ISSN 0012-4966, Doklady Biological Sciences, 2025. © Pleiades Publishing, Ltd., 2025.

Calcipostia guttulata (Basidiomycota, Polyporales) in Russia

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Received July 25, 2025; revised August 11, 2025; accepted August 12, 2025

Abstract—The aim of this work was to summarize the data on the ecological, biological, and morphological features of *Calcipostia guttulata* (Polyporales, Basidiomycota) by using the original materials, revised herbarium specimens, data on molecular barcoding of original collections, the available literature, and iconography and information stored on the GBIF portal. It was shown that *C. guttulata* is a widespread, but rare polypore in the Holarctic; is confined to the early stages of drying of coniferous stands, primarily spruce forests; and is a poorly studied headwood pathogen and a saprotroph that colonizes coniferous deadwood and, less often, fallen trees. The morphological diagnosis of *C. guttulata* was clarified. Its substrate spectrum, distribution, and relationships with insects, which are important for forest pathology, have been identified most fully to date. The conservation status of the species and the prospects for its use in biotechnology are discussed.

Keywords: brown rot, mycetophagous insects, substrate ecology, tinder fungi, *Ips typographus*, Postiaceae

DOI: 10.1134/S0012496625700036

INTRODUCTION

Since 2021, an outburst of mass reproduction of *Ips typographus* (Curculionidae, Coleoptera) has been observed in Leningrad oblast [1]. Drying-out foci have approached protected forests in the Kurortnyi region of St. Petersburg (Gladyshevskii and Ozero Shchuch'e protected territories) [2]. Mass fruiting of *Calcipostia guttulata* has been observed in a recently dried three-year-old *Picea abies* stand in the latter territory. The fungus was part of a pioneer saprotrophic fungal complex, which additionally included *Fomitopsis pinicola*, *Trichaptum abietinum*, *Gloeophyllum sepiarium*, *Armillaria ostoyae*, *Amaropostia stiptica*, *Exidia nigricans*, *E. saccharina*, *Dacrymyces stillatus*, *Heterobasidion parviporum*, *Phlebiopsis gigantea*, *Stereum sanguinolentum*, and *Pleurotus abieticola*.

Calcipostia guttulata is regularly, though rarely, found in various Holarctic regions, but its role in the drying-out of spruce stands, its substrate ecology, and its distribution are still poorly understood. The objective of this work was to summarize the available data on ecological, biological, and morphological specifics of the species (including its relationships with insects, which are of importance in terms of forest pathology). We used our original materials, revised herbarium specimens, data on molecular barcoding of original collections, the available literature, and iconography and information stored on the GBIF portal.

MATERIALS AND METHODS

Specimens collected were examined morphologically under an AxioImager A1 light microscope at the Collective Use Center, Komarov Botanical Institute. Microscopic slides were prepared using 5% KOH and Mezer's reagent. Microstructure measurements were performed in distilled water. Specimens were herbarized in Kirov St. Petersburg State Forest Engineering University (duplicates were stored in Komarov Botanical Institute, LE-F). Specimens collected in the Russian Far East and mentioned in this work were stored in a herbarium (VLA), Bioresource Collection, Federal Research Center of Biodiversity of East Asian Terrestrial Biota (identification no. 2797657).

To isolate DNA, basidiomata pieces were lyophilized in a FreeZone 2.5 Plus freeze dry system (Labconco, United States) at –84°C for 2 days. Then the pieces were homogenized in 2-mL tubes with glass beads on a FastPrep shaker (Precellys 24, Bertin Technologies, Rockville) at 5000 rpm for 2 min. CTAB extraction buffer (3% cetyltrimethylammonium bromide, 2 mM EDTA, 150 mM Tris-HCl, 2.6 M NaCl,

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pH 8) was added at 800 μL per tube, and the tubes were incubated at 65°C for 1 h. The samples were centrifuged, and the supernatant was collected in 1.5-mL tubes, combined with 1 volume of chloroform, and shaken gently. After centrifugation at 14 000 rpm for 8 min, material was precipitated from the supernatant with two volumes of chilled isopropyl alcohol, washed with 70% ethanol, and dissolved in 50 μL of TE buffer.

The PCR mixture (15 μL) contained 3 μL of Screen Mix (Evrogen, Russia), 0.2 μL of each primer (10 μM), 10.5 μL of ddH_2O, and 1 μL of template DNA (100 ng). The ITS nDNA region was amplified with the primers ITS1-F and ITS4 [3, 4]. Amplification included initial denaturation at 95°C for 5 min; 33 cycles of denaturation at 95°C for 30 s, primar annealing at 56°C for 30 s, and elongation at 72°C for 30 s; and final elongation at 72°C for 5 min. Amplification products were resolved by electrophoresis in 1.0% agarose gel in 1× TAE (Tris-acetate) buffer with ethidium bromide and visualized using a ChemiDoc MP imaging system (BioRad, United States). DNA and amplicon concentrations were measured using a SpectroStar Nano spectrometer (BMG Labtech, Germany). Sequencing was carried out by Sintol (Russia). The resulting sequences were compared with reference sequences using the BLASTn algorithm.

