ϕ SC623, a temperate actinophage of *Streptomyces coelicolor* Müller, and its relatives ϕ SC347 and ϕ SC681

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Three species-specific, temperate actinophages of *Streptomyces coelicolor* Müller, ϕ SC623, ϕ SC347 and ϕ SC681, were compared with respect to host range, virion structure, antiserum cross-inactivation, DNA-restriction pattern, DNA hybridization, and DNA base composition. The restriction map of ϕ SC623 (57 kb) was established with eight restriction enzymes; the homologies of this phage with ϕ SC347 and ϕ SC681 suggested that it might be a hybrid phage composed of approximately equal parts homologous to one of the other two phages. No homology was detected between ϕ SC623 and R4, a temperate, wide-host-range phage which can also lysogenize *S. coelicolor* Müller.

Introduction

Streptomyces coelicolor Müller, (Müller, 1908) is one of the most abundant *Streptomyces* species isolated from soil (Flaig & Kutzner, 1960; Kutzner, 1981). It is characterized by the classical criteria (i) *griseus* aerial mycelium, (ii) flexuous aerial hyphae, (iii) smooth spores, and (iv) no melanin pigment. In addition it is more specifically recognized by the production of an antifungal heptaene antibiotic and a blue water-soluble pigment first named amylocyanin by Müller (1908) and later identified as indochrome (Habermehl *et al.*, 1977); unfortunately, the latter is not synthesized by all strains of this species. For a long time *S. coelicolor* was mistaken for *S. violaceoruber*, and vice versa, until the identity of the two species was clarified by Kutzner & Waksman (1959).

Strains of *S. coelicolor* Müller have been described under at least 20 different names; several of these synonyms were recognized by Kutzner (1961) by the host range of a species-specific phage. Our collection presently comprises 56 strains of this species which form a very homogeneous cluster with regard to phage-typing and physiological traits (Korn-Wendisch, 1982) as well as DNA restriction fragment patterns and isoenzyme patterns (F. Korn-Wendisch, unpublished data). This cluster includes synonyms such as *S. albus* P and *S. albus*

G, which are both well known for their restriction-modification systems (Chater & Wilde, 1976; Chater & Carter, 1978). It does not, however, include the best-characterized actinomycete strain *S. coelicolor* A3(2) (Hopwood *et al.*, 1985), which belongs to the species *S. violaceoruber* (Kutzner & Waksman, 1959).

Bacteriophages of *S. coelicolor* have played an important role in streptomycete taxonomy (Kutzner, 1961; Korn-Wendisch, 1982) and for the examination of host restriction barriers (Chater, 1986). Lysogeny in *S. coelicolor* Müller (strain *S. odorifer*) was mentioned, without detailed characterization, by Rautenshtein (1957). The temperate broad-host-range phage R4 (Chater & Carter, 1979) was isolated with *S. albus* G (Chater & Carter, 1978), and together with its close relative SH10 (Klaus *et al.*, 1981) it is one of the best-characterized *Streptomyces* phages (for a review see Chater, 1986).

Here we describe the temperate phage ϕ SC623 and compare it with ϕ SC347 and ϕ SC681, all three isolated from lysogenic strains of *S. coelicolor* (Korn-Wendisch, 1982). The possibility is discussed that ϕ SC623 is a hybrid phage resulting from a recombinational event or a reshuffling of phage modules (Botstein, 1980; Campbell & Botstein, 1983; Krylov *et al.*, 1985; Schneider & Kutzner, 1989*a, b*) between ϕ SC347 and ϕ SC681.

