

Species diversity and pathogenicity of the *Fusarium oxysporum* species complex associated with potato tuber dry rot, including the description of *F. sherbakoffii* sp. nov.

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Research Article

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Abstract

This study clarifies the species diversity of *Fusarium* fungi within the *Fusarium oxysporum* species complex (FOSC) associated with potato dry rot. A total of 23 strains isolated from potato tubers with dry rot symptoms, collected from five regions of Russia, were analysed. Phylogenetic analysis was based on partial sequences of the translation elongation factor (*tef*), RNA polymerase II second largest subunit (*rpb2*), β -tubulin (*tub*), calmodulin (*cmd*), and RNA polymerase II largest subunit (*rpb1*) gene fragments. Among the strains examined, *F. nirenbergiae* (seven strains), *F. oxysporum* s.str. (four), *F. fabacearum* (two), and *F. odoratissimum* (two) were confidently identified. Eight strains from potato tubers of different geographic origins were identified as a new species and are described here as *F. sherbakoffii* sp. nov. Ten previously described species names within the FOSC were synonymised. Morphological features, including the formation of microconidia in false heads on mono- and polyphialides, macroconidia in both aerial mycelium and sporodochia, and the production of chlamydospores and sclerotia, were examined to distinguish species. In pathogenicity tests on potato tubers, *F. nirenbergiae* strains were the most aggressive, causing 1.6–8.2-fold more extensive tissue damage than other species. The strains of *F. oxysporum* s.str. and *F. sherbakoffii* showed variable aggressiveness, whereas *F. odoratissimum* was the least aggressive. In addition to typical necrosis of dry rot, *F. oxysporum* s.str., *F. nirenbergiae*, and *F. sherbakoffii* strains induced atypical symptoms, including dark browning, softening, and a wet appearance of internal tissues around the lesion.

Introduction

The *Fusarium oxysporum* species complex (FOSC) comprises some of the most significant plant-pathogenic fungi, responsible for devastating wilt and rot diseases in numerous economically important crops. Members of the FOSC are also known to occur as plant endophytes and as pathogens of animals and humans (Leslie and Summerell 2006; O'Donnell et al. 2009).

The FOSC is characterized by a complex phylogenetic structure, reflecting a large and highly diverse group of morphologically cryptic anamorphic fungi (O'Donnell et al. 1998; Lombard et al. 2019, 2022). Currently, 51 species are formally recognised within this complex (Mycobank, <https://www.mycobank.org>). Early phylogenetic studies, based on multilocus sequence analyses, delineated 39 species into five major clades (Lombard et al. 2019). The species *Fusarium oxysporum* was originally described by von Schlechtendal in 1824, based on strain isolated from a rotten potato tuber (*Solanum tuberosum* L.) collected in Germany. More recently, researchers at the Westerdijk Fungal Biodiversity Institute (the Netherlands) designated an epitype for *F. oxysporum* sensu stricto (s.str.), using a strain recovered from a diseased potato tuber in Germany (Lombard et al. 2019). This epitypification, together with subsequent multilocus and phylogenomic studies, has substantially expanded the number of formally recognised FOSC species and clarified relationships among several previously ambiguous taxa (Achari et al. 2020; Bugingo et al. 2025). Nevertheless, species boundaries within the FOSC remain an area of active debate: whole-genome and coalescent-based reanalyses continue to propose new taxonomic arrangements and to synonymise or split previously accepted species (Lopez-Jimenez et al. 2026; Le Dinh Thao et al. 2026), reflecting both the genuinely fine-grained divergence within the complex and the methodological sensitivity of species recognition to the dataset and criteria used. This ongoing taxonomic flux underlines the continued need for integrative studies that combine multilocus phylogenetics with detailed morphological and biological characterisation of strains from previously under-sampled regions and hosts (Bugingo et al. 2025).

Dry rot of potato tubers, caused by various *Fusarium* species, represents a significant post-harvest disease that considerably reduces both nutritional value and seed quality (Tiwari et al. 2020). Currently, researchers worldwide are showing increasing interest in the species diversity and biology of the pathogens associated with this disease. Studies have been conducted across various geographical regions, including North and Central America (Schlachter et al. 2024; Castillo-Batista et al. 2025; Christian et al. 2025; Aslam et al. 2026), Europe (Stefańczyk et al. 2016; Catalani et al. 2024; GavriloVA et al. 2024), Asia (Kim et al. 2024; Li et al. 2025; Guo et al. 2025; Muratali et al. 2025; Pooja et al. 2025), and Africa (Gherbawy et al. 2019; Azil et al. 2021; Elansky et al. 2024; Lekota et al. 2025; Kouadri et al. 2026).

A comprehensive tuber survey was conducted between 2018 and 2024, during which 342 potato batches from five different regions of Russia were examined for *Fusarium* infection (Gagkaeva et al. 2025). In total, 82.7% of the analysed batches contained *Fusarium*-infected tubers, and the proportion of infected tubers per batch varied from 5.7 to 13.5%. *Fusarium* fungi isolated from tubers with dry rot symptoms were represented by members of seven species complexes. Overall, *F. sambucinum* was the most common pathogen, followed by representatives of the FOSC, although regional differences in the frequency of occurrence were observed. Notably, members of the FOSC predominated among the *Fusarium* spp. isolated from potato batches originating from the North Caucasus region (Gagkaeva et al. 2025).

This study aimed to accurately identify strains morphologically resembling *F. oxysporum* sensu lato (s.l.) associated with dry rot of potato tubers, and to compare the morphological features and pathogenicity of the identified species.

Materials and methods

Fusarium strains

Fungal strains were isolated from rotten potato tubers collected from various regions of Russia (Table 1). Fragments of diseased tissue were placed onto potato dextrose agar (PDA) supplemented with an antibiotic mixture (1 mL/L, HyClone™, GE Healthcare Life Sciences, Vienna, Austria) and 0.4 µL/L Triton X-100 (Panreac, Castellar del Vallès, Spain), and incubated at room temperature. Twenty-three strains morphologically resembling members of the FOSC were randomly selected for detailed investigation. Subsequently, single-spore isolates were obtained and maintained in the fungal culture collection of the All-Russian Institute of Plant Protection (St. Petersburg, Russia).

DNA isolation, PCR amplification, and sequencing

Genomic DNA was extracted from 10–50 mg of aerial mycelium of each *Fusarium* strain using a standard cetyltrimethylammonium bromide (CTAB) protocol with chloroform (O'Donnell and Cigelnik 1997). Partial fragments of four loci were amplified and sequenced: the translation elongation factor 1- α (*tef*) gene using primers EF1/EF2 (O'Donnell et al. 1998); the RNA polymerase II second largest subunit (*rpb2*) gene using primers RPB2-150f and RPB2-7cR (Jewell and Hsiang 2013; Liu et al. 1999); the beta-tubulin (*tub*) gene using primers T1/T2 (O'Donnell and Cigelnik 1997); and the calmodulin (*cmd*) gene using primers CL1/CL2A (O'Donnell 2000). PCR amplifications were performed under the conditions specified in the corresponding original publications.

Amplicons were purified and sequenced in both directions using the same primers on an ABI Prism 3500 genetic analyser (Applied Biosystems, Hitachi, Japan) with the BigDye Terminator v3.1 cycle sequencing kit (Applied Biosystems, Foster City, CA, USA). The obtained sequences were deposited in the NCBI GenBank database (Table 1).

Phylogenetic analysis

Sequences of 169 reference *Fusarium* strains were retrieved and selected using the FUSARIOID-ID database (www.fusarium.org). For phylogenetic analysis, the *tef*, *rpb2*, *tub*, and *cmd* sequences obtained in this study were combined with the *rpb1* sequences retrieved from the NCBI GenBank database (Supplementary Table S1). The ex-type strain CBS 221.76 of *F. fujikuroi* Nirenberg was used as an outgroup.

Sequence alignment was performed using MEGA X v. 10.1 (Kumar et al. 2018). Bayesian inference was conducted with MrBayes v. 3.2.1 on the Armadillo v. 1.1 platform (Lord et al. 2012), using 2,000,000 generations of Markov chain Monte Carlo with trees sampled every 1,000 generations. The best-fitting nucleotide substitution model was determined, and maximum likelihood (ML) analysis was performed using IQ-TREE2 v.2.1.3 (Minh et al. 2020). For the multilocus analysis of the five loci, the TNe+R2 model was selected. Nodal bootstrap support in maximum likelihood analysis was assessed based on 2,000 replicates. The alignment and phylogenetic trees were deposited in TreeBASE (accession no. S32708).

Morphological characterization

Colony morphology, pigment production, and the presence of chlamydospores and sclerotia were evaluated on PDA after incubation for 7–21 days at 25 °C in constant darkness.

Morphological features were examined after 14–21 days of fungal growth on synthetic nutrient agar (SNA) and on carnation leaves placed on the surface of SNA (CLA), under alternating illumination (12 h light / 12 h dark) at 25 °C. The shape, septation, size and arrangement of conidia were observed in water mounts, on adhesive tape imprints, and directly on the agar surface, as described by Gagkaeva et al. (2023). Whenever possible, at least 30 measurements of each structure were recorded. Micromorphological characters were studied and documented using an Olympus BX53 microscope and an Olympus SZX16 stereomicroscope (Olympus, Hachioji, Japan), both equipped with a PROKYON camera (Jenoptik, Jena, Germany).

