A Phylogenetic Analysis of the Family *Dermatophilaceae*

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The comparative analysis of the 16S ribosomal ribonucleic acid (rRNA) of *Geodermatophilus obscurus* DSM 43060 and *Dermatophilus congolensis* DSM 43037 revealed that these members of the family *Dermatophilaceae* were only remotely related. While *G. obscurus* represented an individual and separate line of descent within the phylogenetically defined order *Actinomycetales*, *D. congolensis* was closely related to representatives of *Arthrobacter*, *Micrococcus*, *Cellulomonas*, *Brevibacterium*, *Promicromonospora* and *Microbacterium*.

INTRODUCTION

The family *Dermatophilaceae* is one of the eight families constituting the order *Actinomycetales* (Gottlieb, 1974). The *Dermatophilaceae* harbours two genera, *Dermatophilus* and *Geodermatophilus*, each with a single species, *D. congolensis* and *G. obscurus*, respectively. *Geodermatophilus* was included in the *Dermatophilaceae* by Luedeman (1968), mainly on the basis of a single morphological character, namely the ability to divide in transverse and longitudinal planes to form masses of cuboid cells. Quoting Roberts (1981), 'This may be an excessive significance to attach to a simple structural characteristic . . . '.

The two species are identical only in peptidoglycan type (Lechevalier *et al.*, 1971), while they show significant differences in DNA G + C content (Samsonoff *et al.*, 1977), in whole cell sugars and phospholipid composition (Lechevalier & Lechevalier, 1981) and in their morphological development (Roberts, 1981). As pointed out by Samsonoff *et al.* (1977) the significant difference in the DNA G + C content of about 15 mol% makes it unlikely that *G. obscurus* and *D. congolensis* are representatives of two closely related genera. Doubt has also been cast on the specific relatedness of *G. obscurus* and *D. congolensis* by the results of a numerical taxonomic study (Goodfellow & Pirouz, 1982). The question is whether the two genera are phylogenetically more closely related to each other than to any organism of another family. Only then can one say that *Dermatophilus* and *Geodermatophilus* are members of one family in the phylogenetic sense.

One of the well-established, reliable methods of elucidating relationships at the family level is the comparative analysis of 16S ribosomal RNA. We have recently applied this method to the determination of the degree of natural relationship within the broad group of actinomycetes and coryneform organisms, including *G. obscurus* (Stackebrandt *et al.*, 1983): *G. obscurus* was found to represent an individual line of descent within this group. We now present the results of 16S rRNA analysis of *D. congolensis*, showing that this species is more closely related to *Arthrobacter* and related taxa than to *G. obscurus*.

METHODS

Organism and cultivation. *Dermatophilus congolensis* DSM 43037 (= IMRU V-1240 = A. Seino A-0081) was obtained from the Deutsche Sammlung von Mikroorganismen (DSM), Göttingen, F.R.G. The identity of this strain was confirmed by the DSM by morphology, analysis of the peptidoglycan and the presence of madurose (Lechevalier & Lechevalier, 1981). The strain was cultivated in 600 ml of a malt extract (Merck)/yeast extract (Oxoid)/glucose broth (1:0.4:0.4%, w/v) for 16 h at 37 °C.

16S rRNA analysis. Cells were broken by passing through a French pressure cell. The isolation of 16S ribosomal RNA followed the methods described by Stackebrandt *et al.* (1981). Controlled digestion of RNA with RNAase T₁, dephosphorylation of the 3' end of oligonucleotides with alkaline phosphatase from calf intestine, enzymic *in vitro* labelling of the 5' ends with [γ -³²P]ATP and polynucleotide kinase, and the determination of the nucleotide sequences, followed the description of Stackebrandt *et al.* (1982a). Binary matching coefficients (S_{AB} values) were calculated according to Fox *et al.* (1977). A dendrogram was generated from the S_{AB} values by average linkage (between the merged groups) clustering.

