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A revision of the lichen genus *Thelotrema* Ach. (Thelotremataceae) in the Sakhalin Region, Far East of Russia

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Keywords. broad-leaved forest, cool-temperate zone, corticolous lichens, old-growth forest, tropical and subtropical lichens.

Summary. As a result of a revision of the lichen genus *Thelotrema* in the Sakhalin Region (Russian Far East), two species are reported as new to the region. *Thelotrema diplostroma* is recorded for the first time in Russia, and *T. suecicum* is reported for the first time in Asia. *T. diplostroma* previously known only from evergreen forests in tropical and subtropical regions of Africa, Australia, and Asia, was found in an old-growth forest with bamboo understory on the bark of deciduous trees on Kunashir Island. This finding represents the northernmost locality of the species in the temperate zone. *T. suecicum*, a widespread lichen of rainforests and wet montane forests in the cool-temperate zones of the Northern and Southern Hemispheres (Europe, North and South America, Australia, and New Zealand), was collected in a warm, humid riparian forest on the bark of *Alnus hirsuta* in southern Sakhalin Island and in an oak forest on the bark of *Quercus crispula* on Iturup Island. Following this revision, three species of *Thelotrema* are confirmed for the Sakhalin Region, including the previously known *T. lepadinum*. Detailed morphological, anatomical, and ecological descriptions are provided, along with illustrations, diagnostic features of similar species, and an identification key for the species of *Thelotrema* and morphologically related taxa occurring in the region.

Ревизия рода лишайников *Thelotrema* Ach. (Thelotremataceae) в Сахалинской области, Дальний Восток России

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Ключевые слова: старовозрастный лес, тропические и субтропические лишайники, широколиственный лес, холодно-умеренная зона, эпифитные лишайники.

Аннотация. В результате ревизии материалов по роду *Thelotrema* в Сахалинской области выявлено два новых для региона вида: *T. diplostroma* – новый вид для России, и *T. suecicum* – новый вид для Азии. *Thelotrema diplostroma*, ранее известный только из вечнозелёных лесов тропических и субтропических районов Африки, Австралии и Азии, обнаружен в старовозрастном лесу с подлеском из курильского бамбука на коре лиственных деревьев на острове Кунашир. Эта находка стала самой северной точкой ареала вида в умеренной зоне. *Thelotrema suecicum*, широко распространённый в дождевых и влажных горных лесах холодно-умеренного пояса Северного и Южного полушарий (Европа, Северная и Южная Америка, Австралия, Новая Зеландия), выявлен в хорошо прогреваемом влажном прирусловом лесу на коре *Alnus hirsuta* на юге острова Сахалин и в дубовом лесу на коре *Quercus crispula* на острове Итуруп. По итогам ревизии для Сахалинской области подтверждено три вида *Thelotrema*, включая ранее известный *T. lepadinum*. В статье приведены подробные описания морфологии, анатомии и экологии видов, проиллюстрированы их диагностические признаки, а также представлен ключ для определения видов *Thelotrema* и морфологически сходных таксонов, встречающихся в регионе.

Introduction

The genus *Thelotrema* Ach., a former member of Graphidaceae (Frisch et al., 2006; Mangold et al., 2009), belongs to Thelotremataceae according to the most recent classification of Ascomycota (Hyde et al., 2024; Thiyagaraja et al., 2025). Representatives of the genus are characterized by immersed-erumpent to sessile, non-carbonized, eolumellate, perithecioid to apothecioid ascomata with a double margin caused by a free proper exciple, and lateral periphysoids (Frisch et al., 2006; Rivas Plata et al., 2010). The genus comprises ca. 150 species, mostly corticolous, with a distribution centered in tropical and subtropical regions and extending into temperate areas (Purvis et al., 1995; Lücking, Breuss, 2012; Hyde et al., 2024). Thelotremoid lichens represent one of the most important components of corticolous rainforest microlichen biotas (Santesson, 1952; Rivas Plata et al., 2008). In Russia, only one species of *Thelotrema* is known: the subcosmopolitan *T. lepadinum* (Ach.) Ach., which occurs throughout the Russian southern Far East (Tchabanenko, 2002). This species is widely distributed in temperate to subtropical regions in both hemispheres, as well as in tropical mountain areas (Frisch et al., 2006; Mangold et al., 2009). The report of *Thelotrema foveolare* Müll. Arg. for Kunashir Island by Insarov and Pchelkin (1988) was considered doubtful (Urbanavichus, 2010) since the specimen was badly damaged by fungi (Konoreva et al., 2020). The palaeotropical species *Austrotrema bicinctulum* (Nyl.) I. Medeiros et al., a former member of *Thelotrema* (Medeiros et al., 2017), is known from Sakhalin and Shikotan Islands (Tchabanenko et al., 2018; Chesnokov, Konoreva, 2022), while globally it occurs in rainforest, coastal, and wet-sclerophyll