Pathogenicity assay

Pathogenicity of all strains was assessed by inoculation of potato tubers of the cultivar Impala. Healthy tubers weighing approximately 40 g were selected, surface-sterilised with 5% sodium hypochlorite for 3–5 min, rinsed with sterile distilled water, and air-dried.

Inoculation was performed by wounding the tuber at the stolon attachment site using a cork borer (5 mm diameter) to a depth of 20 mm, and removing the tissue plug. An agar disk (4 mm diameter) was cut from a 7-day-old fungal culture grown on PDA and placed into the wound, which was then covered with the original tuber plug. At least five tubers were inoculated separately with each strain, placed in plastic containers with loose caps, and incubated at 23 °C for 4 weeks. For the control treatment, a sterile PDA agar disk was inserted into the hole.

After 4 weeks of incubation, each tuber was cut longitudinally through the inoculation site, and the width and depth of the rotted tissue were measured (mm); the average value was calculated for each strain. For each variant, lesion sizes were calculated by subtracting the average dimensions of the inoculation hole measured in control tubers from the values obtained for the inoculated tubers.

Statistical analysis

Statistical analyses were performed using Microsoft Excel 2010, Minitab 17.0, and STATISTICA 12.0. Mean values and confidence intervals were calculated, and differences between treatments were evaluated using Student's t-test at a significance level of $p < 0.05$.

Results

Phylogeny

Phylogenetic analysis of the combined sequences, containing five loci (*tef*, *rpb2*, *tub*, *cmd* and *rpb1*), was used to infer the genetic relationships among *Fusarium* strains belonging to the FOSC. The dataset included concatenated sequences of the 23 strains analysed in this study and 169 reference *Fusarium* strains, and consisted of 4,034 characters (577 bp for *tef*, 861 bp for *rpb2*, 544 bp for *tub*, 602 bp for *cmd*, and 1,450 bp for *rpb1*), of which 3,372 were conserved, 655 were variable (16.2%), and 303 were parsimony-informative (7.5%).

The topologies of the multilocus phylogenetic trees inferred by different methods were largely congruent and consistent with previously reported phylogenetic relationships among species of the FOSC (Lombard et al. 2019; Han et al. 2025; Lopez-Jimenez et al. 2026).

Four strains (MFG 70125, MFG 70127, MFG 70128, and MFG 70145) clustered together with three reference strains of *F. oxysporum* s.str. with strong bootstrap support (BP/ML 0.99/100) (Fig. 1).

Two strains (MFG 70025 and MFG 70165) and eight reference strains of *F. fabacearum* formed a well-supported clade (BP/ML 0.98/99), which also contained the ex-type strain BRIP 70752a of *F. wimaladesilvae*. *Fusarium wimaladesilvae* was recognised as a synonym of *F. fabacearum*.

Seven strains (MFG 70132, MFG 70136, MFG 70137, MFG 70139, MFG 70157, MFG 70159, and MFG 70178) clustered together with 18 reference strains of *F. nirenbergiae* with strong bootstrap support (BP/ML 0.99/99). Within the *F. nirenbergiae* clade, the strains were distributed among several subclades, although these received poor bootstrap support. The ex-type and representative strains of *F. houttuyniae*, *F. idabrowneae*, *F. landiae*, and *F. liriopes* also clustered within the *F. nirenbergiae* clade, and these four species were recognised as synonyms of *this species*.

Two strains (MFG 70138 and MFG 70158) clustered with 18 reference strains predominantly isolated from *Musa* spp. and identified as *F. odoratissimum*, including the ex-type strain InaCC F822. This clade also contained the ex-type strain and nine reference strains of *F. phialophorum*, and comprised three well-supported subclades: one consisting of the ex-type and representative strains of *F. rosae-roxburghii*, a second comprising the ex-type and representative strains of *F. cili*, and a third including five strains of *F. odoratissimum* isolated from sorghum roots. The clade uniting the 39 strains of the four above mentioned species received strong bootstrap support (BP/ML 0.99/100). Based on these phylogenetic results, all strains in this clade were considered to belong to the same species. Consequently, *F. rosae-roxburghii*, *F. phialophorum*, and *F. cili* were recognised as synonyms of *F. odoratissimum*, which has nomenclatural priority.

The remaining eight MFG strains, isolated from potato tubers obtained from five regions of Russia, together with eight other strains isolated from soil in the Netherlands and Belgium and previously named "*Fusarium* sp. 3" (Crous et al. 2021b), formed a monophyletic lineage with strong bootstrap support (BP/ML 0.99/99), which we designate here as *F. sherbakoffii* sp. nov. This new species is closely related to *F. cugenangense* and *F. vaughaniae*.

Based on the phylogenetic analysis conducted in this study, the clade including *F. libertatis* strains also contained the ex-type and representative strains of *F. oxysporum* f. sp. *dactyliferae*. The strains FMBCC 12.1 and FMB-FO-PD-017, previously annotated in GenBank as representatives of *F. oxysporum* s.str., were not recovered within the clade corresponding to this species. These findings indicate that *F. oxysporum* f. sp. *dactyliferae* should be re-identified and recognised as a synonym of *F. libertatis*.

Moreover, the ex-type and representative strains of *F. hordeum* clustered together with *F. agrestense* strains. The *tef*, *tub*, *rpb1*, and *rpb2* sequences of the analysed strains of both species were identical. Thus, *F. hordeum* was recognised as a synonym of *F. agrestense*.

In summary, the multigene phylogeny resolved the 192 strains included in this analysis into 41 clades, representing 38 previously described species and two phylogenetic lineages within the FOSC, as well as one new species described in this study. Ten species names were synonymised.

Morphology of fungi

The morphological characteristics of the strains belonging to the *F. oxysporum* s.l. were similar and readily recognisable by the profuse production of microconidia formed in false heads on relatively short monophialides, macroconidia that are mostly 3-septate and pointed at both ends, and the typically abundant presence of intercalary or terminal rough-walled chlamydospores. The morphological differences between the identified phylogenetic lineages are described below and demonstrate only minor distinctions.

In *F. nirenbergiae* strains MFG 70132, 70139, 70157, and 70159, colony reverse ranged from light yellow to dark brown (Fig. 2A, B). In three-week-old cultures of strains MFG 70139 and 70159, pigment accumulation was so intense that the reverse appeared brown-black. The reverse of the

other three *F. nirenbergiae* strains was colourless. Among the four *F. oxysporum* s.str. strains, only one had a colourless reverse, whereas the remaining three exhibited various shades of purple (Fig. 3A, B). In two *F. sherbakoffii* strains (MFG 70024 and MFG 70112), yellow to dark brown pigment was observed, while the reverse of the other strains was nearly colourless (Fig. 4A, B). One *F. fabacearum* strain (MFG 70025) produced a strong purple-brown pigment, whereas the other strain (MFG 70165) showed a light purple pigmentation (Fig. 5A, B).

The most striking reverse pigmentation was observed in *F. odoratissimum* strains, which displayed a bright purple to wine pigmentation that lightened towards the margins (Fig. 6A, B). The pigment was already intense during the first days of growth, additionally revealing a filiform pattern of even more intensely coloured substrate hyphae. Such dense wine-coloured pigmentation was not detected in the other analysed strains. According to previous descriptions, *F. odoratissimum* strains isolated from banana produce a characteristic odour after one to two weeks of incubation on PDA, described as “peculiarly stale” (Maryani et al. 2019). However, no specific odour was detected in the *F. odoratissimum* strains examined in this study, nor in any of the other strains obtained from potato tubers.

Aerial phialides borne laterally on the hyphae, single, ampulliform, obclavate to subcylindrical and cylindrical, slightly tapering towards the apex and the base, $4\text{--}45 \times 2\text{--}4 \mu\text{m}$. Periclinial thickening often inconspicuous, and the collarette was reduced or flared. In many cases, monophialides reduced to small openings on the surface hyphae, or occasionally formed terminally at the ends of growing hyphae (Figs. 3o,p; 4m; 5f; 6p). Monophialides were dominant in all strains and were quite similar in shape and size. However, polyphialides with two loci were observed in *F. nirenbergiae* (Figs. 2i-l), and, more rarely, in *F. odoratissimum* (Fig. 6q, r) and *F. sherbakoffii* (Fig. 4l). Polyphialides were lateral, short, and morphologically similar, bearing no more than two openings, with collarettes and periclinial thickening inconspicuous or absent.

Aerial microconidia were the most abundant conidia forming in small false heads at the tips of phialides. They were hyaline, ellipsoidal, oval, reniform to falcate, smooth- and relatively thin-walled, 0–2-septate. In *F. fabacearum*, falcate, one-septate microconidia with curved ventral and dorsoventral sides were formed in false heads on monophialides significantly more frequently than in other FOSC species, and were produced on the same locus together with unicellular microconidia (Fig. 5l). In *F. odoratissimum*, microconidia were 1(2)-septate and often narrowed at the septum.

Falcate macroconidia with 2–3 septa in the aerial mycelium were formed on monophialides. They were slightly curved dorsiventrally and ventrally. The outer cells were often distinctly curved; the apical cell was pointed or blunt to papillate, and blunt to foot-like basal cell.

