Streptomyces scabies sp. nov., nom. rev.†

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Revival of the name *Streptomyces scabies* is proposed for the predominant species causing common scab of potato. Common scab strains from the northeastern United States, Atlantic Canada, and Hungary were differentiated by a phenotypic analysis of 42 criteria from six atypical pathogen strains, three saprophytic streptomycetes isolated from scab lesions, and reference strains of *Streptomyces griseus* and *Streptomyces tendae*. The 12 *S. scabies* strains formed a homogeneous group characterized by smooth grey spores borne in spiral chains, melanin production, and usage of all International *Streptomyces* Project sugars. Most *S. scabies* isolates did not degrade xanthine and were susceptible to 25 µg of oleandomycin per ml, 10 IU of penicillin G per ml, 20 µg of streptomycin per ml, 10 µg of thallous acetate per ml, and 0.5 µg of crystal violet per ml. The type strain of *S. scabies* is strain RL-34 (= ATCC 49173).

Scab diseases of potatoes (*Solanum tuberosum*), which are characterized by deep or superficial, corky lesions, are incited by streptomycetes that historically have been referred to as "*Streptomyces scabies*." However, certain scab pathogens may belong in other species. Acid-tolerant strains form the distinct species *Streptomyces acidiscabies* (15). Additional isolates, which are usually less virulent, have been placed in *Streptomyces griseus* (4, 6, 11), *Streptomyces olivaceus* (11), *Streptomyces aureofaciens* (4), *Streptomyces flaveolus* (17), or other species (1, 17). Organisms causing common scab were first isolated in 1890 in Connecticut by Thaxter (29, 30), who named them *Oospora scabies* and characterized the species as a melanin producer with grey spores borne in spiral chains. A type culture was not maintained. The species was renamed *Actinomyces scabies* by Güssow (8) and *Streptomyces scabies* by Waksman and Henrici (32). In 1961, Waksman (31) redescribed the species, erroneously designating strain IMRU 3018 (= ISP 5078) as the neotype strain (5, 13). This choice was made apparently on the basis of pathogenicity because strain IMRU 3018 lacks spiral spore chains and melanin production. Strain IMRU 3018 represented *S. scabies* in the International *Streptomyces* Project (ISP) of the 1960s (22–25) and in all of taxonomic keys derived from the ISP (12, 18, 27). A disproportionate number of "*S. scabies*" reference strains isolated from potatoes have subsequently been placed in the other species mentioned above. For these reasons, the species is considered invalid and was listed in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (3), as species incertae sedis ("type strain not extant, many taxonomically different strains available"). In 1979 Elesaway and Szabó (5) recognized this situation and reevaluated the species, offering an acceptable neotype strain (strain ATCC 33282) and expanding the original description to include smooth spores and use of all ISP sugars. However, the species did not appear on the Approved Lists of Bacterial Names, which was published shortly thereafter (26). The purposes of this paper are to demonstrate that the majority of pathogenic streptomycetes isolated from potatoes form a distinct species consistent with the original description, to provide phenotypic criteria which differentiate this species from other organisms with which it

has been confused, and to revive as a valid name the universal designation for this organism, *Streptomyces scabies*.

MATERIALS AND METHODS

Strains. The following cultures were investigated: 11 common scab strains (strains RL-34^T [T-type strain], RL-39, RL-42, RL-43, RL-70, RL-78, RL-102, RL-131, RL-151, RL-174, and RL-232, which were isolated by R.L. in Maine, New Brunswick [Canada], New York, and West Virginia), whose pathogenicity was confirmed on tubers produced from stem cuttings (16); 3 strains identified as "*S. scabies*" ATCC 33282 (5), ATCC 15485 (Takeda Chemical Co., Ltd.), and ISP 5078 (= IMRU 3018) (31); "*Streptomyces griseus* subsp. *scabies*" ATCC 3352, ATCC 10246, and IMRU 3029 (6); *Streptomyces setonii* ATCC 25497^T, a weak scab pathogen (17) thought to be *S. griseus* by Hütter (11); 3 saprophytes isolated from scab lesions (*Streptomyces sampsonii* ATCC 25495^T [17], DHL-1, and DHL-2); *Streptomyces tendae* ATCC 19812^T, which is considered similar in appearance to certain common scab strains (11); and *S. griseus* ATCC 10137, ATCC 15395, and ATCC 23345^T. (Names in quotation marks are not on the Approved Lists of Bacterial Names [26].)