Methods

Bacterial strains and phages. The 56 strains of *S. coelicolor* Müller which had been screened for lysogeny are listed elsewhere (Korn-

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Wendisch, 1982). Strains DSM 40347 (synonym *S. odorifer*), 40485, 40607, 40623, 40680 and 40681 were sources of the temperate phages ϕ SC347, ϕ SC485, ϕ SC607, ϕ SC623, ϕ SC680 and ϕ SC681, respectively. The two non-lysogenic strains DSM 40622 and 40624 were used for the propagation of the phages. All these strains as well as typical representatives of other streptomycete species were obtained from the German Collection of Micro-organisms (DSM): *S. albus* DSM 40313, *S. griseus* DSM 40236, *S. californicus* DSM 40058, *S. cyaneoflavus* DSM 40672, *S. viridochromogenes* DSM 40666, *S. lavendulae* DSM 40069, *S. prasinus* DSM 40099, and *S. violaceoruber* DSM 40049. *S. lividans* TK64 and phage R4 (Chater & Carter, 1979) were kindly provided by T. Kieser and K. F. Chater (both of the John Innes Institute, Norwich, UK), respectively. The bacteria were grown as described by Kutzner (1981); phages were propagated and used for host range experiments according to Korn *et al.* (1978) and Schneider *et al.* (1989).

Determination of lysogeny. Broth cultures of different growth stages were filtered through a 0.2 μ m pore size membrane filter and 50 μ l volumes were spotted onto fresh lawns of various possible indicator strains. When lysed zones appeared after 36 h incubation at 28 °C, material from these spots was streaked over an agar plate (base layer); in order to obtain single plaques the plates were overlaid with a top layer containing spores of the same strain as was used to detect the phage from the culture supernatant. The phages thus detected usually gave rise to turbid plaques with growth of lysogenized indicator bacteria; the latter were streaked over an agar plate, incubated for 36 h at 28 °C and then overlaid with spores of the indicator strain. Lysogenized colonies released phages and were therefore surrounded by lysis zones within the indicator lawn; in addition, lysogenization of these cultures was demonstrated by their immunity to superinfection.

UV-facilitated enrichment of modified phages. The two host strains DSM 40622 and 40624 exhibited considerable restriction barriers for the phages used in this work. In order to overcome these barriers, high phage titres were used. In some cases, however, this did not result in plaque formation, and the UV enrichment procedure had to be applied. Provided that the host strains have typical type II restriction endonucleases and corresponding methylases, as is very common in *Streptomyces* (Cox & Baltz, 1984), it should be possible to mutate the endonuclease gene by UV irradiation in some spores without affecting the modification enzyme. Phage infection of the germinating restriction-negative spore should then result in modified phage progeny which can survive the infection of mycelia with an active endonuclease. A 3 ml volume of spore suspension (10^8 spores ml⁻¹) was irradiated for 20 s with a 254 nm UV lamp (270 μ W cm⁻²) to achieve a survival rate of approximately 1%. After irradiation, spores were collected by centrifugation and resuspended in 3 ml GPFH broth (Schneider *et al.*, 1987) containing 10^8 – 10^9 phages. After incubation at 28 °C for 48 h the culture supernatant was freed from bacteria by vigorous mixing with chloroform and used as a potential phage lysate (all phages described here were resistant to 30%, v/v, chloroform). The irradiation time necessary to achieve approximately 1% survival was determined by spreading spores in different dilutions over agar plates prior to UV treatment of various durations. Irradiation and subsequent incubation were either carried out in the dark, or plates were irradiated and left on the bench, exposed to laboratory illumination, for 30 min prior to incubation in the dark at 28 °C. After 48 h colonies were counted to obtain UV survival curves.

Handling of DNA. DNA preparation, characterization and hybridization with biotinylated probes were done as described before (Schneider *et al.*, 1987; Schneider & Kutzner, 1989a). The hybridization stringency was determined by two washes for 30 min: high stringency (homology >92%) was achieved with 0.05 $\times$ SSC/0.1% SDS at 70 °C (1 $\times$ SSC is 0.15 M-NaCl, 0.015 M-trisodium citrate, pH 7.0), medium stringency (homology >82%) with 0.2 $\times$ SSC/0.1% SDS

at 70 °C and low stringency (homology >72%) with 0.2 $\times$ SSC/0.1% SDS at 60 °C. For the evaluation of homologies, a G + C content of 71 mol% was assumed. Homologies between bacteriophage genomes were mapped as described by Schneider & Kutzner (1989b).