Whole cell sugar, fatty acid and menaquinone analysis. Isolation and identification of whole cell sugars were done as described by Kroppenstedt (1977). Fatty acids were isolated according to Minnikin *et al.* (1975) and the composition determined using described methods (Kroppenstedt & Kutzner, 1978). The isolation of menaquinones followed the method of Collins *et al.* (1977), modified by Kroppenstedt (1983); their identification was carried out by HPLC (Kroppenstedt, 1983).

RESULTS AND DISCUSSION

The oligonucleotide catalogue of the 16S rRNA of *D. congolensis* DSM 43037 is listed in Table 1, column 1. The presence of the oligonucleotides in catalogues of 18 strains of *Arthrobacter* and related taxa, 3 strains of *Corynebacterium*, 7 strains of *Mycobacterium*, *Nocardia* and *Rhodococcus*, 4 strains of *Actinoplanes* and related taxa, 6 strains of *Streptomyces* and related taxa, *Streptosporangium roseum* DSM 43021, *Thermomonospora curvata* DSM 43183 and *G. obscurus* DSM 43160 are shown in columns 2–9, respectively. Each column represents an individual line of descent within the phylogenetically defined group of the order *Actinomycetales* (Stackebrandt & Woese, 1981; Stackebrandt *et al.*, 1983). Of the 67 oligonucleotides constituting the 16S rRNA catalogue of *D. congolensis*, 28 are also present in the catalogues of almost all strains of the taxa listed in columns 2–9, indicating that these oligonucleotides are highly conserved in the primary structure of the 16S rRNA of these organisms, and hence without significance in determining specific relationships. By far the highest number of additional identical oligonucleotides (17) is found between the catalogues of *D. congolensis* and at least 50% of the strains of that cluster defined by *Arthrobacter* and related organisms (Table 1, column 2). The number of additional common oligonucleotides between the catalogues of *D. congolensis* and the other phylogenetically defined groupings (columns 3–9) are much lower (8–12); *D. congolensis* and *G. obscurus* share only 9 common oligonucleotides in addition to the conserved ones.

The binary matching coefficients (S_{AB} values) for *D. congolensis* DSM 43037 and representatives of the phylogenetically defined groupings listed in Table 1, columns 2–9 are given in Table 2. Figure 1 is a dendrogram, calculated from the S_{AB} values. A more detailed picture of the phylogeny of the various groupings has already been published (Stackebrandt & Woese, 1979, 1981; Stackebrandt *et al.*, 1980, 1983).

Dermatophilus congolensis DSM 43037 shows similar high S_{AB} values to representatives of *Arthrobacter*, *Micrococcus*, *Cellulomonas*, *Promicromonospora*, *Brevibacterium* and *Microbacterium*. The average linkage clustering, however, indicates that *D. congolensis* is slightly more closely related to species of a subcluster defined by the first four genera. No specific relationship can be detected between *D. congolensis* and *G. obscurus*: the degree of relationship found for the two species is only as high as that found between any two species of different main sublines within the order *Actinomycetales*.

The rather low degree of relatedness found between *D. congolensis* and *G. obscurus* is also seen in the lack of similarity of chemotaxonomic properties (Table 3).

Dermatophilus congolensis DSM 43037 possessed tetrahydromenaquinones with eight isoprene units [MK-8(H₄)] as sole component, while *G. obscurus* contained tetrahydromenaquin-

Table 1. RNAase T₁-resistant oligonucleotides from the 16S rRNA of *Dermatophilus congolensis* DSM 43037 (column 1) and occurrence of these oligonucleotides in members of various phylogenetically defined groups (columns 2–9)

The catalogues of organisms constituting the individual groups have been published: *Arthrobacter* group, which is here defined to include *Micrococcus*, *Cellulomonas*, *Oerskovia*, *Promicromonospora*, *Microbacterium* and *Brevibacterium* (Stackebrandt *et al.*, 1980); *Corynebacterium* group and *Mycobacterium/Nocardia* group (Stackebrandt *et al.*, 1980; Stackebrandt *et al.*, 1983); *Actinoplanes* group (Stackebrandt & Woese, 1981; Stackebrandt *et al.*, 1983); *Streptomyces* group, *Streptosporangium roseum* DSM 43021, *Thermomonospora curvata* DSM 43183, and *Geodermatophilus obscurus* DSM 43160 (Stackebrandt *et al.*, 1983).