Carbon source utilization. Sugars were filter sterilized and added to basal agar medium at concentrations of 1.0% (wt/vol). The basal medium contained (per liter) 2.64 g of (NH₄)₂SO₄, 2.38 g of KH₂PO₄, 5.65 g of K₂H₂PO₄ · 3H₂O, 1.00 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 15.0 g of agar; the pH was 6.9 (20).

Nitrogen source utilization. The basal medium for nitrogen source utilization tests contained (per liter) 1 g of amino acid, 10 g of glucose, 5 g of MgSO₄ · 7H₂O, 5 g of NaCl, 10 mg of FeSO₄ · 7H₂O, 1 g of K₂HPO₄, and 12 g of agar; the pH was 7.4 (34).

Antibiotic activity. The toxicities of antibiotics and other inhibitory compounds were determined on modified Bennett agar, which contained (per liter) 1 g of beef extract, 1 g of yeast extract, 2 g of tryptone, 10 g of glycerol, and 15 g of agar. The toxic compounds which we used were selected from those used by Williams et al. (34) and were chosen for their potential to differentiate species or larger groups of streptomycetes.

Wall composition. The diaminopimelic acid isomer type of

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strains RL-39 and RL-151 was determined by the method of Becker et al. (2).

Degradative activity. Xanthine and xylan were added to modified Bennett agar at a rate of 4 g/liter. Soluble starch was added at a concentration of 10 g/liter and was developed after 7 days with the Gram iodine solution. Polygalacturonic acid degradation was observed on modified Hankin pectin medium (34) and on Hildebrand medium at pH 7.3 (9). Arbutin degradation was determined on the medium described by Kutzner (13), using an arbutin-free control.

pH sensitivity. The minimum pH that allowed growth was determined on media containing (per liter) 10.0 g of dextrose, 0.5 g of L-asparagine, 15.0 g of agar, and 40 mM phosphate as the monopotassium, dipotassium, and disodium salts to adjust the pH in 0.5-U increments from pH 3.5 to 6.0 (33).

Inoculation of media. Spores were scraped from salts-starch plates, suspended in 0.001% Triton X-100, filtered through sterile glass wool, washed, and suspended in water. This suspension was spread onto agar media in a single line with a micropipette.

Pigment production and color and morphology. The presence of melanoid pigments on tyrosine and peptone yeast extract iron agar media (21) was recorded. Spore mass and diffusible pigment colors were described simply. The standards used for spore chain morphology were those described by Shirling and Gottlieb (21).

Taxonomy. Strain characteristics were given values of 100 if they were positive or 0 if they were negative. Spore color (grey or not grey) and chain type (spiral or flexuous) were also given values of 0 or 100. These sets of values were averaged by trait to form species composites for the 12 authentic *S. scabies* strains (Loria strains and strain ATCC 33282) and for the three *S. griseus* strains. These composites and the remaining individual strains were then compared with each other in all combinations. Differences in values for each trait were added and divided by the total number of traits. The resulting number was subtracted from 100 to produce values for percentage of similarity. Individual strains within the *S. scabies* and *S. griseus* groups were likewise compared with their group means, and the resulting numbers were averaged to provide a similarity value, which reflected homogeneity within species. In the same manner, species composites or individual strains were compared with corresponding data for 19 major and 2 minor cluster groups of Williams et al. (34). In the numerical taxonomy of the genus *Streptomyces* of Williams et al. (34), strains were organized into clusters whose members were similar to each other in at least 77.5% of the 139 criteria used. The major clusters contained 6 to 71 individual strains. The percentages of strains within the individual cluster groups of Williams et al. having the same characteristic as our individual strains (or composites) were determined for each trait and strain-cluster combination. These percentages were then averaged for each strain-cluster comparison over the ca. 50 traits common to both studies. This produced percentage averages which indicated the most appropriate placement of our strains in the subgeneric classifications derived by Williams et al.

