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Actinoplanes caeruleus sp. nov., a Blue-Pigmented Species of the Genus *Actinoplanes*

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A new, antibiotic-producing species of *Actinoplanes*, *Actinoplanes caeruleus*, was isolated from soil. This organism formed irregular to globose sporangia which upon wetting dehisced to release spherical to oval, polarly flagellated motile spores. It contained arabinose and xylose as characteristic whole-cell sugars. This organism differed from other species of the genus *Actinoplanes* by forming deep blue vegetative mycelial pigments, by the absence of diaminopimelic acid on the cell wall, by its ability to hydrolyze adenine and hypoxanthine, by its resistance to lysozyme, and by its inability to utilize L-arabinose, D-xylose, and succinate as sole carbon sources. The type strain of *A. caeruleus* is strain SCC 1014 (= ATCC 33937).

Wagman et al. (26) described a novel heptaene antifungal antibiotic produced by an unusual, blue-pigmented species of *Actinoplanes*. This antibiotic was of interest because of its broad spectrum of activity against pathogenic fungi, its novel structure (29), and its production by an actinoplanete. Before this description, actinoplanetes had not been reported to produce polyene antibiotics. A comparison of the organism which produced the antibiotic, strain SCC 1014^T (T = type strain), with previously described *Actinoplanes* species clearly indicated that it is a new species. In this paper we describe the characterization, identification, and classification of strain SCC 1014^T.

MATERIALS AND METHODS

Bacterial strains. Table 1 lists the *Actinoplanes* spp. strains used in this study. Strain SCC 1014^T was isolated from a soil sample collected from a sage brush area in Bristol Cone Park, Calif. A subculture of this organism has been deposited in the American Type Culture Collection, Rockville, Md., as strain ATCC 33937^T.

Strain maintenance. The source materials were freeze-dried preparations of pure cultures. The contents of each vial were suspended in 10 ml of liquid ATCC medium 172 (1) in a 25-mm test tube stoppered with a Morton closure. Broth suspensions were incubated at 30°C on a rotary shaker (model G-52; New Brunswick Scientific Co.) at 250 rpm for 3 to 4 days, and then 5 ml of each culture was transferred into 50 ml of fresh medium in a 250-ml Erlenmeyer flask stoppered with cotton and incubated as described above. The flasks were harvested after 3 to 4 days, and sterile glycerol was added to a final concentration of 7% (vol/vol). Portions (5 ml) were dispensed aseptically into sterile screw-cap vials (17 by 60 mm) and stored at −30°C.

Preparation of inocula. A 1-ml sample of thawed cell suspension was used to inoculate each ATCC medium 172 broth tube by using the procedures described above. After 3 days of incubation, a second transfer to fresh broth was made, and the tubes were shaken for an additional 3 days at 30°C. At harvesting the biomass was centrifuged, washed twice with sterile distilled water, and then suspended in sterile distilled water to three times the packed cell volume. The resulting washed suspensions were used as inocula for the tests described below.

Morphological observations. Washed cells were inoculated onto the surfaces of the following media in petri dishes: half-strength starch agar (yeast extract, 2.5 g; potato starch, 5.0 g; agar, 15.0 g; tap water, 1 liter; pH 7.0), dilute YD agar (yeast extract, 1.0 g; dextrose, 1.0 g; agar, 15.0 g; tap water, 1 liter; pH 7.0), and water agar (agar, 15.0 g; tap water, 1 liter; pH 7.0). The inoculated plates were incubated at 30°C for 5, 10, 15, and 20 days and examined after each time period directly under a microscope. Representative plates were flooded with sterile tap water and gently scraped, and the suspension was transferred to sterile tubes and allowed to settle for 15 min. One drop of the suspension was examined microscopically for sporangia and motile spores. When motile spores were present, wet mounts were prepared for electron microscopic observations by using the procedures of Luedemann and Casmer (18).

Chemical analysis of whole cells. The presence and isomeric form of diaminopimelic acid and the presence of carbohydrates in whole-cell hydrolysates were determined by using the methods of Becker et al. (2) and Lechevalier (15).

Growth characteristics. Strain SCC 1014^T was cultivated on standard agar media as described by Shirling and Gottlieb (21) and Waksman (27) and was incubated for 14 to 21 days at 30°C. Each color designation assigned to the vegetative mycelial pigments consisted of a color name (24) and a color chip number (5).

Carbon utilization. Carbohydrate utilization was determined by using the procedure of Luedemann and Brodsky (17), and utilization of organic acids was determined by using the method of Gordon et al. (11).