RESULTS AND DISCUSSION

Taxonomy and Morphology

Calcipostia guttulata (Sacc.) B.K. Cui, L.L. Shen et Y.C. Dai in L.L. Shen, Wang, Zhou, Xing, B.K. Cui et Y.C. Dai, Persoonia 42: 112, 2019. ≡ *Polyporus guttulatus* Sacc., Syll. Fung. 6: 106, 1888. ≡ *Tyromyces guttulatus* (Sacc.) Murrill, N. Amer. Fl. 9 (1): 31, 1907. ≡ *T. stipticus* f. *guttulatus* (Sacc.) Domański, Orloś et Skirg., Flora Polska. Grzyby, II: 135, 1967. ≡ *Spongiporus guttulatus* (Sacc.) A. David, Bull. Mens. Soc. Linn. Lyon 49 (1): 17, 1980. ≡ *Postia guttulata* (Sacc.) Jülich, Persoonia 11 (4): 423, 1982. ≡ *Oligoporus guttulatus* (Sacc.) Gilb. et Ryvarden, Mycotaxon 22 (2): 365, 1985. = *Polyporus maculatus* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 26: 69, 1874. = *Tyromyces tiliophilus* Murrill [ut '*tiliophila*'], N. Amer. Fl. 9 (1): 33, 1907. = *T. substipitatus* Murrill, Mycologia 4 (2): 96, 1912. ≡ *Polyporus substipitatus* (Murrill) Murrill, Mycologia 4 (4): 217, 1912. = *P. grantii* Lloyd, Mycol. Writ. 5: 763, 1918. = *P. tiliophilus* (Murrill) Sacc. et Trotter, Syll. Fung. 21: 281, 1912. = ? *Tyromyces leveilleanus* (Bondartsev) Bondartsev et Singer, Ann. Mycol. 39: 52, 1941.

Icon.: Lowe (1975, p. 43, *f.* 29 [5]) [ut *Tyromyces guttulatus*]; Gilbertson, Ryvarden (1987, p. 469, *f.* 226 [6]) [ut *Oligoporus guttulatus*]; Ryvarden, Gilbertson (1994, p. 413, *f.* 198 [7]) [ut *O. guttulatus*]; Bondartseva (1998, p. 262, *f.* 52; p. 264, *f.* 53 [8]) [ut *O. guttulatus*]; Nitare J. (2000, p. 325 [9]) [ut *O. guttulatus*]; Niemelä (2001, p. 71, *f.* 54 [10]) [ut *Postia guttulata*]; Ryvarden, Melo (2014, p. 274, *f.* 207 [11]); Yurchenko, Kotiranta (2020, p. 5, *f.* 1 [12]).

Exicc.: "Fungi of Washington", Forest Disease Survey, U.S. Forest Service, No 8228 [ut *Polyporus guttulatus* Peck] – USA, Washington, Olympic Peninsula, Soleduck river, on conifer log, J.L. Lowe, R.L. Gilbertson, D. Griffin, 09.1957.

Teleomorph. Basidiomata rather large, 3–15 × 1.5–8.5 × 0.5–3.5 cm (up to 22 × 10 × 1.5 cm according to Lowe [5]), losing one-fifth to one-forth of volume on drying, *Tyromyces*-like in morphotype, annual, sessile or with lateral/dorsal stipe going into substrate, or prostrate-reflexed, in outlines semiorbicular, flabelliform, linguiform, spatulate, rather applanate, often with small protuberance at base, usually asymmetric, with uneven surfaces and margin, solitary or imbricate (Fig. 1a). Pileus surface delicate velvety initially, then glabrous and coated with thin cuticle, rough, radiate fibrous, with age radiate rugose with depressions filled with metabolic fluid when fresh, initially whitish, concolorous, then with cream-colored, pinkish-pale yellow, or brownish irregular spots and zones, finally isabelline at base, drying yellow or brown (Figs. 1a, 1b). Margin rather thin, wavy, incurved, white, drying ivory white or cream colored. Hymenophore tubular, tubes one-layered, 0.3–0.9 cm thick; hymenophore surface concolorous, initially white, then ivory white or cream colored grayish, sometimes with yellowish coating; pores circular-angular, occasionally labyrinthine, 4–6 per mm when fresh, drying 6–8 per mm (Figs. 1b, 1d). Context white, homogenous, 0.4–3 cm thick, initially fleshy-fibrous, dense, then leathery-corky, finally bony, with strong coumarin scent on drying, bitter (like *Amaropostia stiptica*).