RESULTS

Morphological characteristics. On standard agar media, the aerial mycelium of *S. scabies* cultures was sympodially branched and formed spore chains which were generally loose spirals (Fig. 1). The spores of all strains were grey. Fragmentation of the substrate mycelium, sporangium or

FIG. 1. Sporulating aerial mycelium of strain ATCC 49173^T (= RL-34^T): spiral spore chains on inorganic salts starch agar. Scanning electron micrograph. Bar = 10 μ m.

sclerotium formation, and flagellated spores were not observed. Spores were smooth and cylindrical (0.5 by 0.9 to 1.0 μ m) (Fig. 2). The cell walls of representative strains RL-39 and RL-151 contained the LL-diaminopimelic acid isomer.

Pigments. All *S. scabies* strains produced melanin on tyrosine agar and a black pigment on peptone yeast extract

FIG. 2. Smooth spores of strain ATCC 49173^T (= RL-34^T) on inorganic salts starch agar. Bar = 5 μ m.

TABLE 1. Characteristics of *S. scabies* and other *Streptomyces* species and strains^a

Characteristic	<i>S. scabies</i> group	Saprophyte strain 1	Saprophyte strain 2	<i>S. sampsonii</i> ATCC 25495 ^r	<i>S. setonii</i> ATCC 25497 ^r	Strain ATCC 10246	Strain ATCC 3352	Strain IMRU 3029	Strain IMRU 3018	Strain ATCC 15485	<i>S. griseus</i> group	<i>S. tendae</i> ATCC 19812 ^r
Spore color ^b	G	G	G	G	G	G	G	G	G	G	G	G
Chain morphology ^c	S	S	S	RF	RF	RF	RF	RF	RF	RF	RF	RF
Spore ornamentation ^d	Sm	ND	ND	Sm	Sm	ND	ND	ND	Sm	ND	Sm	Sm
Melanin on tyrosine agar	+	+	+	-	-	-	-	-	-	-	-	-
Pigment on PYI ^f	+	+	+	-	-	-	-	-	-	-	-	-
Diffusible pigment ^b	-	-	-	-	-	-	-	-	-	-	-	Y/O
Carbon usage												
L-Arabinose	+	+	+	+	+	+	+	-	+	+	67 ^g	+
D-Fructose	+	+	+	+	+	+	+	+	+	+	+	+
D-Glucose	+	+	+	+	+	+	+	+	+	+	+	+
D-Mannitol	+	+	+	+	+	+	+	+	+	+	+	+
Raffinose	+	-	+	-	-	-	-	-	-	-	-	-
Rhamnose	+	+	+	-	+	-	+	+	+	-	-	+
Sucrose	+	+	+	-	-	+	+	+	-	-	67 ^g	+
D-Xylose	+	+	+	+	+	-	+	+	+	+	+	+
meso-Inositol	+	+	+	-	+	-	-	+	-	-	-	+
Nitrogen usage												
L-Hydroxyproline	+	+	+	-	+	-	-	-	-	+	+	+
L-Methionine	+	+	+	+	+	+	+	-	+	+	-	-
Degradation of:												
Arbutin	P ^h	P	P	+	+	+	+	+	+	+	+	-
Polygalacturonate	+	+	+	-	+	-	+	+	+	+	67 ^g	+
Xanthine	-	+	+	+	+	+	+	-	+	+	+	-
Xylan	+	+	+	-	+	+	+	+	+	+	-	+
Minimum growth pH	5.0	4.0	4.0	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	4.5
Growth with:												
5% NaCl	83 ^g	+	+	+	+	+	+	+	+	+	+	+
6% NaCl	50 ^g	+	+	+	+	+	+	+	+	+	+	+
7% NaCl	-	+	+	+	+	+	+	+	+	+	67 ^g	+
Tellurite (10 µg/ml)	83 ^g	+	+	+	+	+	+	+	+	+	+	+
Tellurite (100 µg/ml)	50 ^g	-	-	+	+	+	+	-	+	+	+	+
Thallium (10 µg/ml)	8 ^g	+	+	+	+	+	-	+	+	+	+	+
Thallium (100 µg/ml)	-	-	-	-	+	+	-	-	-	-	67 ^g	-
Crystal violet (0.5 µg/ml)	-	+	+	+	+	-	+	-	+	+	+	+
Phenol (0.1%)	-	+	+	+	+	+	+	+	+	-	+	+
Penicillin (10 IU/ml)	-	+	+	+	+	+	+	+	+	+	+	+
Oleandomycin (25 µg/ml)	17 ^g	+	+	+	+	+	+	+	+	+	+	+
Oleandomycin (100 µg/ml)	-	+	+	+	+	+	+	+	-	+	+	+
Streptomycin (20 µg/ml)	-	+	-	+	+	+	-	+	-	-	+	-