forests of tropical and subtropical regions (Mangold et al., 2009). Here we present the result of a revision of herbarium material of *Thelotrema* from the Sakhalin Region in the Herbarium of the Institute of Marine Geology and Geophysics (SAK) and Altai State University (ALTB), including reports of two new records of *Thelotrema*: *T. diplostroma* Nyl. with a tropical to subtropical distribution, and *T. suecicum* (H. Magn.) P. James, which occurs mostly in the cool-temperate zone of both hemispheres.

Material and methods

The paper is based on the study of lichens collected from Kunashir Island and southern Sakhalin in 2015, 2017 and 2023 by the first and third authors. Identified specimens from Russia were compared with additional specimens of *Thelotrema* collected in Japan in 2019 by E. A. Davydov. Additional material of *Thelotrema lepadinum* (Ach.) Ach. collected by F. A. Romanyuk was used in the present study.

The climate of the islands is of a temperate monsoon type, with cold winters that are milder than in the continental part and cool, rainy summers. According to Takhtajan (1986), the northern parts of the Sakhalin Region belong to the Okhotsk-Kamchatka Province of the Circumboreal floristic Region, while the southern parts along with Hokkaido are related to the East Asian floristic Region. Voucher specimens were deposited in the herbaria of the Institute of Marine Geology and Geophysics (SAK) and Altai State University (ALTB). The specimens were examined using stereomicroscopes (Olympus SZ-61, MBS-10 and Zeiss Stemi 2000-C) and compound microscopes (LOMO Mikmed 3 and Zeiss Axio Lab.A1).

Secondary metabolites were identified using high-performance thin-layer chromatography (HPTLC) following standardized methods for lichen products (Arup et al., 1993; Orange et al., 2001). Spot tests were made with 10 % potassium hydroxide solution (K), sodium hypochlorite solution (C), 1,4-p-phenylenediamine (PD), and Lugol's solution (I). We accept the species composition of the genus *Thelotrema* following Rivas Plata et al. (2010) with additions by Medeiros et al. (2017). Identifications were made mainly with the help of the published world-wide key to the thelotremoid Graphidaceae by Rivas Plata et al. (2010).

Results

Thelotrema Ach., 1803, Methodus: 130.

Type: *T. lepadinum* (Ach.) Ach.

≡ *Antrocarpum* G. Mey., 1825, Nebenst. Beschäft. Pflanzenk. 1: 326, nom. illeg., based on *Lichen lepadinus* Ach. [= *T. lepadinum* (Ach.) Ach.]

= *Brassia* A. Massal., 1860, Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 3, 5: 259.

Type: *Brassia porinoides* (Mont. et Bosch) A. Massal. [= *T. porinoides* Mont. et Bosch]

Thallus crustose, endophloeodal to epiphloeodal, whitish, cream, yellowish-greyish, greenish or olive, mostly ecorticate or with a protocortex. Photobiont trentepohlioid. Ascomata ± rounded, perithecioid or apothecioid. Proper exciple ± free, rarely fused. Hymenium non-amyloid; paraphyses parallel to ± distinctly interwoven, usually unbranched; lateral paraphyses present; true columella absent. Epihymenium usually hyaline. Asci 1–8-spored, clavate, non-amyloid. Ascospores 1–3-seriate, transversely septate to muriform, hyaline to yellowish or brown, non-amyloid to distinctly amyloid; ascospore wall thin to thick, smooth or occasionally crenate, non-halonate to ± distinctly halonate.

Chemistry: stictic, hypostictic, norstictic, protocetraric, salazinic acids present or absent.

Distribution and ecology: ca. 150 species, most of which are tropical to subtropical in distribution, occurring predominantly on bark.