Hyphal system pseudodimitic [13]. Generative hyphae predominate in tube trama, 1.5–5.5 μm in diam, hyaline, thin-walled or with slightly thickened walls, branching at sharp angle, with usual clamps; gloeoplerous hyphae are found occasionally, 1.9–14.5 μm in diam, sinuous and swollen, staining bright red in phloxine. Pseudoskeletal hyphae predominate in pileus and stipe contexts, 4–8 (17.5) μm in diam, with clamps, thick-walled to nearly solid, often with subopposite swollen clamps; determine leathery-corky texture of mature basidiomata. In hymenium, leptocystidia (cystidioles) common, fusoid, 10–25 × 2.5–6.0 μm; gloeocystidia (endings of gloeoplerous hyphae) occasional, of the same size. Basidia 12.5–25 × 4.3–6.5 μm, clavate with distinct central constriction, four-spored, with a basal clamp, hyaline. Basidiospores 4.0–5.0 (5.7) × 1.9–2.7 μm (4–5 (6) × 2–2.5 (3) μm according to Lowe [5]; 4–5 × 2–2.5 μm according to Ryvarden, Gilbertson [7] and Yurchenko, Kotiranta [12]), short-cylindrical, hyaline (some with unclear granulate contents or one or two lipid globules), thin-walled, nonamyloid, slightly cyanophilic.

Fig. 1. *Calcipostia guttulata* (LE 287757): (a) a cluster of basidiomata at the base of a *Picea abies* tree, (b) hymenophore of a fresh basidioma, (c) surface detail of a dried specimen, and (d) hymenophore of a dried specimen. Bar, (b, d) 1 mm.

Anamorph. Develops in hymenium, tube trama, and pileus context. Cultures usually cottony-wooly, cotton-like with age, smoky, with fluffy margin, white to cream-colored, often with pinkish, pale-yellow to ochraceous tint. Hyphae 1.5–11.0 µm in diam, hyaline, thin-walled or thick-walled, with abundant, often open clamps. Gloeoplerous hyphae 1.9–15 µm in diam, sinuous and swollen, highly cyanophilic. Conidiogenous hyphae nondifferentiated, branching at right angle, with regular clamps approximately 2 µm wide, slightly swollen at the apex. During conidiogenesis, a simple cross-wall (adventive septum) forms at the basis of the anlage, somewhat higher than the first clamp; the cell wall between the clamp and adventive septum undergoes lysis, and a conidium is released. Another adventive septum sometimes forms in the basal and/or apical part of a conidium; the cytoplasm is preserved in the larger of the resulting two cells (a secondary conidium). Conidia initially thin-walled, ellipsoid or cylindrical, sometimes angulate; are rounded upon maturation to become thick-walled and colored, 4.5–7 (7.5) × 2.5–4.5 (5) µm, brownish in mass [14]. Conidia, which are abundant in the hymenium in some specimens, may be misleading because they resemble basidiospores of species of the genus *Perenniporia* s.l.; however, their basidiospores are never as abundant.