Sporodochia were formed on CLA in all strains, and were less abundant on PDA and SNA. The rate of sporodochium formation depended on the strain and increased under alternating UV/dark illumination. The most rapid and abundant sporodochium production on PDA (after 7 days) was observed in *F. oxysporum* s.str. strain MFG 70125 compared to strains of all other identified species; the sporodochia were cream-orange coloured, and this pigmentation was visible on the colony reverse (Fig. 4C).

Conidiophores in the sporodochia were verticillately branched and densely packed, consisting of short, smooth- and thin-walled cells measuring $4\text{--}10 \times 4\text{--}5 \mu\text{m}$. They bore apical whorls of 2–3 monophialides.

Sporodochial phialides were typically subulate to subcylindrical, $8\text{--}13 \times 3\text{--}5 \mu\text{m}$, smooth- and thin-walled, with inconspicuous periclinial thickening and an apical collarette.

Sporodochial conidia falcate, moderately curved dorsiventrally, widest in the central part, and gradually tapering towards both ends. The apical cells were pointed, or blunt to papillate, slightly curved, whereas the basal cells were pedicellate. Typically, sporodochial conidia were 3-septate, hyaline, smooth-walled and thin-walled.

Comparison of the sizes of macroconidia from sporodochia of different species, obtained from CLA, revealed no significant differences between *F. odoratissimum* and *F. fabacearum* represented by two strains of each, however, three other species differed significantly from *F. odoratissimum* (Table 2). In *F. fabacearum* strains, the number of septa in falcate macroconidia was lower than in other species, ranging from 1 to 4, although conidial size did not differ depending on septum number (Fig. 5s). The maximum number of septa (8) was observed in *F. nirenbergiae* strain MFG 70137, where a conidium formed in the aerial mycelium reached $64.6 \times 3.9 \mu\text{m}$.

We compared the sizes of three-septate macroconidia of *F. sherbakoffii* strain MFG 70151 formed in cream-orange sporodochia on CLA and those produced on phialides in aerial mycelium on SNA, and found significant differences between the two types. Macroconidia from sporodochia were significantly longer ($p < 0.00001$), but their size variability was significantly lower than that of macroconidia formed in aerial mycelium. The mean length of sporodochial macroconidia ($n = 66$) was $32.6 \mu\text{m}$ (range $24.5\text{--}37.8 \mu\text{m}$, $SD = 2.9$), whereas the mean length of aerial macroconidia ($n = 60$) was $29.5 \mu\text{m}$ (range $19.7\text{--}40.3 \mu\text{m}$, $SD = 4.3$). In contrast, the width of sporodochial macroconidia ($n = 58$) was significantly smaller ($p < 0.00001$), with a mean of $4.3 \mu\text{m}$ (range $3.6\text{--}5.1 \mu\text{m}$, $SD = 0.31$), compared to aerial macroconidia ($n = 68$), which had a mean width of $4.3 \mu\text{m}$ (range $3.7\text{--}5.1 \mu\text{m}$, $SD = 0.33$).

Chlamydospore formation was typical for all five species, although the rate of formation varied among strains. Chlamydospores were globose to subglobose, rough-walled, $5.0\text{--}12 \mu\text{m}$ in diameter, and were formed terminally or intercalarily in hyphae and in macroconidia. In addition, lateral

chlamydospore formation in conidia was observed in *F. odoratissimum* strains (Fig. 6v, w).

Sclerotia consistently developed in cultures of most strains, with formation typically beginning in the second week of cultivation; however, their abundance depended primarily on the strain. Sclerotia were usually green or blue in colour. In addition to the small, rock-hard sclerotia, which appeared as dark spots on the colony reverse, a dark hyphal pattern was sometimes also visible there (Fig. 2B, d). In two *F. odoratissimum* strains, no conspicuous sclerotia were observed during the cultivation period.

The analysed fungi were characterized by the formation of hyphae of varying diameters, ranging from 0.9 to 4.9 µm. One of the notable mycelial structures observed in substrate hyphae was rhizoid-like hyphae. These structures were laterally located, narrow, curved, often branched, and varied from short to relatively long, measuring $4.0\text{--}83.6 \times 0.9\text{--}1.7$ µm. Rhizoid-like hyphae were detected in strains of all analysed species except *F. odoratissimum*. No phialides were formed on these structures, although intercalary or terminal chlamydospores were frequently observed.

Overall, only minor morphological differences were observed among strains of the different species within the FOSC. Within each taxon comprising multiple strains, some strains differed to a greater or lesser extent from other strains of the same species.

Based on the phylogenetic analysis and morphological characterisation, eight of the analysed strains were recognised as representing a novel species within the FOSC.

Taxonomy

Fusarium sherbakoffii, A.S. Orina, O.P. Gavrilova & T.Yu. Gagkaeva, sp. nov.

Mycobank 864515. FIG. 4.

Typification: Russia, Vologda Oblast, Ustyuzhensky District, 58°50'N 36°26'E.

Holotype: MFG 70151, isolated from a rotten tuber of *Solanum tuberosum* cultivar Arrow, 9 March 2020, T. Gagkaeva. Ex-holotype living culture MFG 70151 = VKM F-5122 (All-Russian Collection of Microorganisms, Moscow, Russia) = ITEM ##### (Agri-Food Microbial Collection, the Institute of Sciences of Food Production (ISPA) of the National Research Council (CNR), Bari, Italy).

GenBank accession numbers (holotype): *tef* = OR020718, *rpb2* = OR727743, *tub* = PX206216, *cmd* = PX206225.

Etymology: The epithet *sherbakoffii* honours Constantine Demetry Sherbakoff, a distinguished American plant pathologist of Russian origin and author of the book "Fusaria of Potatoes" (1915), in recognition of his significant contributions to the understanding of *Fusarium* diversity.

Diagnosis:

Asexual morph:

Colonies on PDA showed optimal growth at 25 and 30 °C, with an average radial growth rate of 5.6–5.7 mm/day.

Colony surface: aerial mycelium comparatively delicate, loosely floccose, sparsely developed, hairy-funiculose, pressed to the edge, white, grey, cream or pale violet to lilac. Colony margins are filiform.

Colony reverse: pale beige to colourless, occasionally with a violet tinge in the centre.

Hyphae hyaline, smooth-walled, variable in diameter (1.1–3.4 µm). Rhizoid-like hyphae with small branches were observed on substrate hyphae.

Odour absent.

Sporodochia rarely formed, small, almost transparent to pale orange in colour; the rate of formation was more abundant under alternating UV/dark illumination. **Conidiophores in sporodochia** and on aerial mycelium, unbranched or sparingly verticillately branched, short, with no more than 2–3 levels of branching. Cells barrel-shaped to subcylindrical, tapering towards the bases, $4\text{--}10 \times 4\text{--}5$ µm, bearing apical whorls of 2–3 monophialides, often reduced to a single lateral monophialide. **Sporodochial phialides** subulate to subcylindrical, smooth- and thin-walled, with an inconspicuous periclinal thickening and an apical collarette, $8\text{--}13 \times 3\text{--}5$ µm.

Conidiophores carried on the aerial mycelium lateral, solitary, unbranched or sparingly branched, bearing monophialides, 10–55 µm tall. **Aerial phialides** obclavate to subcylindrical or cylindrical, straight or slightly curved, smooth- and thin-walled, slightly tapering towards the apex and base, often reduced to small openings, sometimes with a flared collarette; periclinal thickening conspicuous; monophialidic, $2\text{--}32 \times 2\text{--}4$ µm.

Microconidia abundant, formed in small false heads at the tips of phialides; hyaline, oval, reniform to falcate, obovoid, often with a truncate base, smooth-walled and thin-walled, with a distinct pointed end, 0–2-septate.

0-septate conidia (n=54): 5.6–11.6 × 2.4–4.0 µm (av. 8.0 × 2.9 µm); 1-septate conidia (n=10): 6.4–12.7 × 2.6–4.7 µm (av. 9.3 × 3.2 µm); 2-septate conidia (n=7): 12.7–18.8 × 2–4 µm (av. 15.9 × 3.6 µm).

Sporodochial macroconidia (on CLA) falcate, moderately curved dorsiventrally, gradually tapering towards both ends. Apical cells blunt to papillate, uniformly tapering, slightly curved; basal cells foot-like or papillate; 3–4-septate, hyaline, thin-walled.

3-septate conidia (n=58): 24.5–37.8 × 3.6–5.1 µm (av. 32.6 × 4.3 µm); 4-septate conidia (n=41): 24.8–42.3 × 3.0–5.1 µm (av. 32.9 × 4.0 µm).

Falcate conidia formed on phialides in aerial mycelium (on SNA) moderately curved dorsiventrally and ventrally; 3-6 septate: 3-septate conidia (n=60): 19.7–40.3 × 3.7–5.1 µm (av. 29.5 × 4.6 µm); 4-septate conidia (n=30): 25.0–40.7 × 2.6–4.9 µm (av. 31.1 × 3.2 µm); 5-septate conidia (n=2): 36.4–42.4 × 3.9–4.2 µm; 6-septate conidia (n=5): 48.3–65.4 × 3.3–3.8 µm (av. 55.1 × 3.4 µm).