Key to *Thelotrema* s. l. in the Sakhalin Region

The key comprises current and former representatives of *Thelotrema* known in the Sakhalin Region as well as an expected temperate species *Thelotrema subtile* Tuck.

1. Ascospores muriform ***T. lepadinum***
+ Ascospores transversely septate 2
2. Apothecia immersed, pore-like; thallus with prosoplectenchymatous cortex; stictic acid present; ascospores 15–30 µm long
..... ***Austrotrema bicinctulum***
+ Apothecia prominent; thallus ecorticate or with a loose, irregular cortex; lichen substances absent; ascospores 25–110 µm long 3
3. Ascospores mostly over 60 µm long, with thick outer wall ***T. diplotrema***
+ Ascospores up to 60 µm long, with thin to thick outer wall 4
4. Ascospores with thin walls in early stages, becoming partially grey-brown when mature, ± strongly amyloid; proper exciple colorless
..... ***T. subtile***
+ Ascospores with thick outer walls from an early stage, remaining hyaline, weakly amyloid; proper exciple pale brown ***T. sueticum***

The species

Thelotrema diplotrema Nyl., 1859, Ann. Sci. Nat., Bot., Sér. 4, 11: 258 (Figs. 1A, 1B, 2A, 2B).

Examined specimens: “Russia, Sakhalin Region, Kunashir Island, vicinity of Tretyakovo Village, 43°58′34.1″N, 145°39′45.4″E, 191 m, mixed coniferous–broad-leaved forest, on bark of *Kalopanax septemlobus* (Thunb. ex A. Murray) Koidz., 22 VIII 2017. Leg. A. K. Ezhkin” (SAK 3081, 4065, 4066); *ibid.*, “43°58′28.38″N, 145°39′49.28″E, on bark of *Bothrocaryum controversum* (Hemsl. ex Prain) Poyarkova, 163 m, 22 VI 2015. Leg. A. K. Ezhkin” (SAK 3415).

Additional specimens examined: “Japan, Hokkaido Island, Prov. Kushiro, Mt. O-akan, Akan-cho, Kushiro-city, 43°26′05″N, 144°08′29″E, 430 m, coniferous (*Abies–Picea*) forest, on *Abies* sp. 01 IX 2019. Leg. E. A. Davydov 20342” (ALTB).

Description of the studied specimens: Thallus corticolous, endophloeodal to epiphloeodal, loosely corticated or ecorticate, crustose, continuous or cracked, thin, up to ca. 100 µm thick, whitish gray, smooth. Photobiont trentepohlioid. Algal layer well developed, continuous or discontinuous, densely integrated with crystals. Calcium oxalate crystals abundant, small to large, mostly aggregated to dispersed. Medulla indistinct. Ascomata mostly rounded, apothecioid, up to ca. 0.7 mm diam., with grayish to blackish pruinose disc and rounded thalline margin, concolorous with the thallus. Hymenium hyaline, ca. 130 µm high. Epihymenium

hyaline to grayish. Proper exciple mostly hyaline to yellowish to pale brownish, 15–25 µm thick, I–. Lateral paraphyses conspicuous, up to ca. 20 µm long. Asci clavate, 8-spored, 60–90 × 15–18 µm, I–. Ascospores hyaline, transversely septate, (30–)60–72(–80) × (7–)9–12 µm, with 16–20(–22) lenticular locules, I+ faint blue.

Chemistry: Thallus K–, C–, PD–; no secondary metabolites were detected by HPTLC.

Distribution and ecology: The species is most common in tropical and subtropical regions of Africa, Australia and Asia (Frisch et al., 2006; Mangold et al., 2009; Joshi et al., 2012). On Kunashir it is reported only from one location in old-growth, low-disturbed forest with bamboo in the understory, on bark of deciduous trees at an altitude between 160–190 m. It is here recorded from Russia for the first time.

Notes: This species is morphologically similar to *Thelotrema subtile* Tuck. and *T. pseudosubtile* Mangold in having transversely septate, hyaline ascospores and a thallus lacking secondary metabolites, but both of the latter species can be distinguished by their smaller ascospores with thick lateral walls (25–60 × 6–10 µm). Moreover, *Thelotrema diplostroma* has a less compact, sometimes roughened thallus surface and more distinctly emergent ascomata, usually with a less distinctly free proper exciple (Lumbsch et al., 2008; Joshi et al., 2009, 2012).