Material studied. Russia, Arkhangelsk oblast, Krasnoborsky District, Verkhne-Vashkinsk forest, bilberry moss-covered spruce stand with aspen, on *Picea obovata* downed deadwood, collected and identified by V.M. Kotkova, August 8, 2013 [ut *Oligoporus guttulatus*] (LE 295800). Karelia, Muyezersky District, planned Tulos National Park, near Lake Syartijarvi, on spruce downed deadwood [*Picea abies*], collected by V.M. Kotkova, identified by M.A. Bondartseva, August 20, 2004 [ut *Oligoporus guttulatus*] (LE 259081). Ibid., collected and identified by V.M. Kotkova, September 23, 2005 [ut *O. guttulatus*] (LE 258896). Ibid., Pudozhsky District, Besov Nos area, moss-covered pine stand, on *Pinus sylvestris* downed deadwood, collected and identified by V.A. Spirin, August 23, 2002 [ut *Oligoporus guttulatus*] (LE 208171). Ibid., on *Picea abies* downed deadwood, collected and identified by V.A. Spirin, August 26, 2002 [ut *Oligoporus guttulatus*] (LE 208184). Ibid., Kodopozhsky District, Kivach Nature Reserve, bilberry spruce stand, on spruce downed deadwood [*Picea abies*], collected by V.I. Krutov, identified by V.M. Lositskaya, September 10, 1997 [ut *Oligoporus guttulatus*] (LE 206040). Ibid., Suoyarvsky District, Tolvojarvi National Park, on *Picea abies* stub, collected and identified by V.M. Kotkova, August 29, 2002 [ut *Postia guttulata*] (LE 235659). Ibid., Sortavalsky District, protected area Haapalampi–Northern Ladoga, bilberry spruce stand, on *Picea abies* downed deadwood, collected and identified by V.M. Kotkova, September 16, 2017 [ut *Oligoporus guttulatus*] (LE 311349). Ibid., St. Petersburg, Primorsky District, Severnoe Poberezhie Nevskoy Guby Nature Reserve, on spruce downed deadwood [*Picea abies*], collected by S.N. Arslanov, identified by V.M. Kotkova, September 20, 2012 [ut *Oligoporus guttulatus*] (LE 295654). Ibid., collected and identified by V.M. Kotkova, September 28, 2012 [ut *O. guttulatus*]. Ibid., Kurortny District, Gladyshevsky Nature Reserve, mixed forest, on spruce downed deadwood [*Picea abies*], collected and identified by V.M. Kotkova, September 27, 2007 [ut *Oligoporus guttulatus*] (LE 268436). Ibid., collected and identified by V.M. Kotkova, August 1, 2012 [ut *O. guttulatus*] (LE 290530). Ibid., Ozero Shchuch'e Nature Reserve, bilberry moss-coated spruce stand, on spruce stub [*Picea abies*], collected and identified by V.M. Kotkova, August 23, 2013 [ut *Oligoporus guttulatus*] (LE 295555). Ibid., bilberry spruce stand, at the base of *Picea abies*, collected and identified by D.A. Shabunin, July 13, 2024 [ut *Calcipostia guttulata*] (LE 287757). Ibid., Petrodvortsovy District, village Martyshkino, Usad'by Mordvinovykh Park, bilberry moss-covered spruce stand, on *Picea abies* downed deadwood, collected and identified by V.M. Kotkova, November 4, 2023 [ut *Oligoporus guttulatus*]. Ibid., Tver oblast, Nelidovsky District, nemoral spruce stand, on spruce downed deadwood [*Picea abies*], collected and identified by V.M. Kotkova, September 10, 2011 [ut *Oligoporus guttulatus*] (LE 284286). Leningrad oblast, Gatchinsky District, Ontsevskii Forest Park, bilberry moss-covered spruce stand, on *Picea abies* stub, collected and identified by V.M. Kotkova, August 10, 2023 [ut *Oligoporus guttulatus*] (LE F-342993). Ibid., Volosovsky District, planned Mezhdurech'e Rek Vruda, Ukhora, i Ukhta Nature Reserve, River Vruda valley, old spruce growth, on *Picea abies* downed deadwood, collected and identified by V.M. Kotkova, September 18, 2011 [ut *Postia guttulata*] (LE F-342937). Ibid., Vyborgsky District, Berezovye Ostrova Nature Reserve, Bolshoi Berezovyi Island, on pine (*Pinus sylvestris*) downed deadwood, collected by V.N. Khramtsov, identified by V.M. Kotkova [ut *Oligoporus guttulatus*] (LE 257240). Ibid., Vsevolozhsky District, Koltushskie Vysoty Nature Reserve, on spruce downed deadwood [*Picea abies*], collected and identified by V.M. Kotkova, October 5, 2012 [ut *Oligoporus guttulatus*] (LE 290499). Ibid., Toksovskii Nature Park, bilberry moss-covered spruce stand, on *Picea abies* downed deadwood, collected and identified by V.M. Kotkova, September 11, 2016 [ut *Oligoporus guttulatus*] (LE 310783). Ibid., Priozersky District, planned Orekhovskii Nature Reserve, bilberry moss-covered spruce stand, on *Picea abies* downed trunk deadwood, collected and identified by V.M. Kotkova, September 16, 2021 [ut *Oligoporus guttulatus*] (LE F-351218). Ibid., Lodeinopolsky District, Nizhne-Svirskii Nature Reserve, bilberry pine stand, on *Picea abies* stub, collected by N.I. Kalinovskaya, identified by I.V. Zmitrovich, August 2, 2014 [ut *Postia guttulata*] (LE 393837). Ibid., Orel oblast, Livensky District, near village Vakhnovo, forb pine stand, on pine downed deadwood [*Pinus sylvestris*], collected and identified by S.V. Volobuev, August 31, 2011 [ut *Oligoporus guttulatus*] (LE 291960). Ibid., Nizhny Novgorod oblast, Vetluzhsky District, near Klenovik area, silver fir–linden–spruce stand, on spruce roots [*Picea abies*], collected and identified by V.A. Spirin, August 10, 1999 [ut *Oligoporus guttulatus*] (LE 211341). Ibid., on living silver fir trunk [*Abies sibirica*], collected and identified by V.A. Spirin, August 22, 2000 [ut *Oligoporus guttulatus*] (LE 211274). Ibid., Mordovia, Temnikovsky District, Mordovski Nature Reserve, on *Picea abies* stub, collected by T.L. Nikolaeva, August 16, 1937, identified by S.Yu. Bol'shakov (LE F-314950). Ibid., Volgograd oblast, Cherepovetsky District, Darvinski Nature Reserve, bilberry moss-covered pine stand with spruce, on *Picea abies* downed deadwood, collected and identified by V.M. Kotkova, September 7, 2018. Ibid., Kirov oblast, Kotel'nichsky District, Nurgush Nature Reserve, mixed coniferous-broadleaved forest, on downed spruce trunk deadwood [*Picea abies*], collected and identified by V.M. Kotkova, September 12, 2013 [ut *Oligoporus guttulatus*] (LE 295931). Ibid., Samara oblast, Zhigulevskii Nature Reserve, division 19, comb, on downed trunk (LE 227840). Ukraine, Vinnitsa oblast, on trunk and branch downed pine deadwood [*Pinus sylvestris*], collected by S.S. Ganeshin [1910s], identified by A.S. Bondartsev, October 1949 [ut *Tyromyces leveillianus*] (LE 272275). Jewish Autonomous Region, eastern spurs of Shuki-Poktoi Mountain Range, Shuki-Poktoi Nature Reserve, narrow valley, mixed forest dominated by conifers, on old *Pinus koraiensis* downed trunk deadwood, collected by E.A. Erofeeva, identified by N.V. Bukharova, August 12, 2018 (VLA M-26491). Khabarovsk Krai, Bol'shekhekhtsirskii Nature Reserve, Sosninskii Stream basin, on *Picea jezoensis* downed trunk deadwood, collected and identified by N.V. Bukharova, September 3, 2013 (VLA M-23972). Khabarovsk Krai, Nanaisky District, Anyuiskii National Park, River Yaro basin, mixed forest, on *Pinus koraiensis* downed trunk deadwood, collected and identified by E.A. Erofeeva, August 8, 2011 [ut *Postia guttulata*] (VLA M-24125). Sakhalin oblast, Sakhalin Island, Tymovsky District, River Uskovo valley, spruce–silver fir forest, on conifer stub, collected by E.M. Bulakh, identified by O.K. Govorova, August 6, 2001 [ut *Oligoporus guttulatus*] (VLA M-18785). Ibid., Kunashir Island, Kuril'skii Nature Reserve, Stolbovskaya Ecological Trail, spruce–silver fir forest, on *Abies* [*sacchalinensis*] wood, collected and identified by E.A. Eroveeva, September 1, 2016 (VLA M-25225). Ibid., Shikotan Island, southeastern slope of Shikotan Mountain, on *Picea* [*jezoensis*] and *Abies* [*sacchalinensis*] downed deadwood, collected by E.M. Bulakh, identified by N.V. Bukharova, August 25, 2019 (VLA M-27131, 27158). Ibid., Shikotan Island, Trezubets Cap, collected by E.M. Bulakh, identified by N.V. Bukharova, September 1, 2020 (VLA M-27349). Primorsky Krai, near Vladivostok, Okeanskii Range, on conifer downed deadwood, collected by E.M. Bulakh, identified by N.V. Bukharova, October 5, 2016 (VLA M-27320) [ut *Postia guttulata*].