Chlamydospores abundantly produced after 2 weeks, globose to subglobose, rough-walled, formed terminally or intercalarily in hyphae and macroconidia, rarely lateral, single or in pairs, (5–)7–9(–12) µm in diameter.

Sclerotia consistently produced, variable in size and shape, greenish to deep blue, appearing as dark spots on the colony reverse.

Sexual morph not observed.

Habitat and distribution: On potato tubers in North-Western and Central European regions of Russia. Additional strains were isolated from soil in the Netherlands and Belgium and previously referred to as "*Fusarium* sp. 3" (Crous et al. 2021b).

Additional specimens examined: RUSSIA, CENTRAL EUROPEAN REGION: Tula Oblast, Bogoroditsky District, 53°46'N 38°8'E, 27 Apr 2021, potato tuber, cv. Gala, 2020, MFG 70122, MFG 70123; Samara Oblast, 53°27'N 50°27'E, 9 March 2021, potato tuber, cv. Queen Anne, MFG 70144; Kaluga Oblast, 54°26'N 35°26'E, potato tuber, cv. Challenger, MFG 70024; Vologda Oblast, Ustyuzhensky District, 58°50'N 36°26'E, potato tuber, cv. Arrow, 9 March 2020, MFG 70110, MFG 70112; Novgorod Oblast, 58°26'N 32°23'E, 21 April 2021, potato tuber, cv. Aurora, MFG 70104. All isolates were collected by T. Gagkaeva.

In conclusion, the phylogenetic and morphological evidence supports the recognition of these eight strains as a novel species, *F. sherbakoffii*, nested within the *Fusarium oxysporum* species complex.

Here we also synonymise several *Fusarium* species based on the molecular evidence presented above:

Fusarium agrestense J.F. de Mello, A.C.S. Santos & A.R. Machado, Crop Protect. 187 (no. 106947): 4 (2024)

≡ *Fusarium hordeum* S.L. Han, Meng M. Wang & L. Cai, Mycology 16 (4): 1548 (2025).

Fusarium fabacearum L. Lombard, Crous & Lampr., in Lombard, Sandoval-Denis, Lamprecht & Crous, Persoonia 43: 24 (2019)

≡ *Fusarium wimaladesilvae* Y.P. Tan, Gunasinghe & Vaghefi, in Tan, Gunasinghe, Martin & Vaghefi, Index of Australian Fungi 30: 2 (2024).

Fusarium libertatis L. Lombard & Crous, in Lombard, Sandoval-Denis, Lamprecht & Crous, Persoonia 41: 29 (2018)

≡ *Fusarium oxysporum* f.sp. *dactyliferae* I.U. Haq, S. Ijaz, N.A. Khan & I.A. Khan, Plants 11 (no. 2643): 11 (2022).

Fusarium nirenbergiae L. Lombard & Crous, in Lombard, Sandoval-Denis, Lamprecht & Crous, Persoonia 41: 29 (2018)

≡ *Fusarium houttuyniae* Y.K. He & Yong Wang bis, Phytotaxa 603 (3): 264 (2023);

≡ *Fusarium idabrowneae* Y.P. Tan, in Tan & Shivas, Index of Australian Fungi 31: 8 (2024);

≡ *Fusarium landiae* Y.P. Tan & Conroy, Index of Australian Fungi 45: 3 (2024);

≡ *Fusarium liriopes* Y.K. He & Yong Wang bis, Phytotaxa 603 (3): 266 (2023).

Fusarium odoratissimum Maryani, L. Lombard, Kema & Crous, in Maryani, Lombard, Poerba, Subandiyah, Crous & Kema, Stud. Mycol. 92: 159 (2018)

≡ *Fusarium cili* H. Zhang & Y.L. Jiang, in Zhang, Zeng, wiei, Jiang & Zeng, Mycosphere 14 (1): 2114 (2023);

≡ *Fusarium phialophorum* Maryani, L. Lombard, Kema & Crous, in Maryani, Lombard, Poerba, Subandiyah, Crous & Kema, Stud. Mycol. 92: 169 (2018);

≡ *Fusarium rosae-roxburghii* H. Zhang & Y.L. Jiang, in Zhang, Zeng, Wei, Jiang & Zeng, Mycosphere 14 (1): 2120 (2023).

Pathogenicity of fungi

After four weeks of incubation, the control tubers remained symptomless, and the size of the mechanical wound measured on average 13.7 ± 0.1 mm. Typical symptoms of *Fusarium* dry rot included darkening and necrosis around the inoculation point, drying of the affected tissue, and the appearance of concentric rings on the surface, sometimes accompanied by visible sporulation of the fungus on the tuber surface. Depending on the aggressiveness of the strain, internal cavities of varying sizes were observed within the tubers; these cavities were separated from the apparently healthy tissue by a border ranging from light to dark brown in colour, and were often lined with mycelium and visible fungal sporulation. In addition, many strains caused extensive maceration of the surrounding tissue around the cavity, reaching the periderm of the tuber (Fig. 7A).

The lesion sizes caused by strains of different species varied as follows: *F. nirenbergiae* – 32.3–40.5 mm, *F. oxysporum* s.str. – 5.4–31.0 mm, *F. sherbakoffii* – 4.5–33.4 mm, *F. fabacearum* – 15.4–18.8 mm, and *F. odoratissimum* – 3.0–5.7 mm (Fig. 7B). On average, *F. nirenbergiae* strains were 1.6–8.2 times more aggressive towards potato tubers than strains of *F. oxysporum* s.str. ($p = 0.0094$), *F. sherbakoffii* ($p = 0.0044$), *F. fabacearum* ($p = 0.00069$), and *F. odoratissimum* ($p = 0.000022$). The pathogenicity of *F. oxysporum* s.str., *F. sherbakoffii*, and *F. fabacearum* was similar on average. Strains of *F. oxysporum* s.str. and *F. sherbakoffii* exhibited the most variable aggressiveness towards potato tubers. In particular, *F. oxysporum* strain MFG 70127 and *F. sherbakoffii* strain MFG 70110 were significantly less aggressive than the other strains of their respective species. The two *F. odoratissimum* strains caused similarly weak damage and were significantly less aggressive than all other strains.

Successful re-isolation of the fungi from the inoculated tubers and their subsequent identification confirmed the role of the FOSC species as causative agents of *Fusarium* dry rot.

Discussion

In this study, we focused on resolving the taxonomic status of 23 randomly selected strains isolated from potato tubers with dry rot symptoms, which had previously been phenotypically identified as *F. oxysporum* s.l. The results of our multigene phylogenetic analysis confirmed the extraordinary species diversity within the FOSC. In our view, the current practice of subdividing the FOSC into broad clades based on genetic data alone is of limited practical value, as the rapid pace of species discovery continually reshapes our understanding of phylogenetic relationships and clade composition (Lombard et al. 2019; Lopez-Jimenez et al. 2026). Based on the phylogenetic data obtained in this study, the analysed strains were distributed among five clades corresponding to distinct species, four of which had been previously described and one of which is proposed as new. Among the strains, 30.4% corresponded to *F. nirenbergiae*, 17.4% were identified as *F. oxysporum* s.str., and 8.7% represented each of *F. fabacearum* and *F. odoratissimum*. The majority of the analysed strains (34.8%) belonged to the new species *F. sherbakoffii* described in this study.

Significant genetic diversity among the *F. nirenbergiae* strains was revealed in this study, which is consistent with previous findings (Aiello et al. 2021; Mirghasempour et al. 2022). Furthermore, strains of *F. houttuyniae*, *F. idabrowneae*, *F. landiae*, and *F. liriopes* clustered within the *F. nirenbergiae* clade, and these four species were recognised as synonyms of *F. nirenbergiae*. Within the FOSC, *F. nirenbergiae* is one of the most widespread species, having been recorded on a variety of plant hosts worldwide (Lombard et al. 2019; Aiello et al. 2021; Han et al. 2023). Its frequent association with potato has been noted repeatedly (Mamaghani et al. 2024; Li et al. 2025; Elansky et al. 2025).

Two strains (MFG 70025 and MFG 70165) identified as *F. fabacearum* in the present study originated from geographically distant locations in Russia: one from the Central European region and the other from the Volga region. *Fusarium fabacearum* was first described based on the isolates from *Glycine max* and *Zea mays* in South Africa (Lombard et al. 2019) and has since been recovered from seeds of *Striga asiatica*, from *Sorghum* field and rhizosphere soils in Ethiopia (Lombard et al. 2022). In Russia, this species has been reported on fruit and roots of *Solanum lycopersicum* and roots of *Capsicum annuum* in the Krasnodar region, located in southern European Russia (Yarmeeva et al. 2025). A recent study proposed *F. fabacearum* as the most widespread species within the FOSC (Lopez-Jimenez et al. 2026). Nevertheless, we consider this claim to be premature, as it relies on a relatively small and geographically biased dataset comprising five strains from Russia, three from Canada, and four from Colombia, selected specifically for whole-genome sequencing. Additionally, the ex-type strain BRIP 70752a of *F. wimaladesilvae* was recovered within the *F. fabacearum* clade in our analysis, leading us to recognise this taxon as a synonym of *F. fabacearum*.

It should also be emphasised that the synonymised species *F. idabrowneae*, *F. landiae*, and *F. wimaladesilvae* were described based on limited genetic data alone, without any morphological description, and each is represented by a single strain (Tan and Conroy 2024; Tan and Shivas 2024; Tan et al. 2024).