Thelotrema lepadinum (Ach.) Ach., 1803, *Methodus, Sectio prior* (Stockholmia): 132 (Figs. 1C, 1D, 2C, 2D).

Specimens examined: “Russia, Sakhalin Region, Sakhalin Island, Smirnykhovskiy District, foothills of Mt. Vaida, headwaters of the Vitnitsa River, left bank, 49°53′59″N, 143°26′23″E, 400 m, coniferous forest, on bark of *Betula* sp. 12 VIII 2019. Leg. E. A. Davydov 20341” (ALTB); *ibid.*, “vicinity of Vestochka Village, Komissarovka River valley, coniferous forest, on bark of *Betula ermanii*. 25 VI 2013. Leg. A. K. Ezhkin” (SAK 3616); “Iturup Island, vicinity of Baranskogo Volcano, Kipyashaya River valley, 45°4′43.31″N, 147°59′6.97″E, 225 m, oak forest, on bark of *Quercus crispula* Blume. 21 VIII 2015. Leg. A. K. Ezhkin” (SAK 3615); *ibid.*, “Kurilka River valley, 45°07′49.84″N, 147°47′21.44″E, 225 m, oak forest, on bark of *Quercus crispula*. 25 VIII 2012. Leg. A. K. Ezhkin” (SAK 3621); *ibid.*, “Berutarube Volcano, east slope, Andrey Steam valley, 44°28′42.31″N, 146°56′59.05″E, 450 m, birch-rowan forest, on bark of *Sorbus commixta* Hedl. 01 VIII 2023. Leg. F. A. Romanyuk” (SAK 2878); *ibid.*, “on bark of *Abies*

sachalinensis. 01 VIII 2023. Leg. F. A. Romanyuk” (SAK 2856); “Kunashir Island, vicinity of Mendelev Volcano, 43°58′9.08″N, 145°43′41.75″E, 575 m, coniferous forest, on bark of *Sorbus commixta*. 06 VIII 2013. Leg. A. K. Ezhkin” (SAK 3453); *ibid.*, “43°58′33.69″N, 145°43′19.81″E, 468 m, on bark of *Abies sachalinensis* F. Schmidt. 06 VIII 2013. Leg. A. K. Ezhkin” (SAK 3494); *ibid.*, “44°0′15.27″N, 145°41′53.46″E, 201 m, mixed coniferous-broad-leaved forest, on bark of *Quercus crispula*. 01 VIII 2013. Leg. A. K. Ezhkin” (SAK 3593); *ibid.*, “43°59′29.53″N, 145°43′19.98″E, 328 m, coniferous forest, on bark of *Betula ermanii* Cham. 28 VII 2013. Leg. A. K. Ezhkin” (SAK3622); *ibid.*, “43°58′42.02″N, 145°42′52.14″E, 339 m, coniferous forest, on bark of *Sorbus commixta*. 06 VIII 2013. Leg. A.K. Ezhkin” (SAK 3620); “vicinity of Golovnino Volcano, 43°52′51.59″N, 145°36′20.29″E, 89 m, mixed forest, on bark of *Taxus cuspidata* Siebold et Zucc. ex Endl. 22 VIII 2017. Leg. A. K. Ezhkin” (SAK 3624); “Shikotan Island, vicinity of Mt. Shikotan, 43°52′10.31″N, 146°50′40.63″E, mixed forest, on bark of *Acer pictum*. 20 VI 2017. Leg. A. K. Ezhkin” (SAK 3623); *ibid.*, “43°52′15.9″N, 146°50′42.54″E, 157 m, mixed forest, on bark of *Acer pictum* Thunb. 11 VI 2017. Leg. A. K. Ezhkin” (SAK 3618); *ibid.*, “road to Krai Sveta Cape, 43°50′54.47″N, 146°51′03.75″E, 55 m, mixed forest, on bark of *Abies sachalinensis*. 19 VI 2017. Leg. A. K. Ezhkin” (SAK 3619); *ibid.*, “vicinity of Mt. Notoro, 43°46′40.93″N, 146°42′08.05″E, 92 m, mixed forest, on bark of *Padus ssiirii* (Fr. Schmidt) C. K. Schneid. 17 VI 2017. Leg. A. K. Ezhkin” (SAK 3617).

