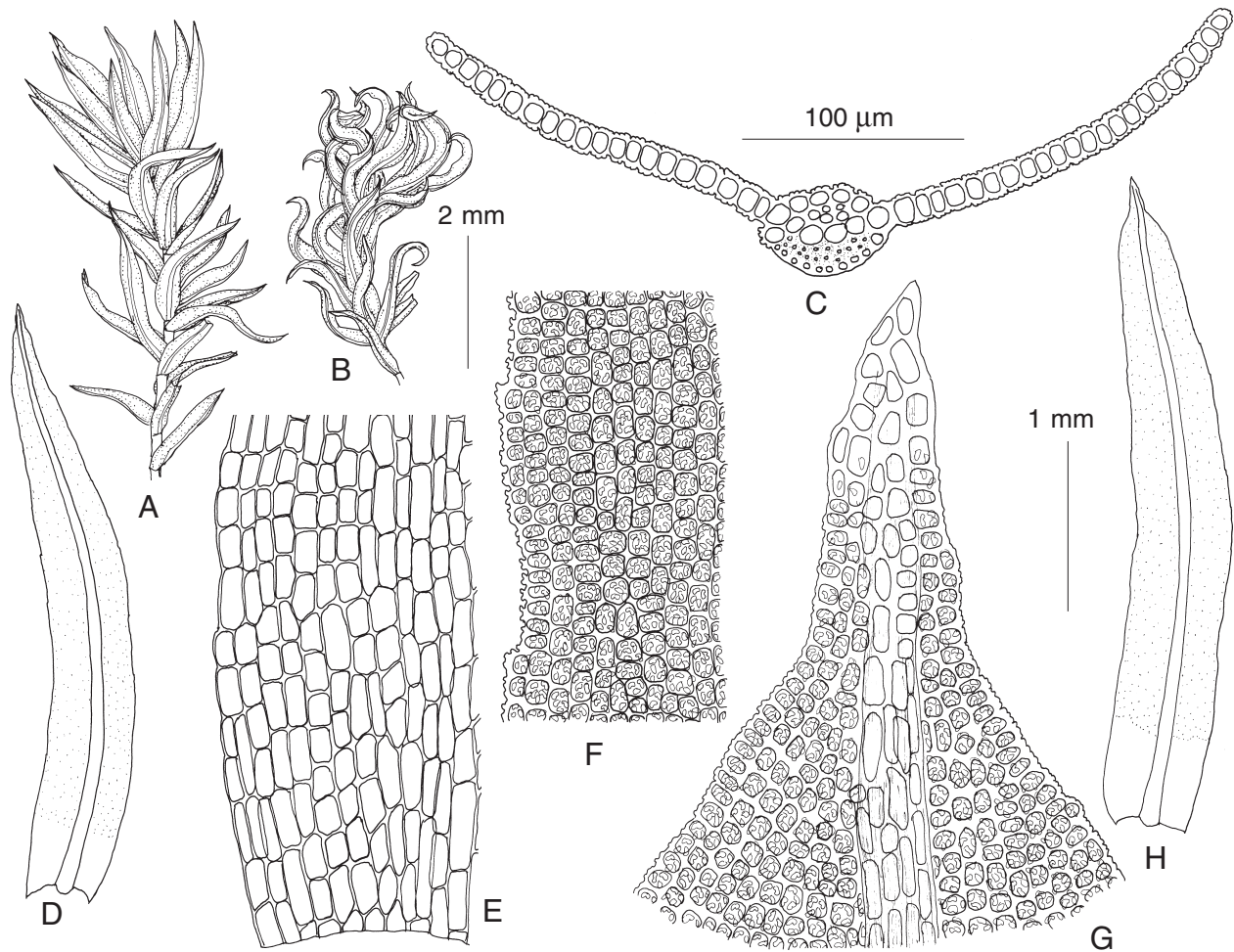


Fig. 4. *Chionoloma cylindrotheca* (from: Russia, Primorsky Territory, Khasansky District, Fedosov & Pisarenko, MW913339). A: habit, wet; B: habit, dry; C: leaf transverse section; D, H: leaves; E: basal laminal cells; F: mid-leaf laminal cells; G: upper laminal cells. Scale bars: 2 mm for A–B; 1 mm for D, H; 100 µm for C, E–G.

specimen of this species grew at base of a tree trunk, unlike American specimens collected from rotten wood and limestone. In the vicinity of Kravtsovka village rock outcrops indeed have base-rich composition, so that many representatives of Pottiaceae occurred there alongside with *C. stenocarpum*. In the vicinity of Khasan Settlement, on foothills of SW slope of Mramornaya Mt., it was collected in cracks of boulders with thin layer of soil (Fig. 6A).