1	2	3	4	5	6	7	8	9
<i>Dermatophilus congolensis</i>	<i>Arthrobacter</i> group	<i>Corynebacterium</i> group	<i>Mycobacterium/Nocardia</i> group	<i>Actinoplanes</i> group	<i>Streptomyces</i> group	<i>Streptosporangium roseum</i>	<i>Thermomonospora curvata</i>	<i>Geodermatophilus obscurus</i>
ACACAG	—	—	—	—	—	—	+	—
CACAAG	18/18	3/3	7/7	4/4	5/6	+	+	+
CUAACG	15/18	3/3	6/7	4/4	6/6	+	+	+
AUAACG	6/18	—	4/6	3/4	4/6	+	+	+
ACACUG	1/18	—	—	—	—	—	—	+
ACUAAG	18/18	—	—	—	—	—	—	—
AAUACG	18/18	3/3	7/7	3/4	6/6	—	+	—
UAAACG	17/18	3/3	7/7	4/4	6/6	+	+	+
UUCCCG	18/18	3/3	7/7	4/4	6/6	+	+	+
CCUUCG	18/18	3/3	7/7	4/4	6/6	+	+	+
UCUCAG	17/18	2/3	7/7	4/4	6/6	+	+	+
UCCAUG	16/18	3/3	—	—	—	—	—	—
AUCCUG	17/18	3/3	4/7	4/4	6/6	+	+	+
UACCUG	17/18	2/3	4/7	4/4	6/6	+	+	+
UAAUCG	17/18	3/3	7/7	4/4	6/6	+	+	+
AAUCUG	—	—	—	—	—	—	—	—
CUAAUG	—	—	—	—	—	—	—	—
UCUCUG	14/18	3/3	7/7	4/4	—	—	—	—
AUUCUG	1/18	—	—	—	—	—	—	—
ACUUUG	—	—	—	—	—	—	—	—
UAACAAG	18/18	3/3	7/7	4/4	6/6	+	+	+
AACACCG	18/18	2/3	6/7	4/4	5/6	+	+	+
CAACUCG	17/18	3/3	7/7	4/4	6/6	+	+	+
CACAACG	18/18	3/3	7/7	4/4	6/6	—	—	—
UAAACG	15/18	3/3	7/7	4/4	6/6	+	+	+
CUUCACG	17/18	—	—	4/4	—	—	—	—
ACUCAUG	8/18	1/3	—	—	—	—	+	+
CAUUACG	18/18	3/3	7/7	4/4	6/6	+	+	+
UAAUACG	18/18	3/3	7/7	—	6/6	+	—	+
AUAUCAG	18/18	3/3	7/7	4/4	6/6	+	—	+