Decomposition of adenine, hypoxanthine, tyrosine, xanthine, and xylan. Two basal media were used, nutrient agar (peptone, 5.0 g; beef extract, 3.0 g; agar, 15.0 g; distilled water, 1 liter; pH 7.0) and YD agar (yeast extract, 10.0 g; dextrose, 10.0 g; agar, 15.0 g; distilled water, 1 liter; pH 7.0). Adenine (0.5 g), hypoxanthine (0.5 g), tyrosine (0.5 g), xanthine (0.4 g), and xylan (0.4 g) were each suspended in duplicate 250-ml Erlenmeyer flasks in 10 ml of distilled water, autoclaved, and mixed with 100 ml of either sterile nutrient agar or sterile YD agar cooled to 45°C. The suspension was thoroughly mixed and poured into sterile petri dishes (15 by 60 mm). Each washed cell suspension was inoculated across the surface of the plates, and these preparations were incubated at 30°C and observed after 14 to 21 days for the disappearance of crystals under and around the growth.

Decomposition of casein, urea, and allantoin. The proce-

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dures of Gordon et al. (11) were used to determine the decomposition of casein, urea, and allantoin.

Hydrolysis of esculin and arbutin. A modification of the method of Cowan and Steel (8) was used to determine hydrolysis of esculin and arbutin. To the basal medium (yeast extract, 10.0 g; ferric citrate, 0.5 g; agar, 15.0 g; distilled water, 1 liter; pH 7.2) either esculin or arbutin was added to a final concentration of 0.1% (wt/vol). For the control, dextrose was added to a final concentration of 0.3% (wt/vol). The resulting agar media were dispensed in 3-ml portions into 13-mm test tubes, autoclaved, slanted, inoculated, and incubated at 30°C for 7 and 14 days. Blackening of the esculin or arbutin agar medium and not the control indicated a positive response.

Hydrolysis of hippurate. To determine whether hippurate was hydrolyzed, the procedure of Gordon (10) was modified as described below. Hippurate broth (sodium hippurate, 10.0 g; dextrose, 2.0 g; tryptone, 2.0 g; beef extract, 2.0 g; yeast extract, 2.0 g; Na_2HPO_4, 5.0 g; distilled water, 1 liter; pH 7.0) was dispensed in 10-ml portions into 25-mm test tubes, which were stoppered with Morton closures and autoclaved. Each tube was inoculated with 0.1 ml of a washed cell suspension and shaken at 250 rpm for 7 days at 30°C. Then 1 ml of broth, free of cells, was removed to a clean test tube and mixed with 1.5 ml of 50% (vol/vol) sulfuric acid. The appearance of finely divided crystals after 4 h indicated the presence of benzoic acid and a positive response.

Resistance to lysozyme. To determine resistance to lysozyme, the procedure of Gordon et al. (11) was modified by replacing glycerol broth with YD broth. YD broth containing lysozyme at a final concentration of 0.005% (wt/vol) was dispensed into tubes, inoculated with organisms, and incubated as described above for hippurate hydrolysis. YD broth without lysozyme was used as the control. The tubes were examined for growth after 7 days.

Resistance to salicylate. The procedure described above for the lysozyme resistance test was used to determine resistance to salicylate. Salicylate broth contained (per liter of distilled water) 2.0 g of sodium salicylate, 10.0 g of yeast extract, and 10.0 g of dextrose (pH 6.8).

Tolerance to salts. To determine tolerance to salts, the appropriate weight of a test salt that resulted in a final concentration in agar of 1.0, 2.0, or 3.0% was placed in a 250-ml Erlenmeyer flask, suspended in 10 ml of distilled water, autoclaved, and mixed thoroughly with 90 ml of sterile molten YD agar (cooled to 45°C), which was then poured into sterile petri dishes (15 by 100 mm). Duplicate plates were inoculated with washed suspensions of cells by using a Steers replicator, incubated at 30°C, and examined after 7 and 14 days for growth.

Temperature relationships. The procedure of Horan and Brodsky (12) was used to determine temperature relationships.

Growth in the presence of antibiotics. The ability of the strains to grow in the presence of the test antibiotics at concentrations of 50 μg/ml was determined by using the procedure of Horan and Brodsky (12).

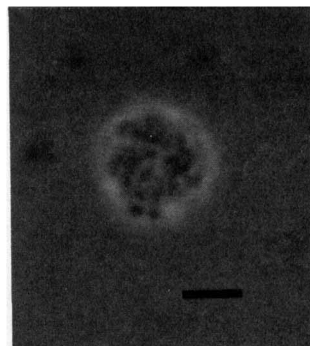

FIG. 1. Strain SCC 1014^T sporangia in water. Phase-contrast microscopy. ×1,000. Bar = 10 μm.