Additional specimens examined: “Japan, Hokkaido Island, Prov. Kushiro, Mt. O-akan, Akancho, Kushiro-city, 43°26′05″N, 144°08′29″E, 430 m, coniferous (*Abies-Picea*) forest, on *Magnolia* sp. 01 IX 2019. Leg E. A. Davydov 20340” (ALTB).

Description of studied specimens: Thallus corticolous, epiphloeodal to endophloeodal, crustose, continuous, thin, up to ca. 150 µm thick, yellow-white, yellow-brown or grayish-green, smooth to rugose. Photobiont trentepohlioid. Algal layer well developed with integration of calcium oxalate crystals. Ascomata apothecioid, up to ca. 1.0 mm diam., usually numerous, deeply immersed in prominent, conical thalline warts with a crater-like summit; the rim is usually incurved, with a whitish membrane at the bottom that disrupts at maturity, leaving small white fragments in the center of the blackish apothecial disc surrounded by a prominent black proper margin which is usually free from the thalline margin. Hymenium ca. 200 µm high, hyaline,

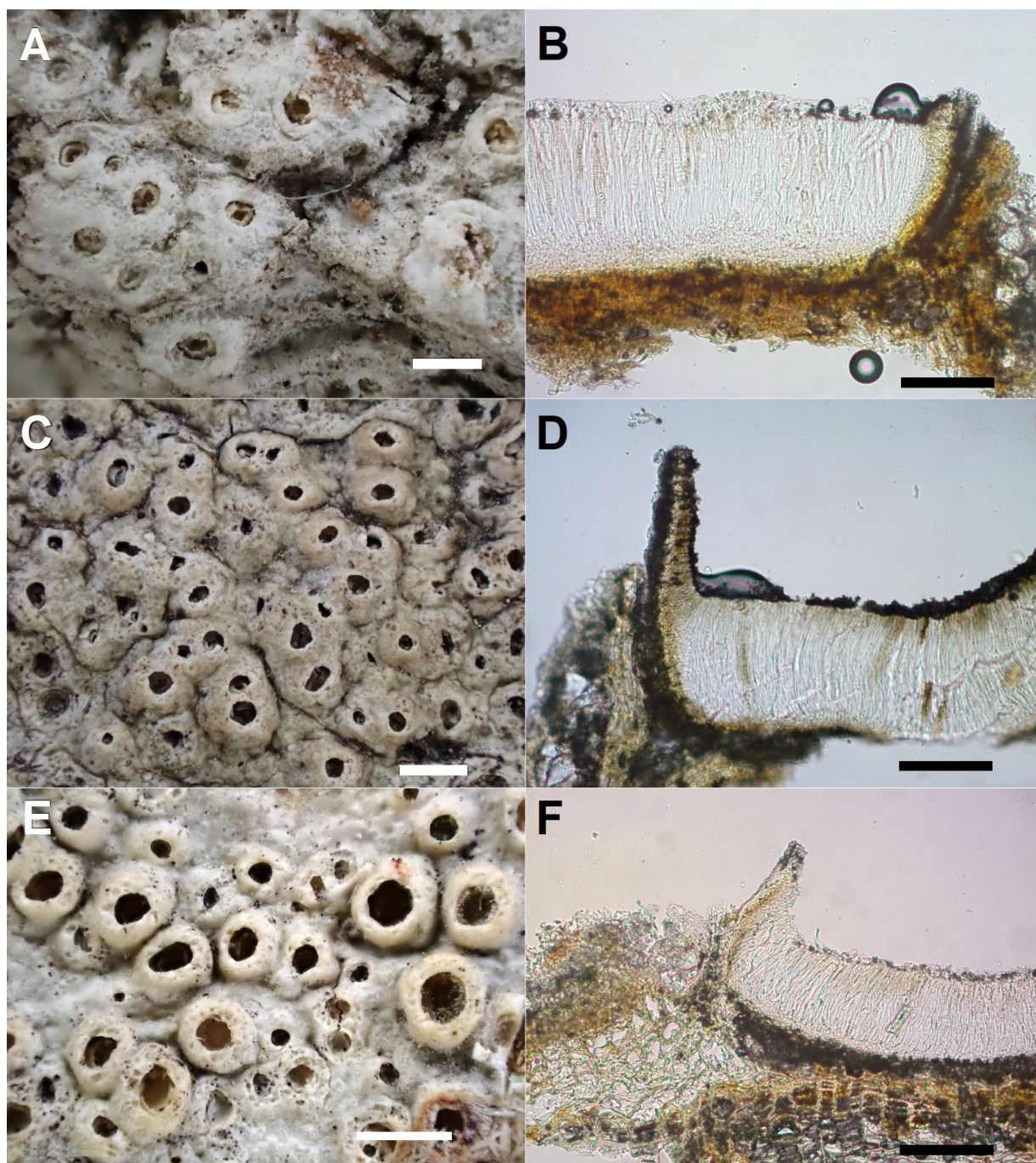


Fig. 1. *Thelotrema* species, thalli and cross sections of apothecia: A, B – *T. diplotrema*; C, D – *T. lepadinum*; E, F – *T. suecicum*. Scale bar: A, C, E = 1 mm; B, D, F = 100 μ m.

not interspersed, weakly conglutinated, non-amyloid; paraphyses slender, thread-like, mostly simple; paraphysoids present, lining the upper inner surface of the exciple; hypothecium colorless. Epiphymenium hyaline to brownish. Asci clavate, 1–4(–5)-spored; ascospores hyaline, muriform, ellipsoidal or broadly fusiform, $(35\text{--})62.5\text{--}92.5\text{(–}150) \times (7.5\text{--})13\text{--}20\text{(–}25)$ μ m, I– or I+ faintly bluish.

Chemistry: Thallus K–, C–, PD–; no secondary metabolites detectable by HPTLC.

Notes: This species most closely resembles *Thelotrema crassisporum* Mangold, but the latter contains stictic acid and has smaller ascospores, up to ca. 30 μ m long (Joshi et al., 2012).

Ecology and distribution: *Thelotrema lepadinum* is a widespread subcosmopolitan lichen in temperate and subtropical regions and tropical mountains and occurs in different types of forests on coniferous and deciduous trees in both hemispheres (Frisch et al., 2006; Mangold et al., 2009). In the Sakhalin Region

