Streptomyces caviscabies sp. nov., from Deep-Pitted Lesions in Potatoes in Québec, Canada

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Eight deep-pitted-scab-inducing streptomycetes isolated from potato lesions in Québec (Canada) were phenotypically compared with representative strains of the principal plant-pathogenic *Streptomyces* species. These eight strains could be distinguished from representatives of *Streptomyces scabies*, *Streptomyces aureofaciens*, *Streptomyces ipomoeae*, and *Streptomyces acidiscabies* on the basis of their morphological or physiological properties. They were characterized by a gold mycelium on yeast-malt extract medium and a white mass of spores borne in flexuous chains. The spores of these organisms were cylindrical and smooth. Their cell walls contained the LL-diaminopimelic acid isomer, and their DNA guanine-plus-cytosine content was 71 mol%. The strains which we studied did not produce melanin. All of the strains grew on proline or methionine as a sole nitrogen source and utilized raffinose as a sole carbon source. Bacterial growth was inhibited at pH 4.5. The levels of DNA relatedness between the deep-pitted-scab-inducing strains and strains of the other plant-pathogenic *Streptomyces* species were low. We place these deep-pitted-scab-inducing strains in a new bacterial species, for which we propose the name *Streptomyces caviscabies*. The type strain of this species is strain ATCC 51928.

Several *Streptomyces* species are causal agents of potato scab, but *Streptomyces scabies* is the predominant pathogen. *S. scabies* induces shallow, raised, or deep-pitted corky lesions on tubers and expanded tap roots. In 1989 this species was revived and redefined by Lambert and Loria (12), who characterized *S. scabies* as a species which has smooth gray spores borne in spiral chains, produces melanin, and utilizes all of the diagnostic sugars recommended by the International *Streptomyces* Project to identify *Streptomyces* species (18). Paradis et al. (15) divided the *S. scabies* strains in Québec into two genetic groups that exhibited relatively low levels of DNA relatedness (between 21 and 60%) (15). Even though *S. scabies* can occasionally induce deep-pitted scab depending on the interaction among cultivar, environmental conditions, and virulence of the isolate, in two independent studies workers identified other *Streptomyces* species as the predominant causal agents of deep-pitted scab of potatoes (1, 5). Archuleta and Easton (1) suggested that most cases of deep-pitted scab in the state of Washington should not be attributed to *S. scabies* but rather should be attributed to four other *Streptomyces* species (*Streptomyces diastatochromogenes*, *Streptomyces atroolivaceus*, *Streptomyces lydicus*, and *Streptomyces resistomyficus*). Unfortunately, this suggestion has never been confirmed.

Recently, a group of streptomycetes isolated from potato scab lesions in Québec was characterized (5, 6). This group of actinomycetes was associated with deep-pitted scab (Fig. 1) and was most commonly isolated from tubers grown in irrigated soil. The members of this group exhibited numerous traits that were not characteristic of *S. scabies*; for example, they produced white spores borne in flexuous chains, they did not produce a melanoid pigment, and they were resistant to streptomycin. In addition, these organisms could not be identified as members of another important potato scab-inducing species, *Streptomyces acidiscabies*, on the basis of their physiological properties (5, 11). Phenotypic characterization, a fatty

acid analysis, and whole-cell protein electrophoresis revealed that these plant-pathogenic bacteria formed a relatively homogeneous group (5). A numerical analysis (5) showed that these deep-pitted-scab-inducing strains shared numerous phenotypic traits (level of similarity, 75.8%) with strains belonging to the *Streptomyces albidoflavus* cluster of Williams et al. (22).

S. scabies, *S. acidiscabies*, and *Streptomyces ipomoeae*, the causal agent of sweet potato pox, produce thaxtomins, a group of phytotoxins that appear to play an important role in the phytopathogenicity of streptomycetes (9, 10). *S. scabies* and *S. acidiscabies* strains produce thaxtomins on potato tubers (10) and also in some culture media made out of oatmeal (2, 14). In contrast to *S. scabies* and *S. acidiscabies* (14) and like *S. ipomoeae* (9), the strains from Québec that cause deep-pitted scab do not produce thaxtomins in oatmeal media. However, they do produce thaxtomins in media made out of potato or sweet potato peels (7).

The purposes of this work were (i) to compare the phenotypic traits of the deep-pitted-scab-inducing bacteria from Québec with the phenotypic traits of the principal phytopathogenic streptomycetes and *S. albidoflavus* and (ii) to determine the levels of DNA complementarity between the deep-pitted-scab-inducing strains and representatives of other *Streptomyces* species. On the basis of our results we propose that the plant-pathogenic bacteria from Québec should be placed in a new species, *Streptomyces caviscabies*.