**Differentiation.** *Chionoloma stenocarpum* has a unique combination of morphological characters which is unknown in other mosses occurring in the Russia. It can be already recognized by its oblong-lingulate leaves, slightly widened distally, with rounded apices, often constricted above bases, in combination with straight, obliquely striolate peristome teeth without basal membrane. Other species of *Chionoloma* known in Russia have leaves not widened distally and acute or acuminate at apices. Some species of *Weissia* from the Russian Far East possess leaves crisped when dry, with almost flat margins, rounded apices and shortly excurrent costa, but they are smaller in size, have much shorter capsules and shorter, papillose peristome teeth.

**Specimens examined: Primorsky Territory:** Khasansky Distr.: vicinity of Kravtsovka village, Black mountains (East Mandzhurian Mountains eastern spurs), Kravtsovskie Waterfalls (43.36475N, 131.64184E, ca. 150 m alt., polydominant forest with rock outcrops along the creek, on rocks with *Timiella anomala*, 24.IX.2024, Fedosov & Pisarenko (MW9133380\*, isolate BF174); vicinity of Andreevka Town (42.66236N, 131.12833E, ca. 35 m alt.), forested slope of hill, dry oak dominated forest with *Lespedeza*, on oak bases, 17.IX.2024, Fedosov & Pisarenko (MW9133385\*, isolate OK4018, MW9133386, MW9133387); *ibid*, Andreevka River valley (42.6608N, 131.1549E, ca. 70 m alt.), grassy S-faced slope with scattered oaks, on oak bases, 19.IX.2024, Fedosov & Pisarenko (NSK2010480); vicinity of Khasan Settl., Reid Pallady Bay southern shore, Mramornaya Mt. foot of SW-slope (42.56856N, 130.80402E, 47 m alt.), boulders among thickets of tall grasses and shrubs, in cracks with thin layer of soil, 21.IX.2024, Fedosov & Pisarenko (NSK2010481); *ibid* (42.5652N, 130.8003E, 183 m alt.), in cracks of the rocks 21.IX.2024, Fedosov & Pisarenko (NSK2010484).

***Chionoloma* cf. *cylindrotheca* (Mitt.) M. Alonso, M. J. Cano & J. A. Jiménez, Ann. Missouri Bot. Gard. 194: 582. 2019. — *Tortula cylindrotheca* Mitt., J. Proc. Linn.**