Two strains (MFG 70138 and MFG 70158) were identified as *F. odoratissimum*, a species also characterised by high genetic diversity and phylogenetic similarity to *F. phialophorum*, *F. rosae-roxburghii*, and *F. cili*. *Fusarium odoratissimum* and *F. phialophorum* were described simultaneously in a single study (Maryani et al. 2019). However, the boundary between these two species has previously been considered vague due to the extremely high similarity of the *tef*, *rpb1*, and *rpb2* sequences of their ex-type strains (Lombard et al. 2022). In the present study, the near-identity of the *tef* and *rpb2* sequences of the ex-type strains of *F. odoratissimum* and *F. phialophorum* was confirmed, and extensive sequence

similarity with other reference strains of these species was also observed. The other two species, *F. rosae-roxburghii* and *F. cili*, were described based on genetic data from a limited number of strains in phylogenetic analyses (Zhang et al. 2023). In our study, strains of both species were nested within the clade containing *F. odoratissimum* and *F. phialophorum*.

Comparison of the morphological descriptions of *F. cili*, *F. odoratissimum*, *F. phialophorum*, and *F. rosae-roxburghii* revealed significant differences among these species and between them and the strains identified in our study. Both MFG strains identified as *F. odoratissimum* were distinguished from strains of other species by the production of a strong wine-coloured pigment. This phenotype contrasts sharply with that of other strains and may be attributable to the fact that the original description of *F. odoratissimum* was based exclusively on strains isolated from bananas in Indonesia (Maryani et al. 2019). In contrast to the 110 banana-derived *F. odoratissimum* strains analysed in that study, the potato-derived strains examined here had a purple-wine pigmentation on the colony reverse. Nevertheless, some subsequent publications have also reported that *F. odoratissimum* cultures isolated from banana grown on PDA exhibit purple-violet pigmentation on both the obverse and colony reverse (Ujat et al. 2021). Similarities included the formation of polyphialides and the shape and size of microconidia, which were comparable between the two sets of strains.

The *F. odoratissimum* strains MFG 70138 and MFG 70158 are more similar to *F. cili* strains in terms of their cultural characteristics, at least in that they produce pink pigment; however, according to the authors (Zhang et al. 2023), the two strains of *F. cili* do not produce macroconidia. The microconidia of these two species are similar in shape and size, are single-celled or septate, and have a rough wall. The authors refer to single-septate, rough-walled microconidia as mesoconidia; however, according to the classical definition, mesoconidia are not simply intermediate in size between microconidia and macroconidia, but rather represent a specific blastic mode of conidiogenesis, in which the terminal cells are conical (Pascoe, 1990; Nirenberg, 1990). Twenty-nine strains of another phylogenetically related species, *F. phialophorum*, isolated exclusively from banana, formed colonies that were uniformly white and unpigmented (Zhang et al. 2023). In two strains of *F. rosae-roxburghii*, sporodochia were not observed, colonies were white, aerial mycelium was abundant, and the reverse was light orange (Zhang et al. 2023).

While *F. odoratissimum* and *F. phialophorum* are primarily recognised as pathogens of banana (Maryani et al. 2019; Ujat et al. 2021), *F. odoratissimum* has been recovered from a diverse range of substrates and geographical regions: garden soils in the Netherlands (Crous et al. 2021a), roots of *Sorghum* plants in Dutch greenhouse soils (Lombard et al. 2022), kiwifruits displaying soft rot symptoms in China (Wang et al. 2026), and *Anoectochilus formosanus* in Taiwan (Chang et al. 2026). The closely related species *F. rosae-roxburghii* and *F. cili* were originally isolated from *Rosa roxburghii* in China (Zhang et al. 2023). In our study, two *F. odoratissimum* strains were obtained from potato tubers collected in two distant regions of Russia: Stavropol Krai in the south of European Russia and Bashkiria, near the Ural Mountains. A previous study also reported a single isolation of this species from potato in Russia (Elansky et al. 2025). These observations indicate that *F. odoratissimum* is not restricted to banana-growing regions; rather, it has a wide area and high diversity of host plants.

In summary, the combined phylogenetic, phenotypic and host association data for *F. odoratissimum*, *F. phialophorum*, *F. rosae-roxburghii* and *F. cili* support the conclusion that the strains of these four species represent a single species, *F. odoratissimum*, which exhibits considerable genetic and ecological plasticity. This conclusion is in line with a recent suggestion that these four taxa represent the same species (Han et al. 2025).

One of the most unexpected findings of this study was that the majority of the randomly selected FOSC strains belonged to a previously undescribed species, which we formally describe here as *F. sherbakoffii*. Eight strains isolated from potato tubers collected in five regions of Russia, together with eight strains previously referred to as "*Fusarium* sp. 3" isolated from soil in the Netherlands and Belgium, formed a monophyletic lineage within the FOSC. Notably, a recent survey in Russia identified 11 *Fusarium* isolates from dry-rotted potato tubers whose *tef* sequences were 100% identical to that of the "*Fusarium* sp. 3" strain JW 10005 (GenBank accession MZ921857) (Elansky et al. 2025). To date, all known records of *F. sherbakoffii* have been associated either with soil or with potato tubers growing in it. Identifying the host range and natural habitats of this species is therefore a priority for future research.

In addition, other taxonomic changes are proposed based on the results of our phylogenetic analyses: *Fusarium oxysporum* f. sp. *dactyliferae* is recognised as a synonym of *F. libertatis*, and *F. hordeum* as a synonym of *F. agrestense*. Furthermore, it is important to note that the definition of a *forma specialis* does not follow the nomenclatural rules established by the International Code of Nomenclature for algae, fungi, and plants. The lack of robust morphological and molecular characterisation of *F. oxysporum* s.l. isolates, combined with an overemphasis on plant–pathogen interactions, often leads to incorrect species identification (Edel-Hermann et al. 2021). A clear illustration of this problem is provided by the re-identification of *F. oxysporum* f. sp. *cepae* strains as *F. nirenbergiae* based on multilocus sequence data (Sakane et al. 2024).

In this study, we also assessed the morphological variability of genetically characterised strains to provide insight into the differences between species. Identification of fungal strains as members of the FOSC is generally straightforward due to the rapid and abundant production of microconidia in false heads, the presence of macroconidia both in aerial mycelium and in sporodochia, and the formation of numerous, typically solitary chlamydospores (Gerlach and Nirenberg 1982; Leslie and Summerell 2006). However, defining clearly distinct, highly specific morphological characteristics and/or their combinations that would allow reliable species delimitation within the FOSC appears to be an extremely challenging task. The difficulty in separating these species under artificial culture conditions is compounded by their considerable

phenotypic instability: even the same strain, grown under identical conditions, can produce divergent morphotypes over successive culture passages.

The formation of **microconidia** in false heads on short monophialides is a basic characteristic of *F. oxysporum* s.l. However, the main feature uniting these species is the production of single-celled microconidia on short, ampulliform monophialides, tapering towards both the base and the apex. Nevertheless, a recent description of a new FOSC species, *F. semanoti*, which is phylogenetically closely related to *F. odoratissimum*, reported the absence of microconidia – a feature completely atypical for this group of fungi (He et al. 2026).

Recent studies focusing on the morphological characterisation of phylogenetically defined species have demonstrated that polyphialide with two loci formation is a feature of several taxa within the FOSC. Polyphialides produced on aerial mycelium have been reported for *F. carminascens*, *F. curvatum*, *F. elaeidis*, *F. libertatis* (Lombard et al. 2019), and *F. odoratissimum* (Maryani et al. 2019). In the protologue of *F. nirenbergiae*, polyphialides were not mentioned in the text, although they were shown in the figures (Lombard et al. 2019). Our isolates of *F. nirenbergiae* consistently produced polyphialides with two loci, and these structures were observed more frequently than in strains of *F. odoratissimum* and *F. sherbakoffii*.

Most of the identified fungi abundantly produced 3-septate macroconidia. According to our data, macroconidia were relatively longer in *F. odoratissimum*, but the range of values for this parameter within each species was too wide to be diagnostically useful. We noted the presence of falcate conidia with a single septum in the aerial mycelium of *F. fabacearum* strains; these did not differ significantly in size from the three-septate macroconidia. Interestingly, the same type of macroconidia in this species was also illustrated in the publication by Lombard et al. (2022).

In general, fungi of the FOSC are typically characterised by abundant sporulation, including the formation of chlamydospores and sclerotia. This ability facilitates their spread, colonisation of various substrates, and long-term survival under harsh environmental conditions. In some descriptions of newly recognised phylogenetic species, the absence of chlamydospores on SNA was noted, possibly because observations were made after only 7 days of growth (Maryani et al. 2019; Lombard et al. 2022). In contrast, we examined micromorphological characteristics on the same medium after 14–21 days and detected chlamydospores in all studied species, not only in hyphae but also within macroconidia.

Another morphological structure commonly observed in *F. oxysporum* s.l. is sclerotia, which form rapidly on agar and exhibit considerable variation in shape and colour. This variability has historically prompted attempts to use them as diagnostic characters for species identification (Sherbakoff 1915). However, the rate of sclerotium formation and their abundance depend primarily on the strain rather than on the fungal species.