RESULTS

Morphological observations. On both water agar and half-strength starch agar, strain SCC 1014^T formed abundant globose to irregularly shaped sporangia ranging in diameter from 6 to 16 μm. On water agar, the sporangial bodies appeared to be embedded in the mycelial mat and contained numerous sporangiospores. When wetted, the sporangia rounded up, and the wall became phase bright (Fig. 1) and appeared to dissolve, with the release of numerous spherical to oval motile spores that were 1.3 to 2.0 μm in diameter (Fig. 2). Electron micrographs of sporangiospores showed

TABLE 1. Strains of *Actinoplanes* used in this study[a]

Laboratory no.	Received as:	
	Species	Strain[b]
SCC 1014^T	Original isolate from soil	67-121
A-15696^T	*Actinoplanes armeniacus*	ATCC 15676^T
A-25844^T	*Actinoplanes brasiliensis*	ATCC 25844^T
A-21983^T	*Actinoplanes deccanensis*	ATCC 21983^T
A-29868^T	*Actinoplanes ferrugineus*	ATCC 29863^T
A-27366^T	*Actinoplanes italicus*	ATCC 27366^T
A-14538^T	*Actinoplanes missouriensis*	ATCC 14538^T
C-188.64	*Actinoplanes missouriensis*	CBS 188.64
A-12427^T	*Actinoplanes philippinensis*	ATCC 12427^T
I-3919^T	*Actinoplanes rectilineatus*	IMRU 3919; LL-7-10^T
A-14539^T	*Actinoplanes utahensis*	ATCC 14539^T
C-367.66	*Actinoplanes utahensis*	CBS 367.66

[a] Species on the Approved Lists of Bacterial Names (22).
[b] CBS, Centraalbureau voor Schimmelcultures Baarn, The Netherlands; IMRU, Institute of Microbiology, Rutgers University-Busch Campus, Piscataway, N.J.; ATCC, American Type Culture Collection, Rockville, Md.

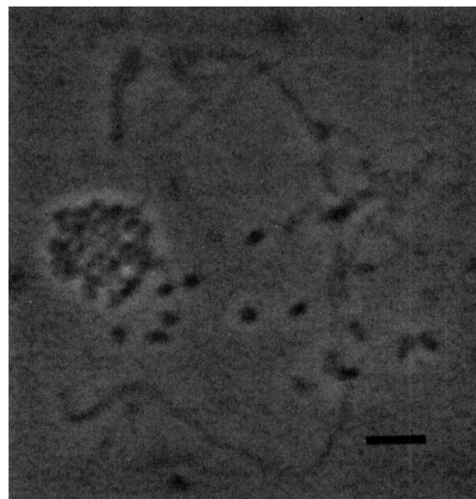

FIG. 2. Dissolution of the sporangial wall, with the release of numerous motile spores. Phase-contrast microscopy. ×1,000. Bar = 10 μm.

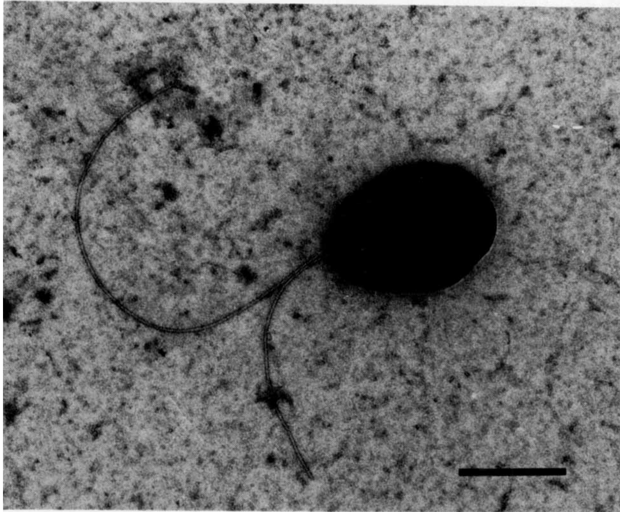

FIG. 3. Polar flagellation of strain SCC 1014^T sporangiospores. ×16,200. Bar = 1 μm.

the presence of a tuft of polar flagella (Fig. 3). Scanning electron microscopy of immature sporangia indicated that sporangium formation followed the steps described by Lechevalier and Holbert (14).