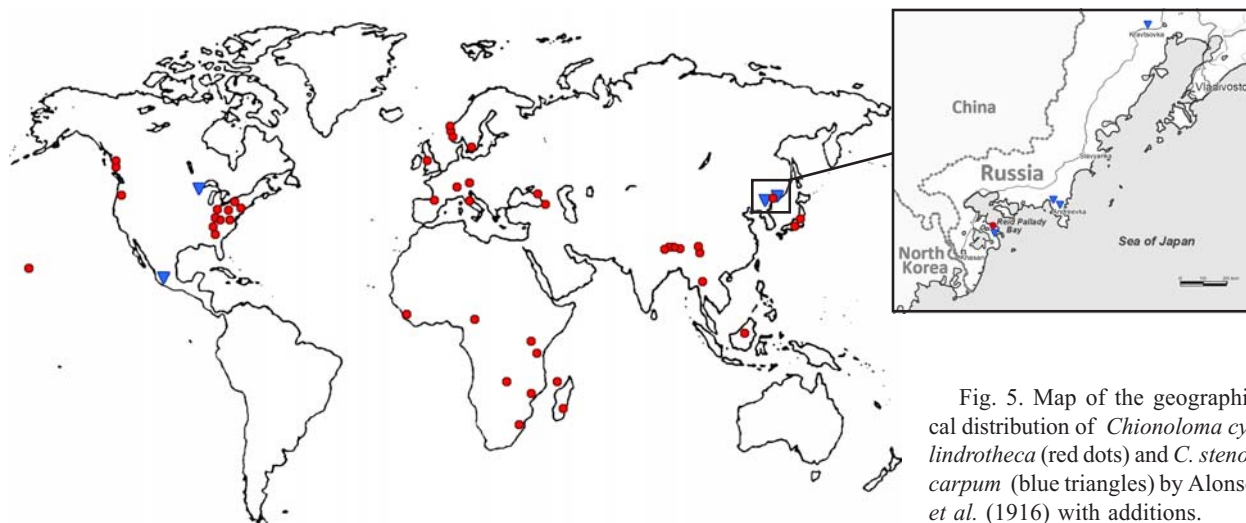


Fig. 5. Map of the geographical distribution of *Chionoloma cylindrotheca* (red dots) and *C. stenocarpum* (blue triangles) by Alonso *et al.* (1916) with additions.

Soc., Bot., Suppl. 1: 30. 1859. — *Oxystegus daldinianus* (De Not.) Köckinger, O. Werner & Ros, Nova Hedwigia Beih. 138: 39. 2010. — *Didymodon cylindricus* (Brid.) Bruch & Schimp. var. *daldinianus* De Not., Atti Reale Univ. Genova 1: 563. 1869. Fig. 4.

*Plants* medium-sized, in low, dense or loose tufts, green or dark-green. *Stems* to 3(5) cm long, simple or branched, without hyalodermis and central strand. *Leaves* incurved and twisted when dry, erect spreading to patent when wet, not fragile, linear-lanceolate, 4–6×0.5–0.6 mm, often cuspidate at apices, with short, canaliculate apiculi (at least in some leaves) or acute, with weakly differentiated bases; margins plane, entire or weakly papillose-crenulate, occasionally also distantly denticulate in upper and middle portion; costa strong, percurrent or short excurrent, 80–100 μm wide at leaf base, smooth on dorsal surface, papillose on ventral surface above base, in transverse section with one layer of guide cells, dorsal stereid band larger than ventral one or equal to it in size, with differentiated ventral epidermis and without dorsal epidermis; upper and median laminal cells quadrate and short transverse rectangular, 8–12(–15) μm wide, moderately densely papillose; basal laminal cells rectangular, 20–65×8–17 μm, smooth, hyaline; transition from hyaline basal cells to chlorophyllose median cells more or less abrupt, straight, not V-shaped. *Dioicous*, sporophytes unknown in Russia.

**Distribution and ecology.** *Chionoloma cylindrotheca* was described from India; it occurs also in Nepal, Buthan, China, Japan, Malaysia, Thailand in Asia, in subatlantic and central regions of Europe, and eastern North America. In Russia it was known only in the western Caucasus, near Sochi. Its finding in Primorsky Territory could be expected, as it occurs in neighboring Japan and China; however, its presence here is confirmed by molecular barcoding for the first time. It was collected in Khasansky District on southern slope of Mramornaya Mt., on rock outcrops under crooked oak canopy (Fig. 6B).

**Differentiation.** Alonso *et al.* (2019) consider the shape of leaf apex to be the main diagnostic character of *C. cylindrotheca*; however, such attenuate, canaliculate apiculi are usually found only in some leaves of its plants. In some cases, it is very difficult to separate *C. cylindrotheca* from *C. tenuirostre*. The latter species possesses a combination of morphological characters similar to that of *C. cylindrotheca*, including linear-lanceolate leaves, costa with dorsal stereid band larger than ventral one, weakly differentiated leaf base, and border between hyaline basal cells and chlorophyllose median cells straight, not V-shaped. It is interesting to note that Alonso *et al.* (2019) do not mention leaf fragility among morphological characters of *C. tenuirostre*; in the key to identification, they separate mainly tropical *C. hyalinoblastum* (Broth.) M. Alonso, M.J. Cano & J.A. Jiménez with strongly fragile leaves from *C. tenuirostre* with usually intact leaves. This contradicts the description of the latter species in some European and Russian handbooks (Guerra, 2006; Hallingbäck *et al.*, 2008; Savicz-Lyubitskaya & Smirnova, 1970; Ignatov & Ignatova, 2003), where its leaves are described and illustrated as having sinuose upper margins, with constrictions marking places of breaking. Actually, specimens of *C. tenuirostre* with strongly fragile leaves prevail in herbarium collections from Russia, and only in the Russian Far East and, partially, Transbaikalia, plants with non-fragile leaves were frequently collected. Both *C. cylindrotheca* and *C. tenuirostre* occasionally have distantly and faintly denticulate upper leaf margins. Dorsal surface of costa is always formed of elongate, smooth cells in *C. cylindrotheca*, but, according to Alonso *et al.* (2019) it can be smooth or papillose (throughout or only distally) in *C. tenuirostre*. Unfortunately, this characters not very helpful for separation these species in the Russian Far East, since most specimens of *C. tenuirostre* have costae with smooth dorsal surface. Thus, study of more leaves and evaluating shape of their apices is the only possibility to separate these species in doubtful cases.



