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Characterization of *Streptomyces* Species Causing Potato Scab in Korea: Distribution, Taxonomy, and Pathogenicity

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From 1996 to 1999, potato-growing areas in Korea were surveyed for identification and distribution of potato scab pathogens. Potato scab was widely distributed in the mass cultivation areas, especially in Jeju island, southern areas of Chonnam and Gyounggi provinces, and the alpine area of Gangwon province. Jeju island was the most affected area by this disease. A total of 55 *Streptomyces* strains were isolated from potato scab lesions, among which 40 strains were pathogenic on progeny tubers. Among the pathogenic strains, 21 strains were identified as previously described *S. scabies*, 7 strains as *S. turgidiscabies*, and 5 strains as *S. acidiscabies*, while 7 strains were observed as having distinct phenotypic properties. These strains were classified into six distinct clusters based on phenotypic characteristics and selected representative strains for each cluster. *S. scabies* (S33) had grey spores in a spiral chain. Meanwhile, *S. turgidiscabies* (S27) had grey spores, *S. acidiscabies* (S71) had white spores, *S. luridiscabiei* (S63) had yellow-white spores, *S. puniciscabiei* (S77) had purple-red spores, and *S. niveiscabiei* (S78) had thin and compact white spores, all in a rectiflexuous chain. Pathogenicity was determined by the production of thaxtomin A and homologs of *necI* and ORF*tnp* genes. In TLC, representative strains S33, S27, S71, S63, S77, and S78 produced a yellow band that co-migrated with the authentic thaxtomin A. However, thaxtomin A was not detected in chloroform extracts from oatmeal broth culture and slice tuber tissue of *S. luridiscabiei* (S63) and *S. puniciscabiei* (S77) by HPLC analysis. In addition, no homologs of *necI* and ORF*tnp* genes in *S. acidiscabies* (S71), *S. luridiscabiei* (S63), *S. puniciscabiei* (S77), and *S. niveiscabiei* (S78) were detected by PCR and Southern hybridization analysis.

Keywords : Epidemics, phylogenetic analysis, phytotoxin, *Solanum tuberosum*, 16S rRNA sequences.

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Hundreds of soil-borne, saprophytic streptomycetes have been described, while relatively few species are known pathogens of plants (Loria et al., 1997). Hence, pathogenicity is considered a rare phenotype in the genus *Streptomyces*. *Streptomyces* spp. are filamentous, gram-positive prokaryotes that produce an array of agriculturally and clinically important secondary metabolites. Members of this genus have a complex morphology that produces spores to aid their dispersal. Spore chains are produced through fragmentation of aerial hyphae that form on the substrate mycelium. The shape of the spore chains, which may be straight, spiral or wavy, is an important taxonomic characteristic. The color of spores on mass sporulation is also a critically important taxon (Goyer et al., 1996; Locci, 1994; Loria et al., 1997). In addition, *Streptomyces* spp. are phenotypically and genetically complex, which are based on fatty acid profiles (Ndowora et al., 1996; Paradis et al., 1994), inhibitory reaction (Ndowora et al., 1996), DNA-DNA relatedness (Healy and Lambert, 1991; Miyajima et al., 1998), and ribosomal sequence analysis (Bouchek-Mechiche et al., 2000; Takeuchi et al., 1996).

Several pathogenic species of potato scab have been described to date. *Streptomyces scabies* was first described by Thaxter (1892) and re-proposed by Lambert and Loria (1989a) as the predominant species causing common scab of potatoes. A distinct acid-tolerant species, *S. acidiscabies*, induces symptoms similar to *S. scabies* (Lambert and Loria,

1989b). *S. turgidiscabies* has been described in Japan (Miyajima et al., 1998). *S. europaeiscabiei* and *S. stelliscabiei* were reported to cause common scab of potato, while *S. reticuliscabiei* was identified as a causal pathogen of netted scab in France (Bouchek-Mechiche et al., 2000).

This paper discuss the characterization of major scab pathogens found in Korea based on their distribution, taxonomy, and pathogenicity.