Growth characteristics. Table 2 indicates the macroscopic appearance of strain SCC 1014^T on various descriptive media. The organism grew well on most organic media; poor growth occurred on calcium malate and calcium citrate agar media. The vegetative mycelial pigments ranged from yellow and various shades of tan to striking blues. Aerial mycelia were not formed. Faint yellowish brown diffusible pigments were produced on several media.

Whole-cell analysis. Hydrolyzed whole cells did not contain diaminopimelic acid. A cell wall analysis indicated the presence of glycine, lysine, and serine as major constituents. Arabinose and xylose, which are characteristic of *Actinoplanes* spp., were the whole-cell sugars.

Physiological and biochemical reactions. The physiological reactions of strain SCC 1014^T and other actinoplanetes are compared in Table 3.

DISCUSSION

The formation of brightly colored, blue colonies on agar along with globose to irregular sporangia which, in the presence of water, dehisced to release motile, polarly flagellated sporangiospores and the presence of arabinose and xylose in whole-cell hydrolysates clearly placed strain SCC 1014^T in the genus *Actinoplanes* (6, 9). Lysine was the dibasic amino acid found in the cell walls. In their survey of actinomycete cell walls, Becker et al. (3) also reported the absence of diaminopimelic acid in a typical *Actinoplanes* sp.; lysine or ornithine was the characteristic cell wall dibasic amino acid.

Strain SCC 1014^T was compared with all of the species of *Actinoplanes* on the Approved Lists of Bacterial Names (22) except *Actinoplanes armeniacus*, an organism that was described by Kalakoutskii and Kusnetsov (13) and was transferred to the genus *Streptomyces* by Wellington and Williams (28). All of the strains examined utilized D-cellobiose, fructose, D-galactose, D-glucose, glycerol, lactose, maltose, D-mannitol, D-mannose, L-rhamnose, sucrose, D-trehalose, acetate, L-glutamate, and pyruvate; all hydrolyzed tyrosine, casein, starch, and esculin, and all grew at 28°C.

Of the strains used in this study, none shared with strain SCC 1014^T the combination of blue vegetative mycelial pigments, absence of diaminopimelic acid in the cell walls, ability to hydrolyze adenine and hypoxanthine, resistance to lysozyme and salicylate, inability to utilize L-arabinose, D-xylose, and succinate, and ability to produce a heptaene antifungal antibiotic during fermentation (Table 3).

Our data indicate that strain SCC 1014^T represents a new, distinct, antibiotic-producing *Actinoplanes* species, for which we propose the name *Actinoplanes caeruleus* (cae. ru′ le. us. L. adj. *caeruleus* dark blue, azure, referring to the blue vegetative mycelial pigments).

Description of *Actinoplanes caeruleus* sp. nov. Irregular to globose sporangia (diameter, 6 to 16 μm) which dehisce to release polarly flagellated motile spores (diameter 1.3 to 2.0 μm). Colonies are blue on oatmeal, inorganic salts-starch,

TABLE 2. Growth characteristics of strain SCC 1014^T on various media

Medium	Growth	Aerial mycelium	Diffusible pigments	Color of growth[a]
Bennett agar	Good	Absent	Light brown	g 3 ne (topaz)
Czapek sucrose agar	Moderate	Absent	Yellow	Center, g 1 ml (dark olive gray); periphery, g 3 ie (camel)
Glucose-asparagine agar	Moderate to good	Absent	Yellow	Center, g 1 (olive gray); periphery, g 2 eu (ecru)
Glycerol-asparagine agar	Good	Absent	Absent	g 24 ih (misteltoe gray)
Nutrient agar	Moderate	Absent	Absent	g 24 ih (misteltoe gray)
Peptone-glucose agar	Fair	Absent	Absent	g 19 ml (charcoal)
Potato-dextrose agar	Good	Absent	Yellowish brown	g 2 li (covert brown)
Emerson agar	Moderate to good	Absent	Absent	g 3 la (light melon yellow)
NZA glucose agar	Moderate to good	Absent	Absent	g 3 ga (melon yellow)
Yeast-dextrose agar	Good	Absent	Absent	g 3 nc (amber)
Tomato paste-oatmeal agar	Moderate to good	Absent	Absent	g p (lamp black)
Yeast extract-malt extract agar (ISP medium 2)	Good	Absent	Absent	g 3 le (yellow maple)
Oatmeal agar (ISP medium 3)	Fair to moderate	Absent	Gray	g 15 li (dark gray blue)
Inorganic salts-starch agar (ISP medium 4)	Fair to moderate	Absent	Absent	g 14 ni (shadow blue)
Starch agar (Waksman medium 21)	Fair to moderate	Absent	Faint gray	g 14 nl (dark gray blue)
Tyrosine agar (ISP medium 7)	Good	Absent	Absent	g 2 ie (light mustard tan)

[a] See references 5 and 24.