MATERIALS AND METHODS

Strains. We characterized the following eight deep-pitted-scab-inducing strains from Québec (Canada): EF-83, EF-86, EF-87^T (T = type strain), EF-88, EF-92, EF-98, EF-104, and EF-123 (Table 1). These deep-pitted-scab-inducing strains were compared phenotypically with representative strains of other phytopathogenic *Streptomyces* species (including *S. acidiscabies* [11], *S. ipomoeae* [13], *S. scabies* [12], and *Streptomyces aureofaciens* [4]), with *S. albidoflavus* ATCC 25422^T, and with strains belonging to *S. albidoflavus* cluster 1 of Williams et al. (22), (Table 2).

Phenotypic characterization. Colony color and spore color were observed after 10 days of growth at 30°C on yeast-malt extract (YME) medium (16). Spore ornamentation and spore chain morphology were determined by scanning electron microscopy as follows. Sporulating colonies were fixed in situ in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.3) for 2 h at room temperature. Small pieces of agar were then cut out with a razor blade and postfixed in 2% osmium tetroxide in the same cacodylate buffer for 2 h at room temperature. The pieces were then dehydrated in a graded ethanol series, critical point dried

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TABLE 1. Bacterial strains used in this study

Strain	Potato cultivar	Geographical origin
<i>S. caviscabies</i> strains		
EF-83	Superior	Saint-Ambroise, Québec, Canada
EF-86	Trent	Saint-Ambroise, Québec, Canada ^a
EF-87 ^T	Trent	Saint-Ambroise, Québec, Canada ^a
EF-88	Trent	Saint-Ambroise, Québec, Canada ^a
EF-92	Trent	Saint-Ambroise, Québec, Canada ^b
EF-98	Trent	Saint-Ambroise, Québec, Canada ^b
EF-104	Norchip	Saint-Arsène, Québec, Canada
EF-123	Superior	Inverness, Québec, Canada
<i>S. acidiscabies</i> strains		
ATCC 49003 ^T	Katahdin	Central New York
EF-9	Unknown	North Hatley, Québec, Canada
EF-12	Kennebec	Rivière-du-Loup, Québec, Canada
EF-81	Trent	Saint-Ambroise, Québec, Canada
<i>S. albidoflavus</i> ATCC 25422 ^T	NA ^c	Unknown
<i>S. aureofaciens</i> strains		
EF-31	Kennebec	Les Buissons, Québec, Canada
EF-38	Acadia Russet	Les Buissons, Québec, Canada
EF-42	Atlantic	Les Buissons, Québec, Canada
EF-62	Atlantic	Les Buissons, Québec, Canada
EF-69	Superior	La Pocatière, Québec, Canada
EF-70	Norland	La Pocatière, Québec, Canada
EF-74	Kennebec	La Pocatière, Québec, Canada
EF-111	Kennebec	Bonaventure, Québec, Canada
EF-112	Kennebec	Bonaventure, Québec, Canada
EF-115	Unknown	Inverness, Québec, Canada
EF-120	Unknown	Péribonka, Québec, Canada
EF-126	Kennebec	Saint-Ambroise, Québec, Canada
EF-130	Unknown	Péribonka, Québec, Canada
EF-138	Belmont	Saint-Léonard-d'Aston, Québec, Canada
<i>S. ipomoeae</i> 91-3	NA	Unknown
<i>S. scabies</i> strains		
EF-5	Unknown	Rivière-du-Loup, Québec, Canada
EF-35	Kennebec	Notre-Dame-de-la-Paix, Québec, Canada
EF-46	F84002	Les Buissons, Québec, Canada
EF-49	Unknown	Rivière du Loup, Québec, Canada
EF-54	Acadia Russet	Les Buissons, Québec, Canada
EF-63	Acadia Russet	Les Buissons, Québec, Canada
EF-64	Kennebec	Notre-Dame-de-la-Paix, Québec, Canada
EF-68	Kennebec	North Hatley, Québec, Canada
EF-84	Superior	Saint-Ambroise, Québec, Canada
ATCC 49173 ^T	Unknown	Maine

^a Strains EF-86, EF-87^T, and EF-88 were isolated from different tubers that came from the same field.

^b Strains EF-92 and EF-98 were isolated from different tubers that came from the same field.