Distribution of Plant Pathogenic *Streptomyces*

The potato scab disease, which is widely distributed all over the world, is a major problem in potato cultivation and marketing. From 1996 to 1999, potato-growing areas in Korea were surveyed for the identification and distribution of potato scab disease. A total of 55 *Streptomyces* strains were isolated from potato scab lesions from different geographic locations in the country. Strains were identified by pathogenicity test previously described by Loria and Kempter (1986), and by physiological and morphological characterization according to Lambert and Loria (1989a; 1989b) and Shirling and Gottlieb (1966). Among the strains identified, 40 strains reproduced the same symptoms on progeny tubers. Based on physiological and morphological characteristics, 21 strains were identified as previously described *S. scabies* (Kim and Lee, 1996), while 7 strains were identified as *S. turgidiscabies* and 5 strains were identified as *S. acidiscabies* (Kim et al., 1998a; Kim et al., 1998b). However, seven strains were identified as having distinct phenotypic properties compared with the rest of the strains. Three strains among the distinct seven strains were identified as novel species such as *S. luridiscabiei*, *S. puniciscabiei*, and *S. niveiscabiei* based on phenotypic and phylogenetic analyses (Park et al., unpublished). In this study, potato scab pathogens were identified as *S. scabies*, *S. turgidiscabies*, and *S. acidiscabies*, while three novel species were identified as *S. luridiscabiei*, *S. puniciscabiei*, and *S. niveiscabiei* in Korea.

Serious potato scab problem was observed in mass cultivation areas, especially in Jeju island, southern areas of Chonnam and Gyounggi provinces, and alpine area of Gangwon province. Among these areas, Jeju island was the most affected. For the analysis of the potato scab problem in Jeju island, this study investigated the relationship between geographical distribution and potato cultivars. Daejima, the most commonly used cultivar in potato growing areas of Jeju island, was found highly susceptible to potato scab pathogens. Cultivars Atlantic and Irish cobbler were found moderately susceptible, while cultivars Superior and Jopung were resistant to potato scab pathogens (Fig. 1).

Daejima is cultivated twice a year to double the yield. Second cultivation time is usually from fall to the next spring. At that time, most farmers prefer to keep potato in natural soil condition without harvesting, so that these can be sold for a higher price in the next spring season. However, these methods may accelerate the rapid increase of pathogens in the soil and consequently, may increase the chance of its outbreak in Jeju island.

In contrast, the cultivar Superior, which is mostly cultivated in Gangwon, Gyounggi, and Chonnam provinces, was found resistant to potato scab pathogens. Farmers in these areas often rotate potato with other crops, which may have contributed to the prevention of the outbreak of potato scab.

Taxonomy

Plant pathogenic *Streptomyces* species has been classified by phenotypic characteristics such as colors of spores and substrate mycelium, spore chain morphology, pigment production, sugar utilization of International *Streptomyces* Project (ISP), and resistance to inhibitory compounds (Lambert and Loria, 1989a; 1989b; Shirling and Gottlieb, 1966). In recent years, phylogenetic analyses using rRNA operon and DNA relatedness, and guanine and cytosine composition have been extensively used for identification at species level (Bouchek-Mechiche et al., 2000; Kreuze et

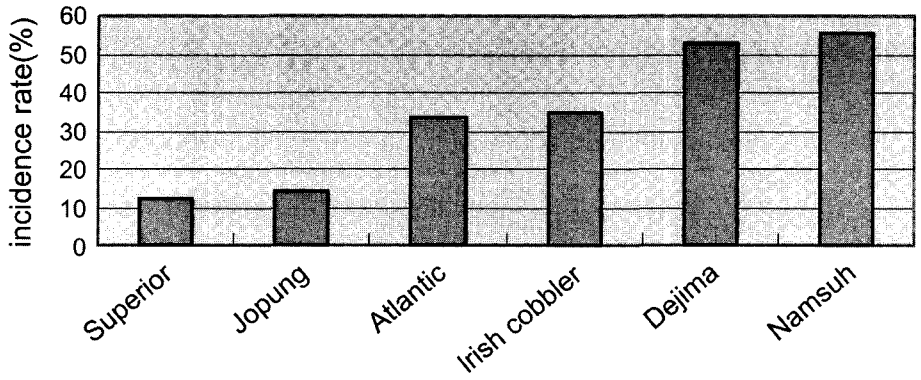

Fig. 1. Occurrence of potato scab disease on various potato cultivars (*Solanum tuberosum*).