Fig. 6. Habitat of *Chionoloma stenocarpa* and *C. cf. cylindrotheca* in southern extremity of Primorsky Territory, Mramornaya Mt. A: rock outcrops on SW slope of Mramornaya Mt.; B: rocks with *Lycopodioides tamariscina*, a characteristic ecotope of *C. cf. cylindrotheca*.

*Specimens examined:* Primorsky Territory, Khasansky Distr., vicinity of Khasan Settl., Reid Pallady Bay southern shore, Mramornaya Mt. SW slope near ridge (42.56695N, 130.80278E, 170 m alt.), meadow with oaks, bushes and rock outcrops, on boulder covered by thin layer of soil with *Lycopodioides tamariscina*, *Grimmia pilifera*, *Hypnum leptothallum* and *Campylopus subulatus*, 21.IX.2024, Fedosov & Pisarenko (MW9133399\*, isolate BF175).

Putative hybridogeneous species with *C. tenuirostre*:

Primorsky Territory, Khasansky Distr., vicinity of Khasan Settl., Reid Pallady Bay southern shore, Prizernaya Mt. NW slope (42.54342N, 130.70530E, 64 m alt.), meadow with, rock outcrops, in niche, 22.IX.2024, Fedosov & Pisarenko (MW133390\*, isolate BF176).

#### KEY TO IDENTIFICATION OF CHIONOLOMA SPECIES OCCURRING IN RUSSIA

1. Leaves acute at apices, often fragile, with sinuose upper leaf margins, or not fragile, with papillose-crenulate or weakly and distantly denticulate upper leaf margins; costa papillose on dorsal surface in distal leaf portion or smooth throughout ..... 1. *C. tenuirostre*
- Leaves rounded, acuminate or cuspidate at apices, not fragile, with entire, papillose-crenulate or weakly and distantly denticulate upper leaf margins; costa smooth on dorsal surface from base to apex .... 2
2. Leaves oblong-lingulate, slightly widened distally, rounded at apices, often with constriction above base ..... 4. *C. stenocarpum*
- Leaves linear-lanceolate or oblong-lanceolate, acute, acuminate or cuspidate at apex, not constricted above base ..... 3
3. Leaves often cuspidate and canaliculate at apex; leaf margins often faintly and distantly denticulate in upper and middle leaf portion; dorsal stereid band usually larger than ventral one; smooth basal cells do not form V-shaped pattern .. 2. *C. cylindrotheca*

- Leaves acute or acuminate at apex, but never cuspidate; leaf margins entire; dorsal stereid band smaller or equal to ventral one; smooth basal cells form V-shaped pattern ..... 3. *C. orthodontum*

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Appendix 1. Specimen voucher information and GenBank accession numbers for the newly obtained sequences and GenBank accessions involved in the plastid dataset (accession numbers for ITS sequences, representing specimens, not involved in the plastid dataset are shown in Fig. 1).