^a All strains used salicin as a sole carbon source, used L-histidine, L-phenylalanine, or L-valine as a sole nitrogen source, and degraded starch. No strain degraded hippurate or grew on media containing 100 µg of sodium azide per ml or 1 µg of crystal violet per ml.

^b G, Grey; R, red; W, white; Y, yellow; O, orange.

^c S, Spiral; RF, rectiflexuous.

^d Sm, Smooth; ND, not determined.

^e +, Positive reaction; -, negative reaction.

^f PYI, Peptone yeast extract iron agar.

^g Percentage of strains in the composite having a positive reaction.

^h P, Reaction obscured by pigment.

iron agar (Table 1). *S. tendae* ATCC 19812^r produced an orange or yellow pH-sensitive pigment, and the mycelia of other strains were tinted yellow on some media.

Physiological characteristics. Within the collection, *S. scabies* strains were unique or nearly so in their use of raffinose, melanin production, inability to degrade xanthine, and susceptibility to 10 IU of penicillin G per ml, 25 µg of oleandomycin per ml, 20 µg of streptomycin per ml, 10 µg of thallous acetate per ml, 0.5 µg of crystal violet per ml, and 1,000 µg of phenol per ml. No strain differed from the most typical

responses by more than two traits. As an independent comparison, nine pathogenicity-tested *S. scabies* strains isolated in Wisconsin by R.L. were tested on several of these media. None grew on crystal violet or streptomycin agar, one grew with thallous acetate at a concentration of 10 µg/ml, two degraded xanthine, four grew on medium containing penicillin G at a concentration of 10 IU/ml, and four grew on medium containing 5 µg of oleandomycin per ml. Raffinose, a component of hemicellulose, was used only by *S. scabies* and by a single saprophyte (strain DHL-2).

TABLE 2. Levels of similarity of *Streptomyces* sp. strains or species composite groups with each other and with selected cluster groups of Williams et al.^a