A detailed study of the hyphal structures of the analysed strains revealed lateral sinuous bundles of short hyphae resembling rhizoid-like hyphae characteristic of some fungi (e.g., *Rhizopus* spp.). To the best of our knowledge, such or similar structures have not previously been described in *F. oxysporum* s.l. The rhizoid-like hyphae are common, and they apparently facilitate maximal nutrient absorption, anchorage of the fungus to the substrate, and penetration of various host tissues.

In our pathogenicity assays, all analysed strains were capable of causing disease on potato tubers. However, differences in aggressiveness were observed among species: *F. nirenbergiae* strains consistently induced the most severe symptoms, whereas *F. odoratissimum* strains caused only weak lesions. The high pathogenic potential of members of the FOSC has been repeatedly noted across different geographic regions (Gherbawy et al. 2019; Azil et al. 2021; Muratali et al. 2025; Christian & Duellman, 2026; Kouadri et al. 2026). Importantly, our results also revealed considerable variation in aggressiveness not only between species but also among strains belonging to the same species, confirming that pathogenicity is a strain-dependent trait. Intraspecific variability in aggressiveness towards potato tubers has been reported previously for *F. oxysporum* (Gashgari and Gherbawy 2013; Muratali et al. 2025; Pooja et al. 2025), and the coexistence of highly aggressive and non-pathogenic strains in the potato mycobiota has also been noted (Akosah et al. 2021). Our study also revealed significant differences in pathogenicity among strains of *F. oxysporum* and *F. sherbakoffii*. Notably, infection with strains of *F. oxysporum* s.str., *F. nirenbergiae*, and *F. sherbakoffii* resulted not only in typical dry rot but also in atypical symptoms, including dark browning, tissue softening, and a wet appearance of the internal tuber tissues surrounding the lesion. These observations are in agreement with previous reports that illustrated similar symptoms caused by the FOSC fungi (Li et al. 2025; Muratali et al. 2025; Christian & Duellman, 2026).

We interpret these atypical symptoms as likely resulting from the activity of secondary metabolites produced by the fungi, and agree with Christian and Duellman (2026), who noted that potential visual differences in symptoms depending on the *Fusarium* species should be taken into account in the diagnosis of tuber diseases. *Fusarium* species associated with potato dry rot are known to produce different metabolites, some of which are phytotoxins (López-Berges et al. 2013; Eranthodi et al. 2020; Steglińska et al. 2023; Mamaghani et al. 2024). Analysis of metabolite production by *Fusarium* strains isolated as endophytes from healthy potato tubers or roots in Iran showed that all *F. nirenbergiae* strains produced the mycotoxins beauvericin and moniliformin, whereas other strains produced enniatin A1, beauvericin, and fusaric acid in various combinations (Mamaghani et al. 2024).

Conclusions

This study highlights the considerable species diversity among FOSC strains associated with potato dry rot. By integrating multilocus phylogenetic analysis with morphological and pathogenicity data, we identified five distinct species, including the newly described *F. sherbakoffii* sp. nov., and synonymised ten previously recognised taxa. Our results demonstrate that morphology alone is insufficient for reliable species identification, and that pathogenicity varies considerably not only among species but also among strains within a species. Continued deposition of well-vouchered strains from previously under-sampled hosts and regions, combined with standardised multilocus and morphological protocols, will remain essential for stabilising FOSC taxonomy going forward.

Declarations

Author Contribution

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Aleksandra S. Orina, Olga P. Gavrilova and Tatiana Yu. Gagkaeva. The first draft of the manuscript was written by T. Yu. Gagkaeva and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests. The authors declare no competing interests.

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Tables

Table 1 *Fusarium* strains isolated from rotten tubers of different potato cultivars collected from various regions of Russia and used in this study.

<i>Fusarium</i> species	MFG*	Origin, region	Source (potato cultivar)	Year of isolation	GenBank accession number			
					<i>tef</i>	<i>rpb2</i>	<i>tub</i>	<i>cmd</i>
<i>F. fabacearum</i>	70025	Russia, Kaluga Oblast	Innovator	2020	OR020703	OR727730	PX206209	na**
<i>F. fabacearum</i>	70165	Russia, Chuvashia	Riviera	2021	OR020727	OR727746	PX206217	na
<i>F. nirenbergiae</i>	70132	Russia, Yaroslavl Oblast	Arrow	2020	OR634787	OR727749	na	na
<i>F. nirenbergiae</i>	70136	Russia, Stavropol Krai	unknown	2020	OR020713	OR727738	na	na
<i>F. nirenbergiae</i>	70137	Russia, Stavropol Krai	unknown	2020	OR634788	OR727739	na	na
<i>F. nirenbergiae</i>	70139	Russia, Stavropol Krai	unknown	2020	OR634790	OR727741	na	na
<i>F. nirenbergiae</i>	70157	Russia, Bashkiria	Udacha	2021	OR020721	OR727744	na	na
<i>F. nirenbergiae</i>	70159	Russia, Bashkiria	Udacha	2021	OR020723	OR727745	na	na
<i>F. nirenbergiae</i>	70178	Russia, Stavropol Krai	unknown	2021	OR020733	OR727747	na	na
<i>F. odoratissimum</i>	70138	Russia, Stavropol Krai	unknown	2020	OR634789	OR727740	na	na
<i>F. odoratissimum</i>	70158	Russia, Bashkiria	Udacha	2021	OR020722	OR727751	na	na
<i>F. oxysporum</i> s.str.	70125	Russia, Tula Oblast	Al'yans	2020	OR634784	OR727735	na	na
<i>F. oxysporum</i> s.str.	70127	Russia, Stavropol Krai	Colombo	2020	OR634785	OR727736	na	na
<i>F. oxysporum</i> s.str.	70128	Russia, Stavropol Krai	Colombo	2020	OR634786	OR727737	na	na
<i>F. oxysporum</i> s.str.	70145	Russia, Samara Oblast	Queen Anne	2020	OR634793	OR727750	na	na
<i>F. sherbakoffii</i> sp. nov.	70024	Russia, Kaluga Oblast	Challenger	2020	OR634773	OR727729	PX206208	PX206218
<i>F. sherbakoffii</i> sp. nov.	70104	Russia, Novgorod Oblast	Aurora	2020	OR634777	OR727731	PX206210	PX206219
<i>F. sherbakoffii</i> sp. nov.	70110	Russia, Vologda Oblast	Arrow	2020	OR634781	OR727732	PX206211	PX206220
<i>F. sherbakoffii</i> sp. nov.	70112	Russia, Vologda Oblast	Arrow	2020	OR634782	OR727748	PX206212	PX206221
<i>F. sherbakoffii</i> sp. nov.	70122	Russia, Tula Oblast	Gala	2020	OR020707	OR727733	PX206213	PX206222
<i>F. sherbakoffii</i> sp. nov.	70123	Russia, Tula Oblast	Al'yans	2020	OR020708	OR727734	PX206214	PX206223
<i>F. sherbakoffii</i> sp. nov.	70144	Russia, Samara Oblast	Queen Anne	2020	OR634792	OR727742	PX206215	PX206224
<i>F. sherbakoffii</i> sp. nov.	70151	Russia, Vologda Oblast	Arrow	2020	OR020718	OR727743	PX206216	PX206225

* strain number in the collection of Laboratory of Mycology and Phytopathology (VIZR, St-Petersburg, Russia);

** not analyzed.

Table 2 Micromorphological features of strains belonging to five species within the FOSC.

<i>Fusarium</i> species (MFG strains)	Septation in macroconidia	Sizes of 3 septate macroconidia in sporodochia, µm	Sizes of 0 septate microconidia, µm	Presence of polyphialides
<i>F. fabacearum</i> (70165, 70025)	3 (1-4)	38.7 × 4.4 (28.5–46.8 × 3.4–5.8)	7.6 × 2.7 (3.9–15 × 2.0–3.7)	no
<i>F. nirenbergiae</i> (70137, 70132, 70136)	3-5 (8)*	34.4 × 4.3 (24.2–47.2 × 3.1–5.7)	7.4 × 2.5 (4.2–13.5 × 2.0–3.9)	rare
<i>F. odoratissimum</i> (70138, 70158)	3-6	43.3 × 4.2 (31.5–58.3 × 3.4–4.9)	6.4 × 2.8 (3.9–9.8 × 2.1–3.7)	rare
<i>F. oxysporum</i> s.str. (70125, 70127, 70128)	3-5 (4, 7)	36.1 × 4.3 (23.7–46.5 × 3.2–5.3)	7.0 × 2.7 (5.0–10.6 × 1.9–3.4)	no
<i>F. sherbakoffii</i> (70151, 70024, 70144)	3-4 (6)	35.0 × 4.3 (24.5–52.3 × 3.2–5.4)	8.0 × 2.9 (5.6–11.6 × 2.4–4.0)	rare

* numbers in parentheses indicate septa observed in rare cases.