^c NA, not applicable.

by using liquid CO₂, and evaporation coated with gold-palladium at 10 mA and 4×10^{-6} Pa with an Edwards sputter coater. The colonies were examined with a JEOL model 840A scanning electron microscope.

Sugar utilization was determined in a minimal medium containing (per liter) 2.64 g of (NH₄)₂SO₄, 2.38 g of KH₂PO₄, 5.65 g of K₂HPO₄ · 3H₂O, 1 g of MgSO₄ · 7H₂O, 6.4 mg of CuSO₄ · 5H₂O, 1.1 mg of FeSO₄ · 7H₂O, 7.9 mg of MnCl₂ · H₂O, 1.5 g of ZnSO₄ · 7H₂O, and 15 g of agar. Sugars were added to this medium at a final concentration of 1% (wt/vol) (12). The basal medium used to test utilization of different nitrogen sources contained (per liter) 10 g of glucose, 5 g of MgSO₄ · 7H₂O, 5 g of NaCl, 1 g of K₂HPO₄, 10 mg of FeSO₄ · 7H₂O, and 15 g of agar. Amino acids (1 g/liter) were added to the basal medium as sole nitrogen sources. Growth was scored after 7 days of incubation at 30°C (12).

Tests to evaluate the ability of the strains to hydrolyze xylan and arbutin were carried out as described by Lambert and Loria (12). Utilization of polygalacturonic acid was determined on a medium containing (per liter) 5 g of polygalacturonic acid, 6 g of Na₂HPO₄, 2 g of (NH₄)₂SO₄, 4 g of KH₂PO₄, 2 g of MgSO₄ · 7H₂O, 6.4 mg of CuSO₄ · 5H₂O, 1 g of yeast extract, 1 mg of FeSO₄ · 7H₂O, 1 mg of CaCl₂ and 10 g of agar (22).

The ability of bacteria to grow at pH 4.5 was tested on YME medium (16) at 30°C. The inhibitory effects of NaCl (4, 7, 10, and 13%), thallous acetate (10 and 100 µg/ml), crystal violet (0.5 µg/ml), phenol (0.1%), penicillin G (10 IU/ml), oleandomycin (100 µg/ml), and streptomycin sulfate (20 µg/ml) on bacterial growth were determined on Bennett medium modified as proposed by Lambert

and Loria (12). Production of melanoid pigment was detected on a peptone-yeast extract-iron agar (PYI) (18).

A diaminopimelic acid analysis was carried out by using the procedure of Becker et al. (3). Isomers were separated by thin-layer chromatography as described by Stanek and Roberts (20).

Genetic characterization. Procedure 3 of Hopwood et al. (8) was used to isolate total DNAs from *Streptomyces* strains. After genomic DNA was dialyzed against 0.1× SSC (17) (1× SSC is 0.15 M NaCl plus 0.015 M sodium citrate) the G+C content of the genome was determined by the method of Ulitzur (21) by using salmon sperm DNA as the standard. DNA-DNA hybridization studies were performed as described by Stall et al. (19), as modified by Paradis et al. (15).

RESULTS

Phenotypic characterization of the deep-pitted-scab-inducing bacteria. The eight deep-pitted-scab-inducing streptomycetes which we studied were characterized by a gold to light brown mycelium on YME medium. The aerial mycelium contained a white mass of spores borne in flexuous chains. The spores were cylindrical, smooth, 0.87 to 1.08 µm long, and 0.5 to 0.63 µm in diameter (Fig. 2). These strains did not produce

TABLE 2. Phenotypic comparison of strains of the plant-pathogenic species *S. caviscabies*, other plant-pathogenic species, and *S. albidoflavus* (cluster 1 of Williams et al.)