Species, strain, or cluster group ^b	% Similarity with:											
	<i>S. scabies</i> group	Saprophyte strain 1	Saprophyte strain 2	<i>S. sampsonii</i> ATCC 25495 ^T	<i>S. setonii</i> ATCC 25497 ^T	Strain ATCC 10246	Strain ATCC 3352	Strain IMRU 3029	Strain IMRU 3018	Strain ATCC 15485	<i>S. griseus</i> group	<i>S. tendae</i> ATCC 19812 ^T
<i>S. scabies</i> group	96	73	78	55	65	58	70	68	68	66	58	68
Saprophyte strain DHL-1	73	100	95	71	83	71	78	78	80	74	74	78
Saprophyte strain DHL-2	78	95	100	67	78	67	78	73	80	74	69	78
<i>S. sampsonii</i> ATCC 25495 ^T	55	71	67	100	84	86	84	75	86	78	87	72
<i>S. setonii</i> ATCC 25497 ^T	65	83	78	84	100	84	86	81	88	80	86	84
ATCC 10246	58	71	67	86	84	100	84	79	81	73	84	72
ATCC 3352	70	78	78	84	86	84	100	81	93	80	81	84
IMRU 3029	68	78	73	75	81	79	81	100	79	71	78	84
IMRU 3018	68	80	80	86	88	81	93	79	100	87	81	81
ATCC 15485	66	74	74	78	80	73	80	71	87	100	77	78
<i>S. griseus</i> group	58	74	69	87	86	84	81	78	81	77	95	79
<i>S. tendae</i> ATCC 19812 ^T	68	78	78	72	84	72	84	84	81	78	79	100
Cluster group 1 (<i>S. albidoflavus</i>)	61	65	65	74	72	71	71	70	76	70	75	66
Cluster group 3 (<i>S. atrolivaceus</i>)	59	59	60	69	68	63	72	66	74	69	68	62
Cluster group 5 (<i>S. exfoliatus</i>)	67	64	65	65	67	63	66	62	70	71	69	63
Cluster group 6 (<i>S. violaceus</i>)	66	66	70	63	63	60	61	59	65	65	66	58
Cluster group 10 (<i>S. fulvissimus</i>)	62	66	69	69	67	66	64	64	67	66	72	63
Cluster group 12 (<i>S. rochei</i>)	65	67	69	68	66	67	70	69	72	63	69	65
Cluster group 15 (<i>S. chromofuscus</i>)	70	61	64	64	62	61	63	63	67	66	62	61
Cluster group 18 (<i>S. cyaneus</i>)	73	69	72	59	60	59	65	62	64	59	61	60
Cluster group 19 (<i>S. diastaticus</i>)	71	66	68	64	63	61	68	66	67	62	65	64
Cluster group 21 (<i>S. griseoruber</i>)	69	68	70	63	67	62	70	68	71	64	66	70
Cluster group 23 (<i>S. microflavus</i>)	71	63	66	59	60	56	67	62	65	58	62	58

^a The table includes cluster groups (34) which exhibit at least 70% similarity with one or more of the strains or species which we investigated.

^b *S. scabies*, *S. setonii*, and strains ATCC 10246, ATCC 3352, IMRU 3029, and IMRU 3018 were pathogenic when they were isolated; strains DHL-1 and DHL-2 and *S. sampsonii* are nonpathogenic organisms that were isolated from scab lesions; the pathogenicity status of "*S. scabies*" ATCC 15485 is not known; and *S. griseus* and *S. tendae* are standards included for comparison. In the numerical taxonomy study of Williams et al. (34), *S. sampsonii* ATCC 25495^T, *S. setonii* ATCC 25497^T, and the *S. griseus* group were placed in cluster group 1, strain IMRU 3018 was placed in cluster group 3, and *S. tendae* ATCC 19812^T was placed in cluster group 12.

Inositol was not generally used by cluster 1 strains (*S. griseus*, "*S. griseus* subsp. *scabies*," *S. setonii*, *S. sampsonii*, and strain IMRU 3018). Xylan and pectin, which are cell wall components, were generally degraded by pathogenic strains.

S. scabies neotype strain RL-34 (= ATCC 49173), which was isolated in 1984 in central New York from the potato variety 'Katahdin', was typical of the majority of *S. scabies* strains (Table 1). For variable traits, growth occurred on media containing 6% NaCl or 100 µg of potassium tellurite per ml. No growth occurred on media containing 10 µg of thallous acetate per ml or 25 µg of oleandomycin per ml.

Taxonomy. The levels of similarity of individual strains or composite groups to each other and to the cluster groups of Williams et al. (34) are shown in Table 2. These data indicate that *S. scabies* strains are not closely related to any of the other strains. The similarity of this species to cluster groups 18, 19, and 23 (*Streptomyces cyaneus*, *Streptomyces diastaticus*, and *Streptomyces microflavus*) confirms the placement of *S. scabies* in the Diastochromogenes group by Elesway and Szabó (5), as the five species (*Streptomyces naya-gawaensis*, *Streptomyces bottropensis*, *Streptomyces diastochromogenes*, *Streptomyces eurythermus*, and *Streptomyces griseosporus*) which these authors considered

similar to *S. scabies* were classified by Williams et al. into the three cluster groups mentioned above. Nonpathogenic strains consistent with *S. scabies* have been isolated (5, 14). The relationship of the nonpathogens in the Diastochromogenes group to *S. scabies* will be determined by a deoxyribonucleic acid homology analysis in a future study.