Figures

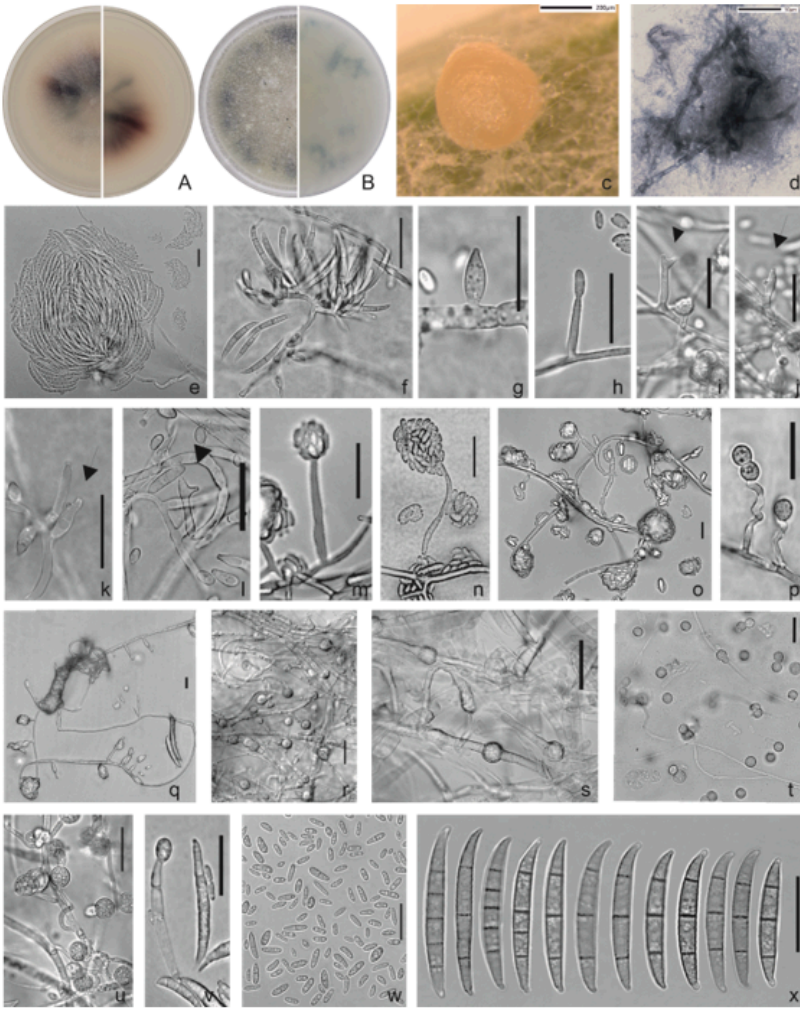


Figure 2

***Fusarium nirenbergiae*.** A. MFG 70159 (PDA, 7 days, dark, 25 °C), B. MFG 70136 (PDA, 14 days, light, 25 °C); c. Sporodochia on carnation leaves; d. Substrate hyphae with dark blue melanin pigmentation; e-f. Sporodochial conidiophores; g-h. Monophialides on aerial mycelium; i-l. Polyphialides on aerial mycelium indicated by arrow; m-o, q. False head carried on a phialide; p, r-u. Chlamydospores in hyphae; v. Chlamydospore in macroconidia; w. Microconidia; x. Sporodochial macroconidia. Bars = 20 μm.

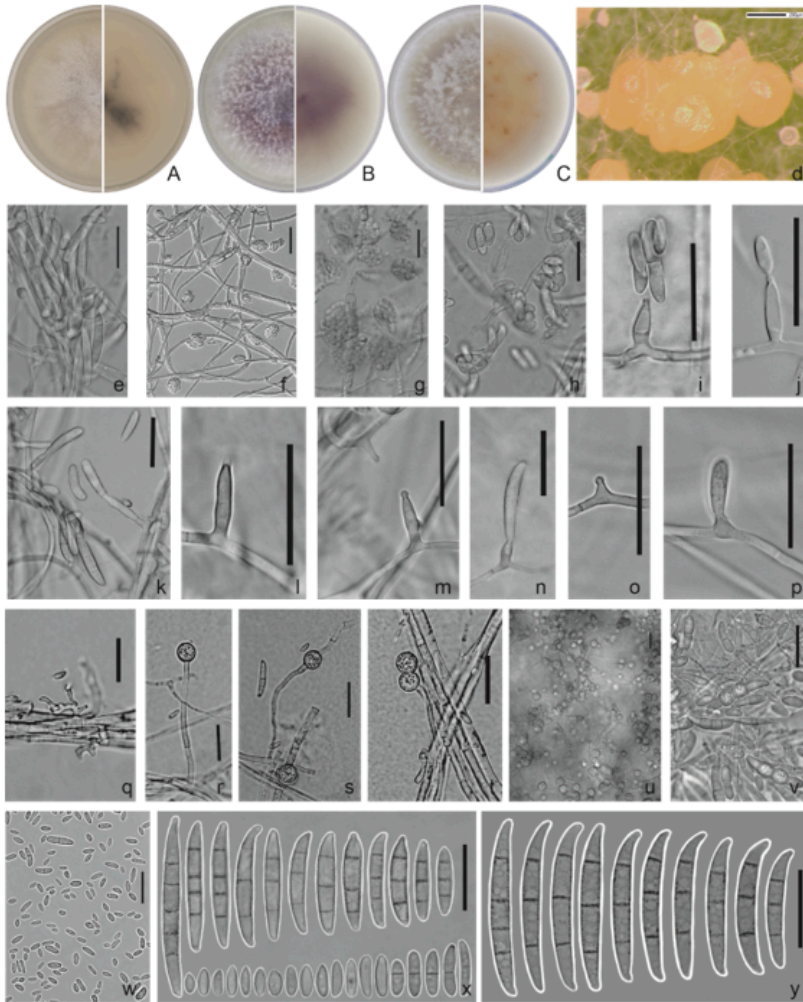


Figure 3

***Fusarium oxysporum* s.str.** A. MFG 70128 and B. MFG 70127 (PDA, 7 days, dark, 25 °C), B. MFG 70125 (PDA, 14 days, light, 25 °C); d. Sporodochia on carnation leaves; e. Sporodochial conidiophores; f-h. False head carried on a phialides; i-p. Phialides; q. Rhizoid-like hyphae; r-u. Chlamydospores in hyphae; v. Chlamydospores in macroconidia; w. Microconidia; x. Conidia in aerial mycelium; y. Sporodochial macroconidia. Bars = 20 µm.

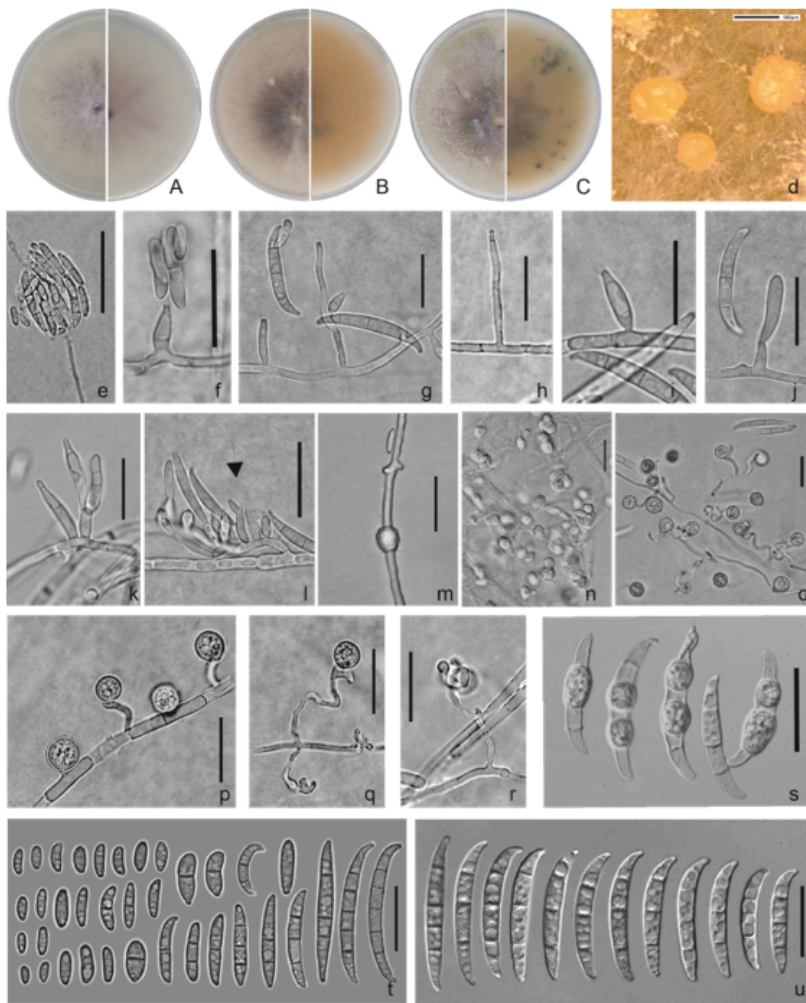


Figure 4

Fusarium sherbakoffii (type culture MFG 70151). Culture on PDA in the dark, 25 °C: A. 7 days and B. 21 days; and C. in the light, 25 °C; d. Sporodochia on carnation leaves; e. False heads of microconidia; f-k. Monophialides; l. Polyphialide indicated by arrow; m, n. Chlamydospores in hyphae; o-r. Rhizoid-like hyphae and chlamydospores; s. Chlamydospores in macroconidia; t. Conidia formed in aerial mycelium, the representation does not reflect the actual ratio; u. Sporodochial macroconidia. Bars = 20 µm.