Characteristic	<i>S. caviscabies</i> strains ^a	<i>S. acidiscabies</i> strains ^b	<i>S. albidoflavus</i> strains ^c	<i>S. aureofaciens</i> strains ^d	<i>S. ipomoeae</i> 91-3	<i>S. scabies</i> strains ^e
Colony color on YME medium	Gold to light brown	Gold to light brown	Gold to light brown	Bright yellow	Gold	Tan to brown
Spore color	White	White	Yellow-brown	Gray	Blue	Grey
Spore ornamentation	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
Spore chain morphology	Flexuous	Flexuous	Rectiflexuous	Flexuous	Spiral	Spiral
Melanin production on PYI medium	— ^f	—	—	—	—	+
Production of diffusible pigment	V	+	—	—	+	—
Utilization of carbon sources						
L-Arabinose	—	+	V	+	+	+
D-Fructose	—	+	+	+	+	+
D-Mannitol	—	V	+	+	+	+
Raffinose	+	V	V	+	+	V
Rhamnose	—	+	V	+	+	V
Sucrose	—	+	V	+	+	V
D-Xylose	—	+	+	+	+	V
Utilization of nitrogen sources						
L-Proline	+	+	V	+	+	+
L-Methionine	+	+	V	+	+	V
Hydrolysis of:						
Arbutin	—	—	+	V	+	V
Polygalacturonic acid	—	—	V	—	+	V
Xylan	+	+	—	V	—	V
Growth at pH 4.5	—	+	—	—	+	—
Growth in the presence of:						
NaCl (4%)	+	V	+	+	+	V
NaCl (7%)	V	—	V	—	—	—
NaCl (10%)	—	—	V	—	—	—
NaCl (13%)	—	—	—	—	—	—
Thallous acetate (10 µg/ml)	+	V	+	—	—	—
Thallous acetate (100 µg/ml)	V	—	—	—	—	—
Crystal violet (0.5 µg/ml)	V	V	V	—	+	V
Phenol (0.1%)	+	V	V	V	+	V
Penicillin (10 IU/ml)	+	+	V	+	+	+
Oleandomycin (100 µg/ml)	V	—	V	V	—	V
Streptomycin (20 µg/ml)	+	+	V	—	+	—

^a Strains EF-83, EF-86, EF-87^T, EF-88, EF-92, EF-98, EF-104, and EF-123 were studied.^b Strains EF-8, EF-12, EF-81, and ATCC 49003^T were studied. On the basis of the morphological and physiological properties proposed by Lambert and Loria (11), the level of similarity between the strains from Québec and the American strains was 88%.^c Data for cluster 1 strains from reference 22.^d Strains EF-31, EF-38, EF-41, EF-42, EF-62, EF-69, EF-70, EF-74, EF-111, EF-112, EF-115, EF-120, EF-126, EF-130, and EF-138 were studied.^e Strains EF-5, EF-35, EF-46, EF-49, EF-54, EF-63, EF-64, EF-68, and EF-84 were studied. On the basis of the morphological and physiological properties proposed by Lambert and Loria (12), the level of similarity between the strains from Québec and the American strains was 80%.^f —, negative; +, positive; V, between 20 and 90% of the strains were positive.

melanin. All of the strains grew on proline or methionine as a sole nitrogen source and hydrolyzed xylan but no polygalacturonic acid and arbutin. Raffinose was the only International *Streptomyces* Project sugar utilized. Most strains grew in the presence of 4% NaCl but not in the presence of an NaCl concentration of 7% or higher. All of the strains grew in the presence of 0.1% phenol, 10 IU of penicillin per ml, 10 µg of thallous acetate per ml, and 20 µg of streptomycin sulfate per ml. Bacterial growth was inhibited at pH 4.5 on YME medium. Some strains produced a diffusible pigment on YME medium. Strains EF-92 and EF-98 produced a red pigment, whereas strain EF-104 produced a yellow pigment (Table 2). The cell walls of the deep-pitted-scab-inducing strains contained LL-diaminopimelic acid.

Genetic characterization. DNA from deep-pitted-scab-inducing strain EF-87^T was hybridized with DNAs from the seven other deep-pitted-scab-inducing strains characterized in this study. The levels of relatedness between strain EF-87^T DNA and the DNAs of the other deep-pitted-scab-inducing strains ranged from 73 to 100% (Table 3). The levels of relat-

edness between the genomic DNA of deep-pitted-scab-inducing strain EF-87^T and the genomic DNAs of representatives of *S. acidiscabies*, *S. aureofaciens*, *S. ipomoeae*, and *S. scabies* were low (between 12 and 33%). Strain EF-87^T also differed genetically from *S. albidoflavus* ATCC 25422^T (level of DNA relatedness, 17%). The guanine-plus-cytosine (G+C) content of strain EF-87^T DNA was 71 ± 3 mol%.