Table 1. Phenotypic characteristics of *Streptomyces* causing potato scab in Korea

Characteristics	S33	S27	S71	S63	S77	S78	*S.s*[a]	*S.t*	*S.a*	*S.c*	*S.e*	*S.st*	*S.r*
Spore color[b]	G	G	W	YW	PO	W	G	G	W	W	G	G	LG
Chain morphology[c]	S	Rf	Rf	Rf	Rf	Rf	S	Rf	Rf	Rf	S	S	Rf
Colony color on YME[d]	TB	RY	LY	OB	GO	LY	TB	Y	Br	GB	ND	ND	ND
Melanin on tyrosine agar	+	+	+	+	+	−	+	+	−	−	+	+	−
Melanin on peptone agar	+	−	−	+	−	−	+	+	−	−	+	+	−
Utilization[e]													
L-Arabinose	+	+	+	+	+	+	+	ND	+	−	+	+	+
D-Fructose	+	+	+	+	+	+	+	ND	+	−	+	+	+
D-Glucose	+	+	+	+	+	+	+	ND	+	−	+	+	+
D-Mannitol	+	+	+	+	+	+	+	ND	+	−	+	+	+
Raffinose	+	+	-	+	+	+	+	+	−	+	+	+	+
Rhanmose	+	+	+	+	+	+	+	ND	+	−	+	+	+
Sucrose	+	+	+	+	+	+	+	ND	+	−	+	+	+
D-Xylose	+	+	+	+	+	+	+	ND	+	−	+	+	+
i-Inositol	+	+	+	+	+	+	+	ND	+	−	+	+	+
Minimun growth pH	5.0	4.5	4.5	4.5	3.5	3.5	5.0	4.5	4.0	5.0	ND	ND	ND
Growth with[f]													
5% NaCl	−	−	+	−	+	−	+	−	−	+	ND	−	−
6% NaCl	−	−	+	−	+	−	+	−	−	v	ND	−	−
7% NaCl	−	−	+	−	+	−	−	−	−	v	ND	−	−
Thallium acetate	−	−	−	+	−	−	−	−	+	ND	ND	ND	ND
Thallium acetate	−	−	−	−	−	−	−	−	−	ND	ND	ND	ND
Crystal violet	−	−	+	+	+	−	−	−	+	v	−	−	−
Phenol	−	−	−	−	+	−	−	−	+	+	ND	ND	ND
Penicillin	+	+	+	+	+	+	−	−	+	+	+	+	+
Oleandomycin	−	+	+	−	+	−	−	−	+	+	+	+	+
Oleandomycin	−	−	+	−	+	−	−	−	−	v	ND	−	−
Streptomycin	−	−	−	−	−	−	−	−	+	+	−	−	−

+ = positive reaction; − = negative reaction; v = between 20 and 90% of the strains were positive.

[a] Data of *S. scabies, S. turgidiscabies, S. acidiscabies, S. caviscabies, S. europaeiscabiei, S. stelliscabiei, S. reticuliscabi* from references Bouchek-Mechiche et al. (2000); Goyer et al. (1996); Lambert and Loria (1989a, 1989b); Miyajima et al. (1998). Type strain of S.s, *S. scabies*; S.t, *S. turgidiscabies*; S.a, *S. acidiscabies*; S.c, *S. caviscabies*; S.e, *S. europaeiscabiei*; S.st, *S. stelliscabiei*; S.r, *S. reticuliscabiei*.

[b] G = grey; W = white; YW = yellowish white; PO = pale orange; LG = light grey.

[c] S = spiral; Rf = rectiflexuous.

[d] YME = yeast malt extract; TB = tan brown; RY = red-yellow; LY = light yellow; OB = olive brown; GO = grey-orange; Y = yellow; Br = brown; GB = golden brown.

[e] ND = not determined.