1	2	3	4	5	6	7	8	9
<i>Dermatophilus</i> <i>congolensis</i>	<i>Arthrobacter</i> group	<i>Corynebacterium</i> group	<i>Mycobacterium</i> <i>Nocardia</i> group	<i>Actinoplanes</i> group	<i>Streptomyces</i> group	<i>Streptosporangium</i> <i>roseum</i>	<i>Thermomonospora</i> <i>curcata</i>	<i>Geodermatophilus</i> <i>obscurus</i>
UAAUUCG	—	—	—	—	—	—	—	—
AAUAUUG	18/18	3/3	7/7	4/4	5/6	+	—	+
CCACACUG	18/18	—	7/7	4/4	6/6	+	+	+
ACCCCAUG	15/18	2/3	1/7	—	6/6	+	+	+
CCUAUCAG	17/18	2/3	7/7	4/4	6/6	+	+	+
AUACCCUG	18/18	3/3	7/7	3/4	6/6	+	+	+
UCAACUCG	18/18	1/3	7/7	4/4	6/6	+	+	+
CUACAAUG	18/18	3/3	7/7	4/4	6/6	+	+	+
AAUUCUG	18/18	3/3	7/7	4/4	6/6	+	+	+
AAUAUUG	18/18	—	—	—	6/6	+	+	+
UUUUUUCG	—	1/3	—	2/4	—	+	—	—
UCUUUUUG	—	—	—	—	—	—	—	—
AAAAUCCCG	—	—	—	—	—	—	—	—
CAACCCUG	16/18	—	—	3/4	—	—	+	+
CUCACCAAG	1/18	—	—	—	3/6	—	—	—
UACACCCG	16/18	3/3	7/7	1/4	6/6	—	—	—
UACACACCG	18/18	3/3	7/7	4/4	6/6	+	+	+
ACUCCUAG	18/18	3/3	7/7	4/4	6/6	+	+	+
CUAACUACG	18/18	3/3	2/7	—	6/6	+	+	—
CCCCUUAUG	17/18	3/3	7/7	4/4	6/6	+	+	—
CCAUUACUG	2/18	—	—	—	4/6	—	—	—
AUUAUUCG	18/18	3/3	7/7	4/4	—	—	—	—
ACAUACACG	5/18	—	4/7	—	2/6	—	—	—
CUUAAACCAUG	—	—	—	—	—	—	—	—
UCUAAUACUG	6/18	—	—	—	—	—	—	—
UCCAUUCCACG	1/18	—	—	—	—	—	—	—
CCUAAACCCUUG	7/18	—	—	—	—	—	—	—
CUUAAACACAUG	17/18	3/3	7/7	4/4	6/6	+	+	+
ACCUUUCUCG	—	—	—	—	—	—	—	—
AACCUUACCAAG	18/18	—	—	—	6/6	+	+	—
CCCCUCACUUUG	—	—	—	—	—	—	—	—
AAUCACUUAAAAG	—	—	—	—	—	—	—	—
CUAAAAUCUCAAAG	18/18	3/3	7/7	4/4	6/6	+	+	+
UCAAAUCAUCAUG	17/18	—	—	—	—	—	—	—
UAAACCUUCUUCAG	10/18	—	5/7	2/4	6/6	+	—	+
UACUCCCCUUUUUG	—	—	—	—	—	—	—	—
AUCACCUCCUUUCU _{OH}	18/18	3/3	7/7	4/4	6/6	+	+	+

Table 2. Binary comparisons among the 16S rRNA catalogues from *Dermatophilus congolensis* DSM 43037 and *Geodermatophilus obscurus* and various representatives of actinomycetes and related taxa, expressed as S_{AB} values