DISCUSSION

In a previous study, in which numerical analysis was used to compare the deep-pitted-scab-inducing strains with members of the *Streptomyces* clusters defined by Williams et al. (22), Faucher et al. established that the level of similarity between the deep-pitted-scab-inducing strains and strains belonging to cluster 1 of Williams et al. (*S. albidoflavus*) was relatively high (75.8%) (5). However, according to the criteria of Williams et al. (22), this level of similarity is not high enough to classify these two groups in the same cluster. The results of the DNA-DNA hybridization study which we conducted also confirmed

FIG. 1. Typical deep-pitted scab lesions on a potato tuber. Note the presence of the white *Streptomyces* spores inside the lesions.

that these two groups of strains should not be included in the same species. Indeed, the level of complementarity between *S. albidoflavus* ATCC 25422^T DNA and DNA from deep-pitted-scab-inducing strain EF-87^T was only 17%.

The deep-pitted-scab-inducing strains also differ from other phytopathogenic streptomycetes. The levels of DNA relatedness between the deep-pitted-scab-inducing strains and other plant-pathogenic streptomycetes did not exceed 33% (Table 3). The deep-pitted-scab-inducing organisms also differed mor-

TABLE 3. Levels of relatedness between *S. caviscabies* EF-87^T DNA and DNAs of other *S. caviscabies* strains and strains belonging to other *Streptomyces* species

Strain	% Hybridization with DNA from strain EF-87 ^T
<i>S. caviscabies</i> strains	
EF-83	73
EF-86	93
EF-87 ^T	100
EF-88	100
EF-92	96
EF-98	76
EF-104	100
EF-123	100
<i>S. acidiscabies</i> strains	
ATCC 49003 ^T	24
EF-81	0
<i>S. albidoflavus</i> ATCC 25422 ^T	17
<i>S. aureofaciens</i> EF-38	12
<i>S. ipomoeae</i> 91-3	22
<i>S. scabies</i> strains	
ATCC 49173 ^T	0
EF-54	24
EF-35	33

FIG. 2. Scanning electron micrograph of smooth spores of strain EF-87^T. Bar = 1 μ m.

phologically and physiologically from *S. albidoflavus*, *S. aureofaciens*, *S. ipomoeae*, and *S. scabies*.

The morphological characteristics of the deep-pitted-scab-inducing bacteria were similar to those of *S. acidiscabies*, but these bacteria differed in the ability to catabolize sugars and in sensitivity to pH 4.5 (Table 2).

The eight deep-pitted-scab-inducing strains formed a homogeneous group, as shown in a previous study in which the fatty acid and protein profiles of these organisms were compared (5). Furthermore, strain EF-87^T exhibited DNA reassociation values of 74% or more with the seven other deep-pitted-scab-inducing strains, suggesting that these organisms should be included in the same bacterial species.

The eight deep-pitted-scab-inducing strains described in this study all originated from Québec (Canada), where they were isolated from deep-pitted lesions on potato tubers of different cultivars (Fig. 1). The pathogenicity of these strains has been evaluated on two potato cultivars, Conestoga and Green Mountain (6), and also on carrots, radishes, and parsnips (6a). The strains which we studied induced severe lesions on potato cultivars Conestoga and Green Mountain compared with the symptoms induced by *S. scabies* strains tested under the same conditions. However, they induced only mild symptoms on carrots, radishes, and parsnips. On potatoes, as well as on other crops, more severe symptoms were obtained when the pathogenicity tests were performed in sand (6).

S. scabies and *S. caviscabies* have never been isolated from the same tuber. This suggests that the potato scab diseases caused by *S. scabies* and *S. caviscabies* may occur under different environmental conditions. Most *S. caviscabies* strains were isolated from tubers produced in irrigated soils.

Description of *Streptomyces caviscabies* sp. nov. *Streptomyces caviscabies* (ca.vi.sca'bies. L. adj. *cavus*, hollow; L. n. *scabies*, mange; *caviscabies*, referring to the ability of the organism to cause deep-pitted scab of potatoes). The eight deep-pitted-scab-inducing strains are characterized by a gold mycelium on YME medium and a white mass of spores borne in flexuous chains. The cylindrical, smooth spores are 0.87 to 1.08 by 0.5 to 0.63 μ m (Fig. 2). The cell walls contain LL-diaminopimelic acid, and the DNA G+C content is 71 mol%. The strains do

not produce melanin. All strains grow on proline or methionine as a sole nitrogen source. They utilize raffinose as a sole carbon source. All strains grow in the presence of 4% NaCl, 0.1% phenol, 10 IU of penicillin per ml, 10 µg of thallos acetate per ml, and 20 µg of streptomycin sulfate per ml. Growth is inhibited at pH 4.5 (Table 2). Strain EF-87 (= ATCC 51928) is the type strain of *S. caviscabies*.

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