[f] thallium acetate10 μg/ml, 100 μg/ml; crystal violet, 0.5 μg/ml; phenol, 0.1%; penicillin, 10 IU/ml; oleandomycin, 25 μg/ml, 100 μg/ml; streptomycin, 20 μg/ml.

al., 1999; Miyajima et al., 1998; Takeuchi et al., 1996). In this study, 40 pathogenic strains have been classified into six distinct clusters based on phenotypic characteristics of selected representative strains (Table 1). Based on its phenotypic characteristics, strain S33 which is a member of the first group, was found identical with the strain type of *S. scabies*, except that it failed to grow in 5% and 6% NaCl and was resistant to penicillin (10 IU/ml). Analysis of 16S rRNA sequences also indicated that it is most similar to *S. scabies* strains (ATCC 49173^T, ATCC 33282, SNS-26) with sequence identities of more than 99.8%. Hence, it was identified as *S. scabies*.

Strain S27, which represents the second group, was identified as *S. turgidiscabies* based on its phenotypic characteristics which were identical with type strain ATCC 700248 from Japan, except that it did not produce melanin on peptone agar and was resistant to penicillin (10 IU/ml) and oleandomycin (25 μg/ml). 16S rRNA sequence was found 99.5% identical with that of *S. turgidiscabies* strain (ATCC 700248^T).

Strain S71, which represents the third group, showed similar characteristics with that of *S. acidiscabies*, except that its growth was inhibited below pH 4.5, produced melanin on tyrosine agar, and varied in its reaction to several antibiotics and other inhibitory compounds. This strain was identified as most similar to *S. acidiscabies* (ATCC 49003^T) with 16S rRNA sequence identities of 99.9%.

Phenotypic and phylogenetic analyses of strains S63, S77, and S78 which were isolated from Jeju island showed distinct characteristics compared with other common pathogens of potato scab. These are characterized as novel

species and their detailed descriptions are presented in Table 1 (Park et al., 2003).

Strain S63, which represents the fourth group, produced yellow-white spores in a rectiflexuous chain, produced melanin on tyrosine or peptone agar, and utilized all the ISP sugars. Growth of this strain was inhibited below pH 4.5 and in the presence of 5, 6, 7% NaCl, thallium acetate (100 μg/ml), phenol (0.1% v/v), oleandomycin (25, 100 μg/ml), and streptomycin (20 μg/ml). Strain S63 was similar to *S. setonii* (ATCC 25497^T) and *S. griseous* subsp. *griseous* (KCTC 9080) with 99.3% and 99.0% 16S rRNA sequence identity, respectively. In DNA relatedness, this strain was less than 16%, 16%, and 10% homologous to *S. scabies*, *S. turgidiscabies*, and *S. acidiscabies*, respectively. Also, this strain showed lower homology with *S. griseus* and *S. setonii* at 10% and 7%. G+C content was 70.3 mol%. Based on these data, it is proposed that this strain be named *S. luridiscabiei* sp. nov.

Strain S77, which represents the fifth group, had pale orange spores in a rectiflexuous chain, produced melanin on tyrosine agar, and utilized all the ISP sugars. The growth was inhibited below pH 3.5 and in the presence of thallium acetate (10, 100 μg/ml) and streptomycin (20 μg/ml). 16S rRNA sequences showed relatively lower homology level (<96.5%) compared with the other pathogenic and saprophytic strains. DNA relatedness of this strain was less than 16%, 13%, and 11% to *S. scabies*, *S. turgidiscabies*, and *S. acidiscabies*, respectively. Also, this strain showed very low DNA relatedness values with other *Streptomyces*. G+C content was 68.3 mol% based on these data. Therefore, the strain was named *S. puniciscabiei* sp. nov.

Strain S78, which represents the sixth group, had thin and compact spores in a rectiflexuous chain, did not produce melanin on tyrosine or peptone agar, and utilized all ISP sugars. The growth was inhibited below pH 3.5 and in the presence of 5, 6, 7% NaCl, thallium acetate (10, 100 μg/ml), crystal violet (0.5 μg/ml), phenol (0.1%), oleandomycin (25, 100 μg/ml), and streptomycin (20 μg/ml). 16S rRNA sequences showed relatively low homology level (< 96.5%) with the other pathogenic and saprophytic strains. DNA relatedness of this strain was less than 21%, 17%, and 17% to *S. scabies*, *S. turgidiscabies*, and *S. acidiscabies*, respectively. This strain also showed very low DNA relatedness values with other *Streptomyces*. G+C content was 70.1 mol%. Based on these data, the strain was named *S. niveiscabiei* sp. nov.