Molecular Identification

The monotypic genus *Calcipostia* B.K. Cui, L.L. Shen et Y.C. Dai belongs to the clade *Antrodia*, subclade *Postia* s.l. The genus is rather separated within the subclade and occupies a near-basal position. The genera *Spongiporus* s.str. и *Oligoporus* s.str. are closely related to *Calcipostia* [15]. We think that a predominance of pseudoskeletal hyphae with a narrow lumen (to nearly solid) in mature basidiomata and hard (*Fomitopsis*-like) texture in the mature state provide additional morphological evidence to distinguish the genus.

Molecular analysis was carried out using two specimens, which were collected in the Ozero Shchuch'e Nature Reserve at the base of a *Picea abies* tree on July 13, 2024. The ITS1–5.8S–ITS2 region was sequenced. A consensus sequence based on four sequencing rounds (two forward and two reverse) is as follows:

ATCCTACCTGATTTGAGGTCAGAGGTCAATAAAGTTGGCGTCCCCCCCTCGGAGGGACGATTCGAAGCTGAGCCCGAGTTTTAAAAGCCTCACAGCCGCGGCGTAGACAGCTATCACACCGATAAGCCGATACAGCATAGGTTCAAGCTAATGCATTCAAGAGGAGCCGACCACCCCTTCACAGAGGGCAAAGCCAGCATGAAACCTCCAAGTCCAAGCCCTCGTCCTCAAAGGTTGAGGGTTGATGATTCCATGACACTCAAACAGGCATGCTCCTCGGAATACCAAGGAGCGCAAGGTGCGTTCAAAGATTCGATGATTCACTGAATTCTGCAATTCACATTACTTATCGCATTTCGCTGCGTTCTTCATCGATGCGAGAGCCAAGAGATCCGTTGCTGAAAGTTGTATAAAAATGCGTCGCACGCGTTCAACATTCTAAACATACATAGAGTTCGTGGCATGACATAGAGCACAGCCTTTCGACCGCGACCCTACAAAAGGTGCACAGGGGTGTAAAGGTTGGAATCGATCGAAGCGTGCACATGCCCCGAGAGGCCAGCAGACAGCTCCTTTGAAAATTCAATAATGATCCTTCCGCAGGTTCACCTACGGAAACCTTGTTACGACTTTTACTTC,

showing 100% identity to the KF727432 sequence, which has been established using a Chinese specimen in China [15].

Distribution

The species has a pan-Holarctic range and forms a single tropical exclave in East Africa (Ethiopia) (Table 1).

Finds of *C. guttulata* have been especially numerous in Europe (Austria, Belarus, Czech Republic, Denmark, Estonia, Finland, Germany, Italy, Latvia, the Nether lands, Norway, Poland, Russia, Spain, Sweden, Switzerland, and the United Kingdom). In Asia, finds of the species are known from India, China, Asian Russia, and Japan. In East Africa, the species has been detected in Ethiopia, as mentioned before. In North America, the species is rather widespread in both the United States and Canada.