	<i>Dermatophilus congolensis</i>	<i>Geodermatophilus obscurus</i>
<i>Arthrobacter</i> group		
<i>Arthrobacter globiformis</i> DSM 20124	0.65	0.53
<i>Arthrobacter oxydans</i> DSM 20119	0.63	0.50
<i>Micrococcus luteus</i> ATCC 23262	0.70	0.51
<i>Micrococcus roseus</i> UWO 1057	0.67	0.47
<i>Micrococcus varians</i> DSM 20033	0.71	0.46
<i>Cellulomonas</i> group		
<i>Cellulomonas flavigena</i> DSM 20109	0.66	0.49
<i>Cellulomonas cartae</i> DSM 20106	0.67	0.56
<i>Oerskovia turbata</i> NCIB 10587	0.65	0.52
<i>Microbacterium</i> group		
<i>Microbacterium lacticum</i> DSM 20172	0.61	0.45
<i>Corynebacterium betae</i> DSM 20141	0.69	0.50
<i>Promicromonospora citrea</i> DSM 43110	0.63	0.56
<i>Brevibacterium linens</i> DSM 20158	0.58	0.43
<i>Corynebacterium</i> group		
<i>Corynebacterium diphtheriae</i> ATCC 11913	0.50	0.43
<i>Corynebacterium glutamicum</i> ATCC 13059	0.47	0.38
<i>Arthrobacter variabilis</i> DSM 20132	0.50	0.39
<i>Mycobacterium/Nocardia</i> group		
<i>Mycobacterium phlei</i> ATCC 11758	0.50	0.43
' <i>Nocardia corallina</i> ' ATCC 4273	0.53	0.49
<i>Nocardia calcareo</i> ATCC 19369	0.55	0.46
<i>Nocardia asteroides</i> DSM 43245	0.60	0.51
<i>Corynebacterium fascians</i> DSM 20131	0.57	0.47
<i>Actinoplanes</i> group		
<i>Actinoplanes philippinensis</i> DSM 43019	0.55	0.49
<i>Ampullariella regularis</i> DSM 43151	0.51	0.50
<i>Dactylosporangium aurantiacum</i> NRRL B8111	0.55	0.51
<i>Micromonospora chalybeata</i> NRRL B2344	0.52	0.50
<i>Streptomyces</i> group		
<i>Streptomyces griseus</i> strain 1947	0.60	0.52
<i>Kitasatoa kawaiensis</i> DSM 43360	0.62	0.55
<i>Streptovercillium baldacii</i> DSM 40845	0.57	0.52
<i>Elytrosporangium brasiliensis</i> DSM 43159	0.59	0.52
<i>Streptosporangium roseum</i> DSM 43021	0.57	0.57
<i>Thermomonospora curvata</i> DSM 43183	0.51	0.46
<i>Geodermatophilus obscurus</i> DSM 43160	0.59	1.00
<i>Dermatophilus congolensis</i> DSM 43037	1.00	0.59

ones with nine isoprene units [MK-9(H_4)] as sole component. The fatty acid composition of the two strains differed markedly. Thus *D. congolensis* had predominantly straight-chain fatty acids (65% of total fatty acids) (14:0 : 15:0 : 16:0 : 17:0 : 18:0 in ratios 14 : 10 : 33 : 17 : 7%) while 35% were composed of almost equal amounts of C16, C17 and C18 monounsaturated branched components. In contrast, *G. obscurus* had small amounts of straight-chain, anteiso branched and monounsaturated branched fatty acids (20, 19 and 5%, respectively) while 52% of total fatty acids were iso-branched components (i-14 : i-15 : i-16 : i-17 in ratios 4 : 26 : 20 : 2%). Differences were also found in the whole cell sugar composition: *D. congolensis* contained madurose (Lechevalier and Lechevalier, 1981) in addition to smaller amounts of glucose and ribose, while in agreement with Lechevalier & Lechevalier (1981) no sugar of diagnostic value was found in *G. obscurus*, which contained only small amounts of galactose, glucose and ribose.

Fig. 1. Dendrogram derived by average linkage clustering using a Dice-type similarity coefficient, S_{AB} (Fox *et al.*, 1977).

Table 3. Chemical characters of *Dermatophilus* and phylogenetically related genera and of *Geodermatophilus*

Literature references are indicated by superscript letters: *a*, Samsonoff *et al.* (1977); *b*, Keddie & Jones (1981); *c*, Kloos *et al.* (1974); *d*, Stackebrandt *et al.* (1982*b*); *e*, Goodfellow & Minnikin (1981); *f*, Schleifer & Kandler (1972); *g*, Collins & Jones (1981); *h*, Kroppenstedt (1977); *i*, Collins *et al.* (1982).