Determination of the G + C content and electron microscopy. The methods applied were recently described (Schneider *et al.*, 1989).

Serological studies. Antisera against the phages were prepared by immunization of rabbits and were used for serum spot tests and serum inactivation assays (Eisenstark, 1967; Shirling & Speer, 1967; Korn *et al.*, 1978).

Results

Out of the 56 strains of *S. coelicolor* Müller tested, only six proved to be lysogenic: DSM 40347, 40485, 40607, 40623, 40680 and 40681. The phages from DSM 40485 and 40607 (ϕ SC485 and ϕ SC607) were not included in the studies presented here. The phages from 40623 and 40680 (ϕ SC623 and ϕ SC680) turned out to have identical host ranges and restriction maps; even the restriction fragment patterns generated by enzymes which created a large number of fragments (e.g. *Bst*EII or *Sal*I) could not be distinguished. Our studies were therefore carried out with one of these (ϕ SC623) and with the two remaining phages (ϕ SC681 and ϕ SC347, isolated from DSM 40681 and 40347, respectively). The three phages were tested for infection of all *Streptomyces* species listed above by spotting high-titre phage suspensions (10^5 – 10^6 phages per spot) on bacterial lawns; plaques were only observed on strains of *S. coelicolor*.

Cross-immunity of the three phages

In order to study the cross-immunity of the temperate phages it was necessary to find at least one or two host strains which could be infected and lysogenized by all three phages. Furthermore, possible restriction barriers of these strains had to be considered to ensure that they would not interfere with the cross-immunity studies. *S. coelicolor* Müller strains DSM 40622 and 40624 were selected although they exhibited considerable restriction barriers (see below). These barriers, however, could be overcome either by applying high phage titres or by the UV-facilitated enrichment method (Table 1). Thus it was possible to use lysogenized derivatives of DSM 40622 (Table 1) and DSM 40624 (data not shown) for cross-immunity studies, revealing that ϕ SC623 and ϕ SC681 are homoimmune whereas both phages are heteroimmune with respect to ϕ SC347.

UV treatment as well as the subsequent incubation were carried out in the dark, because DSM 40622 and

Table 1. Cross-immunity test

These results were obtained by spot tests: +, plaque formation with diluted phage suspensions (10–30 phage per spot); ÷, single plaques (1–3) with high m.o.i. (10^5 – 10^6 phage per spot); #, plaque formation after UV enrichment; –, no plaque formation despite all attempts; ND, not determined, as interference with restriction barriers was expected.

Indicator strain	Lysogen of	Phages, and strains on which they were propagated								
		ϕ SC623			ϕ SC681			ϕ SC347		
		DSM 40623*	DSM 40622	DSM 40624	DSM 40681*	DSM 40622	DSM 40624	DSM 40347*	DSM 40622	DSM 40624
40622	–	+	+	#	#	+	#	+	+	÷
40624	–	#	#	+	+	#	+	+	÷	+
40622 ⁶²³	ϕ SC623	–	–	ND	ND	–	ND	+	+	÷
40622 ⁶⁸¹	ϕ SC681	–	–	ND	ND	–	ND	+	+	÷
40622 ³⁴⁷	ϕ SC347	+	+	ND	ND	+	ND	–	–	–

* Phages were obtained from supernatants of these lysogenic strains, which were the original source of the phages.

40624 exhibited a powerful photoreactivation system as shown by the comparison of the 'dark' and 'light' survival results (Table 2). For example, 30 s of UV irradiation in the dark resulted in 0.015% survival, whereas 30 min subsequent exposure to laboratory illumination increased survival 147-fold. Photoreactivation systems are widely distributed in bacteria and have also been reported for various *Streptomyces* species (Sutherland, 1977; Parson, 1983; Hopwood *et al.*, 1985).

Table 2. Photoreactivation after UV treatment of DSM 40624

Spores were irradiated with UV and either (a) exposed to laboratory illumination for 30 min prior to incubation in the dark, or (b) directly incubated in the dark (see text for further explanation). Similar results were obtained with DSM 40622 and DSM 40623.