TABLE 3. Differentiating characteristics of *Actinoplanes* spp.

Characteristic	*A. caeruleus* SCC 1014[T]	*A. brasiliensis* ATCC 25844[T]	*A. decannensis* ATCC 21983[T]	*A. ferrugineus* ATCC 29868[T]	*A. italicus* ATCC 27366[T]	*A. missouriensis* ATCC 14538[T] and CBS 188.64	*A. philippinensis* ATCC 12427[T]	*A. rectilineatus* IMRU 3919	*A. utahensis* ATCC 14539[T] and CBS 367.66
Morphology									
Mycelial pigments	Tan to blue	Orange	Tan to orange	Tan to deep brown	Orangeish tan to reddish brown	Tan to orange	Tan to brown	Tan to brown	Tan to orange
Shape of sporangia	Irregular	Irregular	Globose	Globose	Globose to irregular	Globose	Globose	Cylindrical	Irregular
Diam of sporangia (μm)	6–16	3.5–11.5	4–7	4–12	6–11	6–15	8–25	8–15	5–18
Shape of sporangiospores	Spherical to oval	Subspherical to rod shaped	Globose	Globose	Globose	Globose	Globose	Globose	Globose
Size of sporangiospores (μm)	1.3–2.0	2.3 by 1.2 to 1.7 by 1.2	1–1.5	0.9–1.0	1–2	1.0–1.2	1.0–1.2	1.5–2.0	1.0–2.0
Diaminopimelic acid	Absent	*meso*-DAP[a]	*meso*-DAP	Hydroxy- and *meso*-DAP[b]	*meso*-DAP	Hydroxy- and *meso*-DAP	*meso*-DAP	*meso*-DAP	Hydroxy- and *meso*-DAP
Utilization of:									
L-Arabinose	−	+	+	+	+	+	+	+	+
D-Xylose	−	+	+	+	+	+	+	+	+
D-Mellezitose	+	−	+	−	+	−	+	−	−
i-Inositol	+	−	+	−	+	−	+	+	−
Gluconate	−	+	+	+	+	+	−	+	+
Succinate	−	+	+	+	+	+	+	+	+
Hydrolysis of:									
Adenine	+	−	−	−	−	−	−	−	−
Hypoxanthine	+	−	−	−	−	−	−	−	−
Resistance to:									
Lysozyme	+	−	−	−	−	−	−	−	−
Salicylate	+	−	−	−	−	−	−	−	−
Growth in the presence of:									
Novobiocin (50 μg/ml)	−	+	+	+	+	+	+	±	+
Spectinomycin (50 μg/ml)	+	+	−	−	+	+	−	−	±
Cephalothin (50 μg/ml)	−	+	+	−	−	−	−	−	−
Reference		25	20	19	4	7	6	16	7

[a] DAP, Diaminopimelic acid.
[b] See reference 23.

and starch agar media. Aerial mycelia are not formed. Soluble pigments are yellow to yellowish brown. The cell walls contain glycine, lysine, and serine. Diaminopimelic acid is not present. Type D whole-cell sugar pattern. Fructose, D-glucose, D-mannitol, D-mannose, L-rhamnose, sucrose, and D-trehalose are utilized, with the formation of blue colonies; D-cellobiose, D-galactose, glycerol, i-inositol, lactose, maltose, D-melezitose, acetate, butyrate, glutamate, propionate, and pyruvate are also utilized. Adonitol, D-arabinose, L-arabinose, dulcitol, erythritol, D-melibiose, D-raffinose, D-ribose, D-xylose, benzoate, citrate, succinate, and tartrate are not utilized. Adenine and hypoxanthine are hydrolyzed in the presence of yeast extract, but not beef extract; tyrosine, starch, gelatin, esculin, and arbutin are also hydrolyzed. Casein hydrolysis is weak; xanthine, xylan, and hippurate are not hydrolyzed. Nitrate reductase positive; urease and allantoinase negative. Lysozyme and salicylate resistant. Grows in the presence of 50 μg of rosaramicin per ml and 50 μg of spectinomycin per ml but not in the presence of gentamicin, kanamycin, streptomycin, erythromycin, rifamycin, everninomicin, novobiocin, tetracycline, penicillin G, or cephalothin. No growth in the presence of 2% NaCl or 2% $Na_2S_2O_3$. Grows well at 28 and 35°C. Growth fair at 40°C; no growth at 45°C. Produces a heptaene antifungal antibiotic.

The type strain is strain SCC 1014 (= ATCC 33937).

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