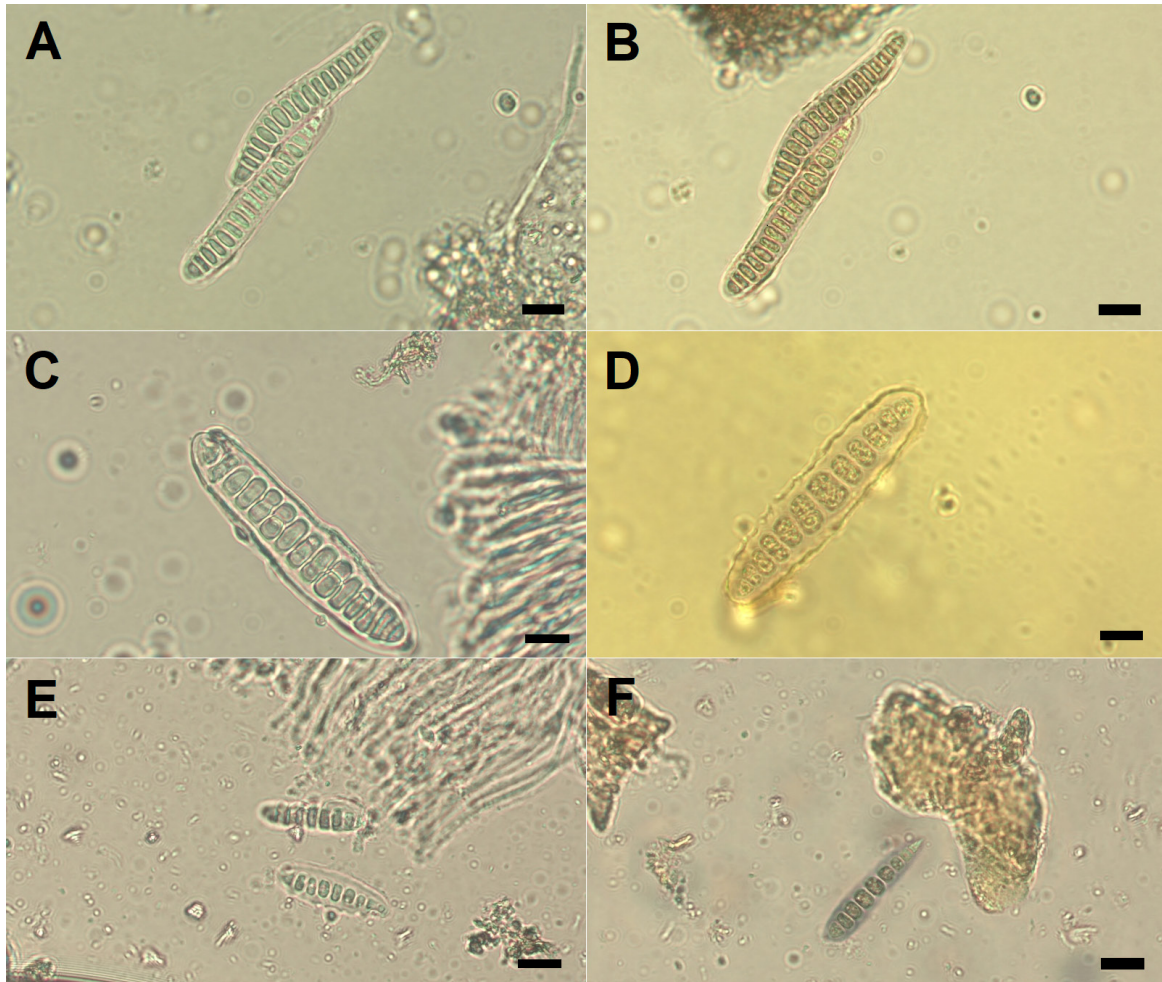


Fig. 2. *Thelotrema* species, spores in water solution and spores in iodine: A, B – *T. diplotrema*; C, D – *T. lepadinum*; E, F – *T. suecicum*. Scale bar: 10 µm.

it has been collected from coniferous and deciduous trees in mixed and coniferous forests on Sakhalin and the South Kuril Islands.

Thelotrema suecicum (H. Magn.) P. James, 1977, *Lichenologist* 9: 186 (Figs. 1E, 1F, 2E, 2F).

Specimens examined: “Russia, Sakhalin Region, Sakhalin Island, Aniva Bay, Cryllion Peninsula, right bank of the Nacha River, 1 km above the mouth, 46°08′34.93″N, 142°12′57.64″E, 5 m, valley alder forest, on bark of *Alnus hirsuta* (Spach.) Rupr. 21 VIII 2023. Leg. E. A. Davydov 20530” (ALTB); *ibid.*, “46°08′32.13″N, 142°12′50.31″E, 10 m, spruce-fir forest, on bark of *Abies sachalinensis*. 21 VIII 2023. Leg. E. A. Davydov 22283” (ALTB); “Iturup Island, vicinity of Baranskogo Volcano, Kipyashaya River valley, 45°05′25.6″N, 147°59′21.9″E, 361 m, oak forest, on bark of *Quercus crispula*. 11 VIII 2012. Leg. A. K. Ezhkin” (SAK 4108).

Additional specimens examined: “Japan, Hokkaido Island, Prov. Kushiro, Mt. O-akan, Akan-

cho, Kushiro-city vicinity, 43°26′05″N, 144°08′29″E, 430 m, coniferous (*Abies-Picea*) forest, on *Magnolia* sp. 01 IX 2019. Leg. E. A. Davydov 20343” (ALTB).

Description of studied specimens: Thallus corticolous, endophloeodal to epiphloeodal, crustose, continuous, up to ca. 100 µm thick, pale yellowish grey, smooth to ± distinctly verruculose. Protocortex discontinuous, up to ca. 20 µm thick, occasionally becoming conglutinated and forming a thin true cortex. Photobiont trentepohlioid. Algal layer well developed and continuous, often becoming discontinuous due to calcium oxalate crystal inclusions. Ascomata apothecoid, up to ca. 1.0 mm diam., hemispherical, sessile, solitary, occasionally marginally fused, rarely immersed, usually emergent, rarely urceolate or subglobose. Disc usually partly visible, greyish, pruinose. Thalline margin thin to thick, entire to split or somewhat eroded, ± rounded, usually becoming wide to gaping, incurved to slightly erect, concolorous with the thallus or yellowish to pale orange. Proper exciple free, thin,