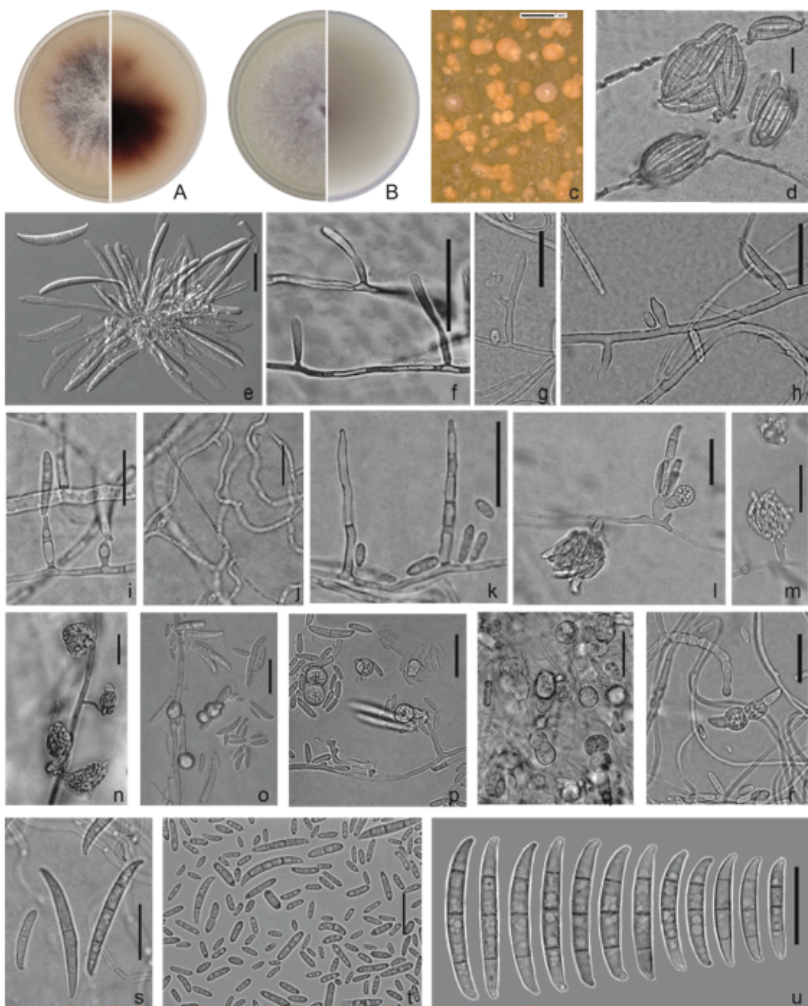


Figure 5

Fusarium fabacearum. A. MFG 70025, B. MFG 70165 (PDA, 7 days, dark, 25 °C); d. Sporodochia on carnation leaves; e. Sporodochial conidiophores; f-k. Phialides; l-n. False head carried on a phialide; o-q. Chlamydospore in hyphae; r. Chlamydospore in macroconidia; s-t. Conidia in aerial mycelium; u. Sporodochial macroconidia. Bars = 20 µm.

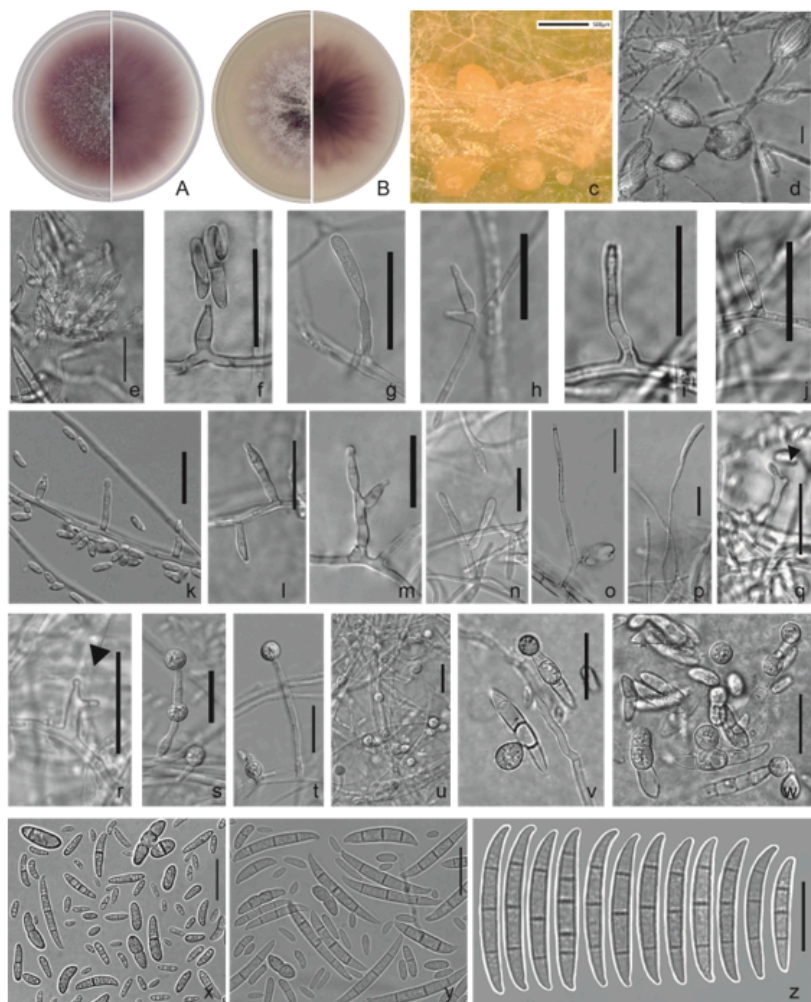


Figure 6

***Fusarium odoratissimum*.** A. MFG 70158 (PDA, 7 days, dark, 25 °C), B. MFG 70138 (PDA, 7 days, light, 25 °C); c. Sporodochia on carnation leaves; d-e. Sporodochia and sporodochial conidiophores; f. False head carried on a phialide; g-p. Conidiophores and phialides; q, r. Polyphialides on aerial mycelium (indicated by arrow); s, t. Chlamydospore in conidiophores; u. Chlamydospore in hyphae; v, w. Chlamydospore in macroconidia; x, y. Conidia in aerial mycelium; z. Sporodochial macroconidia. Bars = 20 μ m.

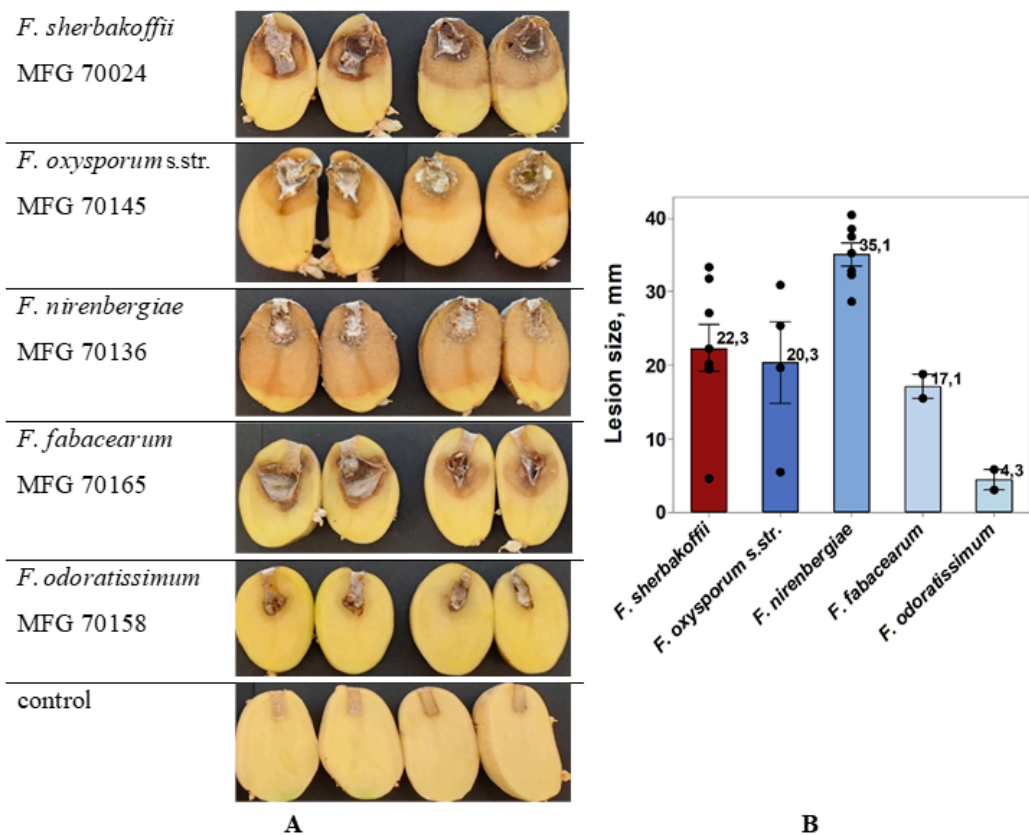


Figure 7

Symptoms of *Fusarium* dry rot (A) and lesion sizes (B) on potato tubers of cv. Impala caused by representative strains of different species within the FOSC after 4 weeks of incubation at 23 °C in the dark. Bars represent standard error of the mean.