Isolate	Species	Locality	specimen_voucher	ITS	<i>atpB</i>	<i>trnG</i>	<i>trnL-trnF</i>
-	<i>Chionoloma angustatum</i> (as <i>Chionoloma schimperiana</i> )	-	Vital & Buck 19678	KT380398	KT380172	KT380244	KT380319
-	<i>Chionoloma arboreum</i>	-	Peralta 12224	KT380432	KT380204	KT380278	KT380357
-	<i>Chionoloma</i> cf. <i>tenuirostre</i>	-	Hedderson 16717	KT380455	KT380225	KT380298	KT380377
-	<i>Chionoloma</i> cf. <i>tenuirostre</i>	-	Long 42872	KT380441	KT380212	KT380286	KT380365
<b>OK322</b>	<i>Chionoloma</i> cf. <i>tenuirostre</i>	-	Ignatov & Ignatova 05-3381	KC121303	-	-	-
-	<i>Chionoloma</i> cf. <i>tenuirostre</i>	-	Porley REU9766	KT380454	KT380224	KT380297	KT380376
-	<i>Chionoloma crassicoatum</i>	-	Muller NC367	KT380449	KT380219	KT380292	KT380371
<b>BF175</b>	<i>Chionoloma cylindrotheca</i>	Russia: Primorsky Terr., Mramornaya Mt.	MW9133399	PQ659507	-	PQ778423	-
-	<i>Chionoloma cylindrotheca</i> s.str.	-	Long & Hodd 41071	KT380442	KT380213	KT380287	KT380366
-	<i>Chionoloma cylindrotheca</i> s.str.	-	Hedenäs s.n.	KT380461	-	KT380304	KT380383
-	<i>Chionoloma dubium</i>	-	Muller NC383	KT380450	KT380220	KT380293	KT380372
-	<i>Chionoloma dubium</i>	-	Koponen 34350	KT380458	KT380228	KT380301	KT380380
-	<i>Chionoloma duriuscula</i>	-	Long 35145	KT380448	KT380218	KT380291	KT380370
-	<i>Chionoloma hibernicum</i>	-	Hakelier s.n.	KT380460	KT380230	KT380303	KT380382
-	<i>Chionoloma hibernicum</i>	-	Long 30538	KT380424	KT380196	KT380271	KT380349
-	<i>Chionoloma leptocylindricum</i>	-	Soares et al. 2042	KT380392	KT380167	KT380239	KT380313
-	<i>Chionoloma leptocylindricum</i>	-	Soares et al. 2004	KT380391	KT380166	KT380238	KT380312
-	<i>Chionoloma minus</i>	-	Long 29105	KT380453	KT380223	KT380296	KT380375
<b>OK3926</b>	<i>Chionoloma orthodontum</i>	Russia: Ingushetia, Erzi Nature Reserve	MHA9026821	PQ066787	-	PQ778426	-
-	<i>Chionoloma richardsii</i>	-	Allen 19066	KT380418	KT380192	KT380267	KT380343
-	<i>Chionoloma schlimii</i>	-	Soares et al. 2255	KT380416	KT380190	KT380265	KT380341
<b>BF174</b>	<i>Chionoloma stenocarpum</i>	Russia: Primorsky Territory, Kravtsovka	MW9133380	PQ659508	-	PQ778424	-
<b>OK4018</b>	<i>Chionoloma stenocarpum</i>	Russia: Primorsky Territory, Andreevka	MW9133385	PQ659509	-	PQ77842	-
-	<i>Chionoloma tenuirostre</i>	-	Soares et al. 1783	KT380394	KT380168	KT380241	KT380315
-	<i>Chionoloma tenuirostre</i>	-	Cano 2687c	KT380395	KT380169	-	KT380316
-	<i>Chionoloma tenuirostre</i>	-	Cano 7875	KT380436	KT380208	KT380282	KT380361
-	<i>Chionoloma tenuirostre</i>	-	Hedenäs s.n.	KT380462	-	KT380305	KT380384
<b>BF173</b>	<i>Chionoloma tenuirostris</i>	Russia: Primorsky Territory, Vladivostok City	MW9133383	PQ659504	-	PQ778420	-
<b>BF194</b>	<i>Chionoloma tenuirostris</i>	Russia: Ingushetia, Dzeirakh Distr	MW9090762	PQ807500	-	PQ778421	-
<b>BF176</b>	<i>Chionoloma tenuirostris</i>	Russia: Primorsky Territory, Priozernaya Mt	MW9133390	PQ659506	-	PQ778422	-
<b>BF193</b>	<i>Tortella fragilis</i>	Russia: Krasnodar Territory, Utrish	MW9092410	PQ807499	-	-	PQ778427-