In European Russia, *C. guttulata* has been detected in Arkhangelsk oblast, Vologda oblast, Kirov oblast, Leningrad oblast, Nizhny Novgorod oblast, Novgorod oblast, Orenburg oblast, Orel oblast, Perm Krai, Republic of Adygea, Republic of Altai, Republic of Bashkortostan, Republic of Karelia, Republic of Komi, Republic of Mordovia, Republic of Tatarstan, Samara oblast, St. Petersburg, Sverdlovsk oblast, Tver oblast, and Chelyabinsk oblast (Bolshakov et al., 2022; Volobuev et al., 2022; herbarium of Komarov Botanical Institute).

In Asian Russia, *C. guttulata* finds are somewhat fewer, but still have been reported from the total area from Southern and Western Siberia to the Russian Far East (the easternmost finds are from the Sakhalin Island).

In Siberia, the species has been detected in the Republic of Altai [16], Tomsk Oblast [16, 17], Khanty-Mansi Autonomous Okrug [16], Krasnoyarsk Krai [16, 18], and the Republic of Yakutia [19].

In the Russian Far East, *C. guttulata* finds are known from Jewish Autonomous Oblast [16, 20], Khabarovsk Krai [16, 20], Primorsky Krai [16, 21, 22], and Sakhalin Oblast [23].

It is noteworthy that the species has not been detected in northern taiga forests and forest tundra. The northernmost find has been made at 62.5° N (Vodlozersky National Park, Karelia), in a western taiga sector with softened climate. The greatest number of finds of the species have been reported from the

Table 1. Geographical distribution and substrate specialization of *C. guttulata*

Country	Substrate	Reference
	Europe	
Austria	*Picea* [*abies*]	[28]
Belarus	*P. abies*	[8, 12]
United Kingdom	*Pinus* [*sylvestris*]	[29]
Germany	[*Abies alba*]	[30]
Germany	[*Picea abies*]	[31, 32]
Germany	[*Pinus sylvestris*]	[33]
Denmark	[*Picea abies*]	[34, 35]
Denmark	*Fagus* [*sylvatica*]	[36]
Spain	[*Pinophyta*]	[37]
Italy	*Cedrus* [*deodara*]	[38]
Latvia	[*Pinus sylvestris*]	[39]
Latvia	[*Picea abies*]	[40]
Netherlands	[*P. abies*]	[41, 42]
	[*Pinus sylvestris*]	[43]
Norway	*Picea abies*	[44], etc.
Norway	*Pinus sylvestris*	[45]
Poland	*Picea abies*	[46], etc.
Russia (European)	*P. abies*	LE 208184, etc.
Russia (European)	*P. obovata*	LE 295800
Russia (European)	*Pinus sylvestris*	LE 208171, etc.
Russia (European)	*Abies sibirica*	[47]; LE 211274
Finland	*Picea abies*	[10, 48]
	Pinus sylvestris	[10, 48]
Czechia	*Picea abies*	[49], etc.
Switzerland	[*Abies alba*]	[50]
	[*Picea abies*]	[51]
Sweden	*P. abies*	[9]
Sweden	*Pinus sylvestris*	[9]
Estonia	[*Picea abies*]	[52]
	[*Pinus sylvestris*]	[53]
	Asia	
India	[*Pinophyta*]	[54]
China	*Abies* sp.	[55]
China	*Picea* sp.	[56]
China	*Pinus* sp.	[57]
China	*Larix* sp.	[58]
Russia (Asian)	*Abies* [*sacchalinensis*]	[59]; VLA M-25225
Russia (Asian)	*Picea jezoensis*	VLA M-23972
Russia (Asian)	*Pinus koraiensis*	[60]; VLA M-26491
Japan	*Castanopsis* [*cuspidata*]	[61]
	Africa	
Ethiopia	*Podocarpus* [*falcatus*]	[62]
	North America	
United States	*Tsuga heterophylla*	[63], etc.

Table 1. (Contd.)

Country	Substrate	Reference
United States	*Populus tricarpa*	[64]
United States	*Picea sitchensis*	[65]
Canada	*P. sitchensis*	[66]
Canada	*P. sitchensis*	[67]
Canada	*P. sitchensis*	[68]
Canada	*P.* [*glauca*]	[69]

Substrates identified on the basis of their images or geographical locations of the finds are given in brackets.

southern taiga subzone of the taiga zone. In addition, *C. guttulala* is found in the sub-taiga zone [24], broad-leaved forest zone [25], and forest steppes [26]; there are also finds associated with subtropical (Japan and the United States) and tropical (East Africa) climate (Table 1).

Europe accounts for more than half of the 3354 *C. guttulata* finds mentioned in GBIF [27].

Ecology

Substrate ecology. *Calcipostia guttulata* is associated with conifer woods and, less often, hardwoods; the species causes brown rot of wood [7].

In Europe, most finds of the species have been made on *Picea abies* (and *P. obovata* in Northeastern Europe); the species is found on *Pinus sylvestris* additionally (Table 1). The species is associated with *Abies alba* in mountain regions of Europe, has been noted in association with *A. sibirica* in sub-taiga forests of the eastern part of European Russia, and has been detected on *Cedrus deodara* in Southern Europe. A *C. guttulata* find on a deciduous tree (*Fagus sylvatica*) is known from Denmark.