In summary, pathogens of potato scab in Korea were identified as *S. scabies*, *S. turgidiscabies*, *S. acidiscabies*, and three novel species (Park et al., 2003). *S. scabies* (S33) had grey spores in a spiral chain, while *S. turgidiscabies* (S27) had grey spores, *S. acidiscabies* (S71) had white spores, *S. luridiscabiei* (S63) had yellow-white spores, *S. puniciscabiei* (S77) had purple-red spores, and *S. niveiscabiei* (S78) had thin and compact white spores, all in a rectiflexuous chain. Therefore, color of spores and spore chain morphology of the *Streptomyces* are the main characteristic features for taxonomic position rather than other physiological characters. Moreover, molecular analyses such as 16S rRNA sequences (more than 98% similarity), pairwise hybridization of DNA (more than 70% DNA relatedness), and G+C content (68% to 73%) are equally important for correct taxonomy position of any species of pathogenic *Streptomyces*.

Table 2. *Streptomyces* strains used in this study, pathogenicity on whole plant (pot) and tuber slices (TB), thaxtomin A production by TLC and HPLC analysis, and hybridization to *nec*1 and ORF*tnp* genes

Strains[a]	Pathogenicity[b]		TLC[c]	HPLC[d]		Hybridization[e]	
	Pot	TB		OA	TB	*nec1*	ORF tnp
S. scabies							
ATCC 49173^T	+	+	+	+	+	+	+
S33	+	+	+	+	+	+	+
ATCC33282	NA	NA	NA	NA	NA	NA	NA
SNS-26	NA	NA	NA	NA	NA	NA	NA
S. turgidiscabies							
ATCC 700248^T	+	+	+	+	+	+	+
S27	+	+	+	+	+	+	+
S. acidiscabies							
ATCC 49003^T	+	+	+	+	+	+	+
S71	+	+	+	+	+	−	−
S. luridiscabiei							
S63	+	+	+	−	−	−	−
S. puniciscabiei							
S77	+	+	+	−	−	−	−
S. niveiscabiei							
S78	+	+	+	+	+	−	−
S. lividans							
TK21	−	−	−	−	−	−	−

[a] T = type strain of the species; NA = not known or applicable.
[b] Pot = pot test; TB = tuber slices; + = pathogenicity on pot test and tuber slices assay; − = non-pathogenicity on both tests.
[c] TLC = thin layer chromatography; + = co-migrated spot similar to authentic thaxtomin A; − = no co-migrated spot similar to authentic thaxtomin A.
[d] HPLC = high pressure liquid chromatography; OA = oatmeal broth culture; TB = tuber slices; + = detection of thaxtomin A; − = no detection of thaxtomin A.
[e] + = hybridization; − = no hybridization.

Pathogenicity

Pathogenicity test for all isolates was performed according to standard Koch's postulates. Generally, pathogenicity test of strains was by whole plant test and tuber slice tissue test and was repeated several times (Loria and Kempter, 1986; Loria et al., 1995). To date, all the species of *Streptomyces*