The other pathogenic strains fell into a group with similarities to cluster group 1 (*Streptomyces albidoflavus*) ≥70% (Table 2). These strains were not as homogeneous as the *S. scabies* strains, nor did they reduce to distinct subgroups. This may indicate that atypical scab-causing strains are taxonomically diverse and, by inference, that there are few physiological requirements for evolution to pathogenicity. Alternately, trivial differences may be obscuring similarities within a group which has diverged from a single pathogenic population. In the past, most investigators encountering such diverse nontypical strains have placed them into multiple species (4, 10, 17). The 81 and 87% levels of similarity of the three *S. griseus* strains to strain IMRU 3018 and *S. sampsonii* ATCC 25495^T, respectively (Table 2), may be related to deoxyribonucleic acid homology data (19), which indicate little relationship at the species level for these two strains and *S. griseus* ATCC 23345^T (42% homology in both cases). The three "*S. griseus* subsp. *scabies*" strains (strains

ATCC 10246, ATCC 3352, and IMRU 3029) have an average level of phenotypic similarity of 81% to the three *S. griseus* strains and are probably related to *S. griseus* at the group level rather than the species level. The average level of similarity of the non-*S. scabies* pathogenic strains to *S. setonii* ATCC 25497^T is slightly higher than the level of similarity to *S. griseus* (85 versus 81%).

DISCUSSION

Following original studies of Thaxter, the pathologists recognized organisms fitting his description of *S. scabies* as the major incitants of common scab and, in most instances, differentiated pathogenic isolates which did not resemble *S. scabies* (4, 10, 14, 16, 27). The only recent exception occurred in a study (1) in which neither the "*S. scabies*" reference strain (strain ATCC 3352) nor the reference strain on which the taxonomic key (18) was based (strain IMRU 3018) was actually *S. scabies*. A virulent isolate identified in this case as *S. diastatochromogenes* was presumably *S. scabies*, as the criteria for *S. diastatochromogenes* in the key used (18) are identical to those for *S. scabies* (grey smooth spores in spirals, melanin produced, all ISP sugars used). These primary characteristics are supplemented in our description of the species by secondary characteristics, including lack of xanthine degradation and the susceptibility of *S. scabies* to a number of toxic compounds. Although melanin production is consistently associated with pathogenicity (28), it is neither essential (7) nor invariable (5) in *S. scabies* and might also be considered secondary.

In our opinion, the original descriptions of *S. scabies* (29, 30) are correct and have been consistently substantiated by those workers familiar with phytopathogenic streptomycetes (4, 5, 7, 10, 14, 17, 28). Strains belonging to this species form a coherent group and are easily distinguishable from other pathogenic strains by numerous characteristics. Failure to disregard strains placed in the species only on the basis of their pathogenicity and errors made in assigning a neotype resulted in exclusion of the species from the Approved Lists of Bacterial Names. We believe that the early discovery of *S. scabies* and the universal recognition of the major scab pathogen by this name make it important to revive the species as *Streptomyces scabies*, designating Thaxter as the original authority.

Streptomyces scabies sp. nov., nom. rev. *Streptomyces scabies* (sca'bies. L. n. *scabies*, mange, the name originally given by Thaxter [29] in reference to the ability of this organism to cause potato scab). Spores are 0.5 by 0.9 to 1.0 μ m, smooth, and grey and are borne in mature spiral chains containing 20 or more spores. Melanin is produced on tyrosine agar and peptone iron agar, and growth does generally not occur below an agar medium pH of 5. All ISP sugars are used (i.e., L-arabinose, D-fructose, D-glucose, D-mannitol, rhamnose, sucrose, D-xylose, and raffinose). Most strains which have been studied do not degrade xanthine and are susceptible to 20 μ g of streptomycin per ml and 0.5 μ g of crystal violet per ml. The guanine-plus-cytosine content of this species is 71 mol%. *S. scabies* differs from other virulent potato pathogens in having spiral spore chains.

The species is placed in the genus *Streptomyces* as it possesses morphology typical of this genus and cell walls with the LL-diaminopimelic acid isomer. The type strain of *S. scabies* is strain RL-34 (= ATCC 49173). This strain was isolated in central New York in 1984.

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