In Asian Russia, the species has been found on *Abies sibirica*, *A. sacchalinensis*, *Picea obovata*, *P. jezoensis*, and *Pinus koraiensis*. In Japan, *C. guttulata* is know in association with *Castanopsis cuspidata*. In India, several *C. guttulata* finds have been made on unidentified conifer woods. In China, the species is characteristic of *Abies* spp., *Larix* spp., *Picea* spp., and *Pinus* spp. In Africa (Ethiopia), the species is associated with *Podocarpus falcatus* wood (Table 1).

In the United States, the species has been detected in association with *Tsuga heterophylla* and *Picea sitchensis*; and a find on *Populus tricarpa* should be noted among the finds on hardwoods in the region. In Canada, the species has been found on *Picea sitchensis* in western mountain regions and on *P. glauca* in eastern regions near the Great Lakes (Table 1).

The number of finds on dead standing trees is higher than that on downed deadwood. The species has occasionally been found on living trees, causing heart rot. The number of *Calcipostia guttulata* finds reported from moist regions of the globe is greater than from the arid zone.

Interactions with insects. As mentioned above, the fungus is capable of colonizing dry stands, which form two or three years after infection of spruce forests by the European spruce bark beetle *Ips typographus*. Bark beetle larvae and pathogenic ascomycetes infecting the cambium cause trees to dry out rapidly, and the saprotroph *C. guttulata* colonizes their wood (mostly heartwood) once a port of infection has formed.

Along with *C. guttulata*, various insects affect the soft bark and sapwood. Insect larvae make galleries under the bark and in wood and pupate usually the next year. Figure 2 shows the entrance and exit holes typical for the black spruce beetle *Tetropium castaneum* and striped ambrosia beetle *Trypodendron lineatum*[1].

Apart from the insects accompanying *Calcipostia guttulata* and causing fast death and degradation of dry trees, facultative and obligate mycetophages are associated with the fungus. Larvae and adults of several insect species are attracted by the *Tyromyces*-like polypore *C. guttulata*, which is relatively easily colonized by insects.

It has been observed that *C. guttulata* basidiomata are visited by *Clambus nigrellus* and *Hallomenus binotatus* adults and provide room for developing larvae and adults of *Rhizophagus dispar* [70, 71]. *Clambus nigrellus* is a moisture-loving species that inhabits moist forests, river regions, and mud banks and is found, for example, in the forest litter, often near mycelia of saprophytic fungi, and on sedge litter in eutrophic bogs [72]. *Hallomenus binotatus* in found in forests and sparse stands and inhabits tree trunks and branches. Adult beetles are often observed in association with *Tyromyces*-like polypore basidiomata, where they feed and mate [73]. *Rhizophagus dispar* lives and develops under the dead bark colonized by ascomycete and basidiomycete mycelia on conifers and hardwood trees. The species can additionally develop in galleries of Scolytidae under the spruce bark, feeding on their pre-imaginal stages, and in sterile parts of *Fomes*

[1] Information about the specifics of entrance and exit holes is insufficient for correct determination of the borer species (B.K. Popovichev, personal communication).

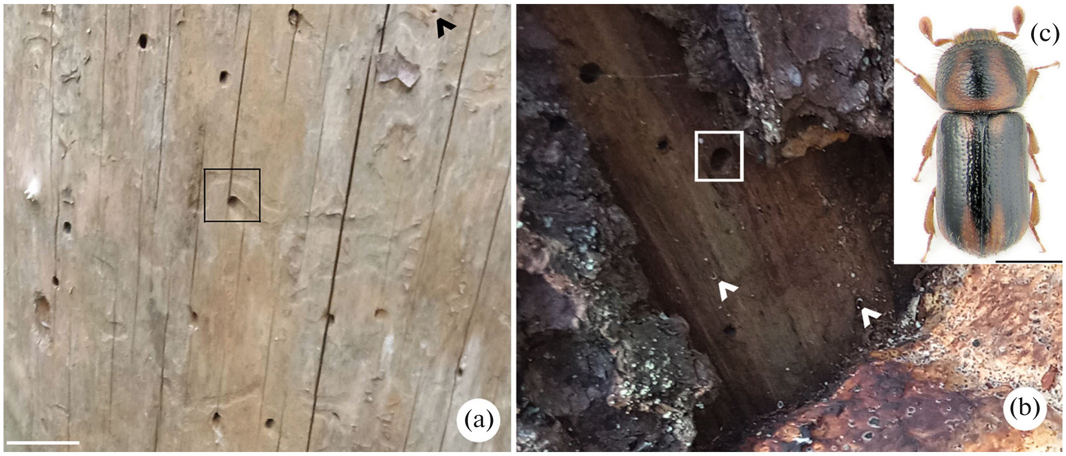

Fig. 2. (a) Debarked and (b) barked spruce wood affected by *C. guttulata*. Entrance (a black frame) and exit (a white frame) holes typical of *Tetropium castaneum* are indicated. Entrance and exit holes created by *Trypodendron lineatum* ae indicated with arrowheads. Bar, (a, b) 10 or (c) 1 mm. Permission to reproduce the photo of *T. lineatum* was obtained from the site https://www.zin.ru/Animalia/Coleoptera/Rus/trylinkm.htm by Prof. A.V. Selikhovkin.

fomentarius and *Trichaptum biforme* basidiomata. Pupation occurs in soil or within the bark of the trees where larvae have developed. Adults can additionally feed on basidiomata of certain xylotrophic fungi [74, 75].