Irradiation time (s)	Surviving c.f.u.(%)		Ratio a/b
	(a) Light	(b) Dark	
0	100	100	1
5	91.5	63	1.5
10	48.5	23.5	2.1
15	16	2.25	7.1
20	11.7	0.77	15.2
25	3.15	0.04	78.8
30	2.2	0.015	147
35	0.7	0.0073	95.9
40	0.22	0.0035	62.9
45	0.05	0.00083	60.2
50	0.019	0.00071	26.8
55	0.01	0.00053	18.9
60	0.006	0.00054	11.1
75	0.00095	0.00048	2
90	0.0006	0.00043	1.4

Restriction-modification systems of the host strains

The presumed restriction-modification systems of DSM 40622 and 40624 obviously have different specificities (Table 3) as shown by testing diluted phage suspensions (10–30 phages per spot) of different origin for plaque formation on the two strains; phages propagated on DSM 40622 did not form plaques on DSM 40624, and vice versa; 40624-grown phages did not plaque on DSM 40622. Furthermore, ϕ SC347 obtained from the culture supernatant of its original host strain, DSM 40347, could be propagated on either of the two strains, whereas ϕ SC623 from DSM 40623 only formed plaques on DSM 40622 and ϕ SC681 from DSM 40681 on DSM 40624. The restriction-modification systems were not investigated further, but total DNA from both strains as well as phage DNA replicated by them could be digested with *SalI* and *PstI* – both restriction-modification systems are known from other strains of *S. coelicolor* (Chater & Carter, 1978; Chater & Wilde, 1976) – as well as with *SacI*, *SacII*, *ScaI*, *SmaI* and *XhoI*, all known to be produced by other

Table 3. Restriction barriers of DSM 40622 and 40624

Indicator strain	Phage lysates obtained with DSM:				
	40622*	40624*	40623†	40681†	40347†
40622	+	–	+	–	+
40624	–	+	–	+	+

*† Phages (ϕ SC623, ϕ SC681 or ϕ SC347) were propagated on 40622 or 40624 (*), or obtained from supernatants of the corresponding lysogenic strains (†). +/–, Plaques/no plaques were observed when diluted phage suspensions (10–30 phages per spot) were used in spot tests (compare Table 1).

streptomycetes (Cox & Baltz, 1984). This indicated that in both cases new restriction-modification systems might be involved.

Characterization of the phages

The three phages produced small, turbid plaques of variable size (0.1–2 mm in diameter) from which lysogenized bacteria could easily be isolated. The virions (not shown) were of the B1 morphotype (Ackermann & Dubow, 1987) with isometric heads (ϕ SC623 and ϕ SC681, 66×68 nm; ϕ SC347, 63×65 nm) and medium-length tails (ϕ SC623 and ϕ SC681, 230×10 nm; ϕ SC347, 190×10 nm). Antisera prepared against ϕ SC623 and ϕ SC347 inactivated all three phages equally well. The phages have a linear dsDNA genome with cohesive ends and a size of about 57 kb as determined by adding up the restriction fragments generated with three or four enzymes. The DNA of ϕ SC681 had a G + C content of 69 mol%, whereas the G + C content of the other two phages was somewhat higher (71.5 mol%). The physical properties of the three genomes therefore resemble those of other temperate streptomycete phages (Chater, 1980, 1986; Ackermann & Dubow, 1987). The host strains DSM 40622 and 40624 have a G + C content of 72.4 mol%.

Fig. 1. The DNA of the three phages was digested with *BsrEII*, separated by agarose gel electrophoresis (a), transferred to nitrocellulose filters, and hybridized with biotinylated DNA of ϕ SC681 (b) and ϕ SC347 (c). Lanes: 1, ϕ SC347; 2, ϕ SC681; 3, ϕ SC623. Stringency > 82% homology with high probe concentrations (approx. 200 ng biotinylated DNA ml⁻¹). Note that the two probes hybridized with different fragments of ϕ SC623 and that ϕ SC681 and ϕ SC347 showed hardly any homology with each other.