hyaline to pale yellowish internally, yellowish to brownish marginally, apically covered by greyish granules, occasionally slightly amyloid at the base. Hymenium up to ca. 90 μm thick, not inspersed, weakly conglutinated; paraphyses parallel to slightly interwoven, unbranched, the tips thickened; lateral paraphyses usually inconspicuous, up to ca. 25 μm long. Epithymenium hyaline, with greyish granules and small crystals. Asci (4–)6–8-spored. Ascospores hyaline, transversely septate, ellipsoidal to broadly fusiform, thick-walled, the ends narrowly rounded to subacute, non-amyloid to faintly amyloid, 20–38 \times 7.5–10 μm , with 6–9(–12) locules; locules \pm rounded to angular, subglobose to cuboid or irregular.

Chemistry: Thallus K–, C–, PD–; no secondary metabolites detectable by HPTLC.

Ecology and distribution: The species occurs on bark in cool-temperate rainforests and wet-sclerophyll forest in both hemispheres, recorded from Europe, North and South America (Purvis et al., 1995), Australia (Mangold et al., 2009) and New Zealand (Lumbsch et al., 2010). In the Sakhalin Region it is reported from a warm humid valley with riparian alder forest on bark of *Alnus hirsuta* and coniferous forest on bark of *Abies sachalinensis* on Sakhalin Island, and from a mountain location with oak forest on bark of *Quercus crispula* on Iturup Island. It is here recorded from Russia and Asia for the first time.

Notes: This species closely resembles *Thelotrema defossum* and *T. subtile*. *Thelotrema defossum* differs by larger ascospores with regularly formed loci and thin septa. *Thelotrema subtile* has strongly amyloid ascospores, less thickened cell walls often with a crenate surface, larger loci, and older ascospores with a brown pigmentation (Lumbsch et al., 2010).

Discussion

After revising all collected material from Sakhalin and the Kuril Islands, we identified two additional species of *Thelotrema*, including *T. diplotrema* which is new to Russia, and *T. suecicum* – a new record for Asia. *Thelotrema foveolare*, previously recorded for Kunashir (Insarov, Pchelkin, 1988; Urbanavichus, 2010), is excluded from the list, following Konoreva et al. (2020). In total, the occurrence of three species of *Thelotrema* was confirmed for the Sakhalin Region. The low number of species is explained by the fact that the Sakhalin Region belongs to the Northern East Asian floristic Province, which represents a northern outlier of the enormous East Asian diversity centered in tropical regions. The diversity of *Thelotrema* in the Sakhalin Region and in the

southern Russian Far East in general is relatively high in comparison with other Russian macro-regions. Only one species, *Thelotrema lepadinum*, recognized in the area treated is known in Russia outside the Russian Far East from South Siberia, the Caucasus and the European part (Urbanavichus, 2010). This mild-temperate lichen, occurring on broad-leaved trees in humid montane forests with frequent fog or near rivers and in coastal humid forests, is also known from Europe and North America in the Northern Hemisphere (Nimis, 2016; McCune, 2017). In the Sakhalin Region *Thelotrema lepadinum* is the most common thelotremoid lichen, occurring on the bark of many deciduous and coniferous trees in almost all forest types. *Thelotrema suecicum* may be under-recorded or overlooked as it was found in three types of forest which had been disturbed or managed previously. So, it may be more widespread than currently documented. The most interesting discovery here is *Thelotrema diplotrema*, found only in one location with old-growth and little-disturbed mixed coniferous-broad-leaved forest on Kunashir Island but was abundant on tree trunks there. As it grows mainly in evergreen forests in the tropics and subtropics, this finding, as the first report of the species in the temperate zone, may indicate a possible relict origin dating back to the Holocene optimum (7380–6200 cal. yr BP) (Razjigaeva et al., 2022). Thus, with the exception of *Thelotrema lepadinum*, species of *Thelotrema* occurring in the Sakhalin Region (as well as most members of the genus worldwide) are very sensitive to air humidity. The latter circumstance may explain their occurrence in the middle elevation belt, which provides more suitable microhabitats to accommodate the mostly tropical species, as well as along the rivers, especially at the mouths of rivers moistened by the Pacific monsoon.

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