Conservation Status

A wide distribution within the Holarctic has provided an argument for assigning *C. guttulata* the LC (least concern) category [76]. The International Union for Conservation of Nature and Natural Resources assigns the LC status to species and intraspecific taxa that do not qualify for any other category (the set includes the most widespread and flourishing species, such as *Homo sapiens, Apis mellifera, Rattus norvegicus*, and *Columba livia*).

However, it is worth noting that *C. guttulata* is missing in many regional lists, is absent from urbanized territories, and is often found in protected natural areas. Finnish mycologists have assigned the NT (near-threatened) category to the species [77]. Moreover, *C. guttulata* is considered to be a VU (vulnerable) species by Swedish researchers [9, 78]. We think that this interpretation is better grounded. The species *C. guttulata* is an indicator species of biologically valuable forests in Northwestern Russia [79].

Biotechnological Potential

Calcipostia guttulata is a poorly known species in biotechnology, although there is evidence that the species was used in traditional medicine [80].

Methanol extracts of the fungus have been shown to possess considerable antibacterial activity, and the species is a component of a patented kit designed to fight pestis americana larvae apium, which is a destructive disease of honey bee larvae. The disease is widespread globally, and burning an infected colony was thought to provide the only efficient means to prevent its spreading until recently. Honeycomb treatment with a complex extract including *C. guttulata* metabolites has been shown to exert a substantial inhibitory effect on the development of the bacterium *Paenibacillus larvae* [81].

The antibacterial effect of *C. guttulata* is most likely due to a bitter substance that is identical in scent to an *Amaropostia stiptica* bitter substance. The latter has been studied recently and found to contain two known triterpene glucosides, oligoporins A and B, along with previously undescribed oligoporins D–F and the bitter indolalkaloid infractopicrin [82].

The species *C. guttulata*, which produces biomass in large amounts, certainly provides a promising, although almost unknown subject for metabolomics and biomedical research.

CONCLUSIONS

C. guttulata is a widespread, but rare polypore in the Holarctic; is confined to the early stages of drying of coniferous stands, primarily spruce forests; and is a poorly studied headwood pathogen and a saprotroph that colonizes coniferous deadwood and, less often, fallen trees.

Our detailed characterization of the hyphal system of the species made it possible to extend the set of its diagnostic features. Its hyphal system is pseudoditimic with nearly solid pseudoskeletal hyphae predominating in the basidiomata, thus determining hard (*Fomitopsis*-like) texture of mature basidiomata.

The ITS barcode of the species showed lack of variation throughout the vast area from European Russia to China.

In the Holarctic, *C. guttulata* is widespread in Europe; Asia; and Africa, where the species is found in tropical regions; and in the temperate and subtropical zones of North America. Most finds of the species have been made in Europe.

The substrates specialization of *C. guttulata* differs between different Holarctic regions. Most finds are associated with species of the genus *Picea*. The fungus has been detected on *Abies alba*, *A. sibirica*, *Picea abies/P. obovata*, and *Pinus sylvestris* in Europe; *Cedrus deodara* in Southern Europe (a find on hardwood *Fagus sylvatica* is known additionally); *Abies sibirica*, *A. sacchalinensis*, *Castanopsis cuspidata*, *Larix* spp., *Picea obovata*, *P. jezoensis*, and *Pinus koraiensis* in Asia; *Podocarpus falcatus* in Africa (Ethiopia); and the conifers *Picea sitchensis*, *P. glauca*, and *Tsuga heterophylla* and deciduous *Populus tricarpa* in North America.

The species follows pathogenic insects and, in particular, *Ips typographus* at early stages of stand drying. Simultaneously with *Calcipostia guttulata* or after wood colonization by the species, secondary species of bark beetles and borers enter woods. Several species of facultative and obligate (*Rhizophagus dispar*) mycetophages are associated with *Calcipostia guttulata* basidiomata and mycelia.

Being associated mostly with least damaged forests and mature stands, *C. guttulata* provides an indicator of biologically valuable forests.

C. guttulata is capable of rapidly producing biomass in large amounts and provides a promising, although still poorly studied subject for metabolomics and biomedical research.

ACKNOWLEDGMENTS

We are grateful to Prof., Doct. Sci. (biol.) A.V. Selikhovkin (Kirov St. Petersburg State Forest Engineering University) for discussion of the manuscript and help with permission to reproduce the *Trypodendron lineatum* photo from https://www.zin.ru/Animalia/Coleoptera/Rus/trylinkm.htm and Ass. Prof., Cand. Sci. (biol.) B.K. Popovichev for valuable advice.

FUNDING

Studies by I.V. Zmitrovich and D.A. Shabunin were supported by the Russian Science Foundation, project no. 24-16-00092.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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Translated by T. Tkacheva

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