Fig. 2. Restriction map of ϕ SC623. (a) Restriction enzymes: B, *Bam*HI; Bg, *Bgl*II; E, *Eco*RV; H, *Hind*III; K, *Kpn*I; P, *Pst*I; S, *Sac*I; Sc, *Sc*I. The size of the restriction fragments is given in kb. In addition, ϕ SC623 has many sites (> 15) for *BsrEII*, *Pvu*II, *Sac*II, *Sal*I, *Sma*I and *Xho*I. (b) The fragments created by multiple digests with *Bam*HI + *Bgl*II + *Pst*I and with *Kpn*I + *Sac*I are shown. The homologies of these fragments with ϕ SC681 and ϕ SC347 are indicated by hatching: ▨, ϕ SC347; ▩, ϕ SC681; ▤, both phages. The lines beneath indicate the highest resolution in mapping the homologies which could be obtained with different combinations of restriction enzymes; the interrupted lines represent regions of lower homology.

Homologies between the three phage genomes

Restriction fragment patterns of the phage genomes created with frequently cutting enzymes (Fig. 1) demonstrated that the three DNAs were different. DNA-DNA hybridization, however, revealed an interesting distribution of homologies: when ϕ SC681 or ϕ SC347 DNAs were used as biotinylated probes, each of them hybridized with different fragments of ϕ SC623 generated by a *Bst*EII digest. On the other hand, ϕ SC681 and ϕ SC347 showed hardly any homology with each other (Fig. 1). For a more detailed investigation of this observation, a restriction map of ϕ SC623 was established and used for mapping the homologies between this and the other two phages (Fig. 2). Approximately 50% of the ϕ SC623 genome exhibited strong homology with ϕ SC347 whereas the other half hybridized with ϕ SC681. Within this part, however, one region also gave weak signals with ϕ SC347. The homologies between ϕ SC623 and ϕ SC347 were observed using high-stringency conditions whereas ϕ SC681 gave good signals only at medium stringency. The two cohesive ends of the linear ϕ SC623 genome hybridized with ϕ SC347 only. The genome of the temperate phage R4 exhibited no homologies with DNA of ϕ SC623.

Discussion

The hypothesis of modular evolution of bacteriophages suggests a colinear organization of the genomes of a wide range of tailed phages which enables them to undergo recombination at short, conserved 'recombination spacers' which are located between the individual functional genetic modules (Botstein, 1980; Campbell & Botstein, 1983). This recombination could then result in viable phages with a new combination of genetic information, leading to the spread of successful phage modules among phage populations which are not necessarily closely related (Schneider & Kutzner, 1989a).

ϕ SC623 may be considered as an example for modular evolution in actinophages: one can imagine a recombinational event between the hardly related (in terms of DNA homology) ϕ SC681 and ϕ SC347, involving at least two crossovers at two conserved 'recombination spacers' which might account for the homologies observed between the two phages. This event would result in a phage with mixed genetic information from ϕ SC347 (e.g. the cohesive ends and presumably the determinant for the endonuclease recognizing them) and from ϕ SC681 (e.g. the region responsible for the homoinmunity between ϕ SC681 and ϕ SC623, perhaps the phage repressor gene). It seems that the ϕ SC347-derived modules of ϕ SC623 have changed less during evolution

than those that the phage has in common with ϕ SC681; this is indicated by the different stringencies which had to be applied in order to detect homologies and by the differences in G + C content.

This model is only a preliminary speculation, as ϕ SC623 is not necessarily a progeny of the two other phages; it might have collected modules, some of which were also acquired by ϕ SC347, others by ϕ SC681. Further studies, especially focusing on the genetic functions of possible modules, are needed. In order to identify individual modules, it will be necessary to examine other *Streptomyces* phages, such as the different homology groups recently described by Diaz *et al.* (1989), for homology with ϕ SC623. These studies should not be limited to temperate phages but could include virulent ones, as the exchange of modules can also occur between temperate and virulent phages (Schneider & Kutzner, 1989a, b).

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