Abbreviations. Peptidoglycan: Ala, alanine; m-Dpm, *meso*-diaminopimelic acid; Glu, glutamic acid; Lys, lysine; Orn, ornithine; Ib*, interpeptide bridge with variable amino acids. Isoprenoid quinones: MK, menaquinone (the numbers indicate the number of isoprenoid units, and H₂, etc., indicates the degree of hydrogenation). Fatty acids: S, straight chain; U, monounsaturated; I, *iso*; A, *anteiso* (main components italicized). Sugars: Gal, galactose; Glc, glucose; Mad, madurose; Man, mannose; Rham, rhamnose; Rib, ribose.

Taxon	DNA G + C content (mol %)	Peptidoglycan		Major isoprenoid quinone	Fatty acids	Cell sugars
		Type ^f	Group ^f			
<i>Dermatophilus</i>	57.4–58.7 ^a	m-Dpm	A	MK-8(H ₄)	S, U ^h	Glc, Mad, Rib
<i>Arthrobacter sensu stricto</i> †	59–66 ^b	L-Lys-Ib*		MK-9(H ₂) ^g	S, I, A ^e	Gal ^e
<i>Micrococcus</i>	64–73 ^c	L-Lys-Ib*		MK-7/8(H ₂) ^g	ND	ND
<i>Cellulomonas/Oerskovia</i>	70.5–76.6 ^d	L-Orn-Ib*/L-Lys-Ib*		MK-9(H ₄) ^g	S, I, A ^e	Man, Rham, Rib ^e Gal ^e
<i>Promicromonospora</i>	73–74 ^e	L-Lys-L-Ala ₂		MK-9(H ₄) ^g	S, I, A ^e	Gal, Glc ^e
<i>Brevibacterium</i>	60–64 ^b	m-Dpm		MK-8(H ₂) ^g	S, I, A ^e	Glc, Gal, Rib ^e
<i>Microbacterium</i>	69–70 ^b	L-Lys-D-Glu	B	MK-10/11/12 ⁱ	S, I, A ⁱ	Gal, Rham ^e
<i>Geodermatophilus</i>	72.9–74.6 ^a	m-Dpm	A	MK-9(H ₄)	S, I, A ^h	Glc, Gal, Rib

ND, Not determined.

† As defined by Keddie & Jones (1981).

The work reported here supports earlier findings concerning the genetic and phenotypical heterogeneity of the family *Dermatophilaceae* (Samsonoff *et al.*, 1977; Goodfellow & Pirouz, 1982; Roberts, 1981) although the extent to which the two species are related could not be detected previously. Our results exclude the possibility that *Dermatophilus* and *Geodermatophilus* are members of one phylogenetically defined family. The data on *G. obscurus* point towards its classification in a family of its own, because of the isolated position of this species within the phylogenetic tree of the actinomycetes and related taxa. In contrast, *D. congolensis* cannot be defined as a genus representing a family of its own and is rather a representative of a genus which is phylogenetically equivalent to the genera of the coryneform and actinomycete group of organisms, i.e. *Arthrobacter*, *Micrococcus*, *Cellulomonas*, *Promicromonospora*, *Brevibacterium* and *Microbacterium*. The distinct position of *Dermatophilus* within this group is also shown by the differences in chemotaxonomic markers (Table 3).

It is surprising to find an organism with such complex morphology to belong in the same phylogenetic grouping as mainly rod-shaped or even spherical bacteria. However, other morphologically fairly complex forms, such as branched or even mycelium-producing organisms, have recently been shown to be closely related to the morphologically simpler forms (Stackebrandt & Woese, 1979; Stackebrandt *et al.*, 1982*b*; Döpfer *et al.*, 1982). Our result on the relationship between *D. congolensis* and *G. obscurus* is another example of the unsuitability of morphological features in the systematics of bacteria, if a taxonomic rank above the species level is to mirror a true natural relationship.

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