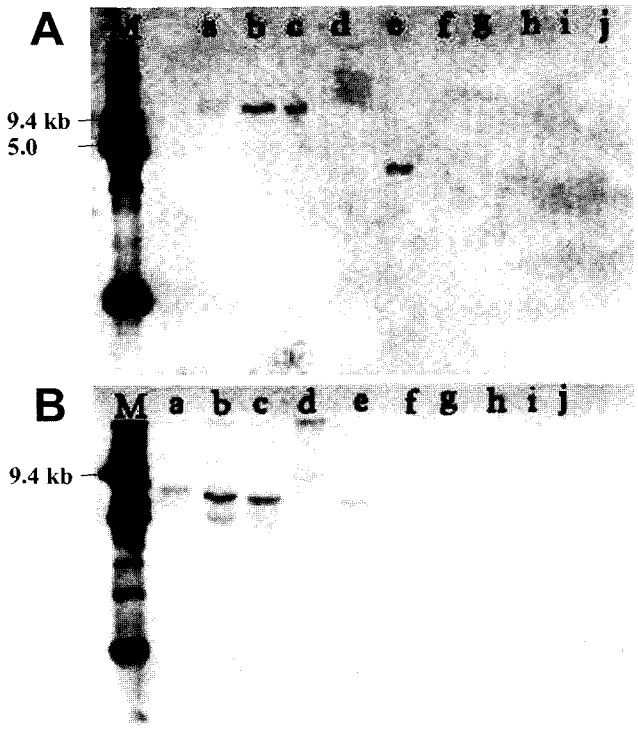

Fig. 2. Southern hybridization analysis of a *Bam*HI digest of representative *Streptomyces* strains with (A) *nec1* (720bp) and (B) ORF*tnp* (550bp) used as DNA probes. Lanes a and b are *S. scabies* ATCC 49173^T and S33; c and d are *S. turgidiscabies* ATCC 700248^T and S27; e and f are *S. acidiscabies* ATCC 49003^T and S71; g, S63; h, S77; i, S78; and j, *S. lividans* ATCC 19844. Sizes in base pairs are indicated for detected fragment of the *nec1* and ORF*tnp* based on reference (Bukhalid et al., 1998).

related to potato scab have been reported to produce thaxtomin A of the phytotoxin family. Thus, this study confirmed which of the representative strains of the six Korean group produces thaxtomin A or not from the extracts of oatmeal broth culture. Results showed that representative strains S33, S27, S71, S63, S77, and S78 produced a yellow band that co-migrated with authentic thaxtomin A by TLC analysis (Table 2). However, thaxtomin A was not detected from chloroform extracts of oatmeal broth culture of *S. luridiscabiei* (S63) and *S. puniciscabiei* (S77) by HPLC analysis. However, it was speculated that the production of thaxtomin A by scab pathogens would require component or signal from potato tissue. Therefore, all six Korean strains were inoculated onto tuber slices, and chloroform extracts from the inoculated tuber slices were analyzed by HPLC for the detection of thaxtomin A. Thaxtomin A was not detected from *S. luridiscabiei* (S63) and *S. puniciscabiei* (S77), which clearly indicated that novel species *S. luridiscabiei* (S63) and *S. puniciscabiei* (S77) did not produce thaxtomin A neither in the media nor from infected potato tissue (Table 2). Therefore, it was concluded that the absence of thaxtomin A from these two strains was not due to any artifact. This is the first result which showed that some pathogenic strains of *Streptomyces* did not produce thaxtomin A, which is a characteristic of potato scab pathogens.

Streptomyces strains having *nec1*, necrosis gene and ORF*tnp*, necrosis gene and transposase pseudogene located 5' to *nec1*, have also been reported from pathogens of potato tubers (Bukhalid et al, 1998; Healy et al., 2000). Therefore, this study investigated the relationship between pathogenicty of the six strains and the presence of homologous genes to *nec1* and ORF*tnp* genes by PCR and Southern hybridization analysis. It sought to determine whether these two genes exist in six representative strains by PCR and southern blotting. In this study, *nec1* gene and the 5' transposase pseudogene ORF*tnp* were successfully amplified by polymerase chain reaction (PCR) from all studied strains except for *S. acidiscabies* (S71) and three novel Korean strains, *S. luridiscabiei* (S63), *S. puniciscabiei* (S77) and *S. niveiscabiei* (S78), where multiple or no bands were produced. However, successful amplification by PCR only shows the possibility of homologous DNA sequences matched to primers, not the presence of *nec1* and ORF*tnp* homologs. Thus, to confirm the presence of *nec1* and ORF*tnp* homolog genes in Korean strains, total genomic DNA from all strains was restricted with the endonuclease *Bam*H1 and subjected to Southern hybridization analysis. The *nec1* and ORF*tnp* homologs were present in all strains tested except for *S. acidiscabies* (S71) and the three novel Korean strains, *S. luridiscabiei* (S63), *S. puniciscabiei* (S77), and *S. niveiscabiei* (S78) (Fig. 2). This is the first report of a *S. acidiscabies* strain lacking a *nec1* gene homolog. Surprisingly, the presence or absence of homologs *nec1* and ORF*tnp* homologs was not related with thaxtomin A biosynthesis genes in Korean strains *S. luridiscabiei* (S63) and *S. puniciscabiei* (S77). These two novel strains were also morphologically, physiologically, and pathologically diverse. Results of this study suggested that these novel pathogens may have a unique mechanism for pathogenicity which may have evolved separately from known scab pathogens.

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