Phylogenetic Analysis of the Genera *Cellulomonas*, *Promicromonospora*, and *Jonesia* and Proposal To Exclude the Genus *Jonesia* from the Family *Cellulomonadaceae*

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The 16S rRNA gene sequences of eight *Cellulomonas* species, two *Promicromonospora* species, and *Jonesia denitrificans* were determined, and these sequences were compared with the sequences of about 50 representatives of the *Arthrobacter* line of descent in the order *Actinomycetales*. We found that in spite of its current assignment to the family *Cellulomonadaceae*, *J. denitrificans* branches outside the radiation of this taxon and cannot be considered a member of it. The two *Promicromonospora* species do not cluster separately from *Cellulomonas* species and are more closely related to *Cellulomonas* species than to each other.

The family *Cellulomonadaceae* currently contains the following four genera, which have been deemed to be phylogenetically related on the basis of partial 16S rRNA sequence data: *Cellulomonas*, *Oerskovia*, *Promicromonospora*, and *Jonesia* (18, 21, 22, 24–27). One of these genera, the genus *Jonesia*, is the most dissimilar genus in terms of chemotaxonomic properties, as exemplified by a DNA G+C content that is about 15 mol% lower than the G+C contents found in the other members of the family and by the presence of fully saturated isoprenologs (MK-9); the other members of the family possess hydrogenated menaquinones of the MK-9(H₄) type (18). The placement of the genus *Jonesia* in the family *Cellulomonadaceae* was not unambiguous (26, 27) because the branching point of the only species, *Jonesia denitrificans*, did not fall consistently within the radiation of cellulomonads but changed according to the number and choice of reference organisms included in analyses of 16S rRNA catalogs.

A second problem concerns the relatedness of the genera *Cellulomonas* and *Oerskovia*. Members of these two genera have been found to be phylogenetically intermixed (22), which has led to the transfer of *Oerskovia* species to the genus *Cellulomonas* (28). On the other hand, morphological characteristics and the amino acid compositions of peptidoglycans, characteristics which have been used in the past to delineate actinomycete genera, differ in members of these two genera (5, 20, 21, 22). A taxon name does not become invalid because of a proposed taxonomic rearrangement (13), and the genus *Oerskovia* was included as a separate genus in the description of the family *Cellulomonadaceae* (27).

To provide a phylogenetically more stable basis for the genera of the family *Cellulomonadaceae* and to identify the position of the genera mentioned above within the radiation of the *Arthrobacter* branch of the order *Actinomycetales*, we sequenced the almost complete 16S ribosomal DNAs (rDNAs) of the type strains of all validly described *Cellulomonas* species and compared these sequences with the homologous sequences available for other actinomycetes.

MATERIALS AND METHODS

Strains investigated. *Cellulomonas biazotea* DSM 20112^T (T = type strain), *Cellulomonas cellasea* DSM 20118^T, *Cellulomonas cellulans* DSM 43879^T, *Cellulomonas fermentans* DSM 3133^T, *Cellulomonas fimi* DSM 20113^T, *Cellulomonas flavigena* DSM 20109^T, *Cellulomonas gelida* DSM 20111^T, *Cellulomonas (Oerskovia) turbata* DSM 20577^T, *Cellulomonas uda* DSM 20107^T, *J. denitrificans* DSM 20603^T, *Promicromonospora citrea* DSM 43110^T, *Promicromonospora enterophila* DSM 43852^T, *Brachybacterium faecium* DSM 4810^T, *Terrabacter tumescens* DSM 20308^T, and *Brevibacterium iodinum* DSM 20626^T are deposited in the DSM-German Collection of Microorganisms and Cell Cultures GmbH. *Cellulomonas*, *Terrabacter*, and *Brevibacterium*, *Jonesia*, *Promicromonospora*, and *Brachybacterium* strains were cultivated on media 53, 215, 65, and 92, as described in the DSM-Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH catalog of strains.

Analysis of 16S rDNA. Extraction of genomic DNA and amplification of the 16S rDNA were carried out as described previously (16). PCR products were sequenced directly by using a *Taq* DyeDeoxy Terminator Cycle Sequencing Kit (Applied Biosystems) according to the manufacturer's protocol. The sequence reaction mixtures were electrophoresed by using an Applied Biosystems model 373A DNA sequencer.

Phylogenetic analysis. The 16S rDNA sequences which we determined were compared with a 16S rDNA database consisting of the sequences of members of the *Arthrobacter* line of descent in the subphylum containing the order *Actinomycetales*, including sequences deposited in the Ribosomal Database Project (14) and recent releases (1, 11, 12, 17). Dissimilarity values were transformed into phylogenetic distance values that compensated for multiple substitutions at any given site in the sequence (10). Phylogenetic trees were reconstructed by additive treeing methods, such as the algorithms of De Soete (3) and Saitou and Nei (19), by using the corrected dissimilarity values. To calculate bootstrap values for 930 polymorphic sites, we analyzed 300 trees.

Peptidoglycan analysis. Preparation of cell walls and determination of peptidoglycan structure were carried out by previously described methods (20), except that thin-layer chromatography on cellulose sheets (TLC plastic sheets; Cellulose 5577; Merck, Darmstadt, Germany) was used instead of paper chromatography. Portions (1 mg) of freeze-dried cell walls were hydrolyzed in 0.2 ml of 4 N HCl at 100°C for 16 h and for 45 min to prepare total hydrolysates and partial hydrolysates, respectively. Diamino acids in the total hydrolysates were identified by using one-dimensional chromatography with a methanol-pyridine-water-10 N HCl (320:40:70:10, vol/vol/vol/vol) solvent system. Amino acids and peptides in the partial and total hydrolysates were identified by their mobilities and ninhydrin staining characteristics following two-dimensional chromatography with the system described by Schleifer and Kandler (20). The resulting fingerprints were compared with the fingerprints of known peptidoglycan structures.

Nucleotide sequence accession numbers. The 16S rDNA sequences which we determined have been deposited in the EMBL database under accession numbers X83799 to X83813.

RESULTS AND DISCUSSION

The almost complete 16S rDNA sequences of the 13 strains which we investigated, which consisted of between 1,420 and 1,480 nucleotides, were aligned with other sequences available

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TABLE 1. 16S rDNA similarity values for the type strains of species belonging to the family *Cellulomonadaceae* and some reference species investigated in this study

Organism	% 16S rDNA dissimilarity with:												
	<i>Cellulomonas flavigena</i>	<i>Cellulomonas gelida</i>	<i>Cellulomonas uda</i>	<i>Cellulomonas biasotea</i>	<i>Cellulomonas fimi</i>	<i>Cellulomonas cellasea</i>	<i>Cellulomonas fermentans</i>	<i>Cellulomonas cellulans</i>	<i>Cellulomonas turbata</i>	<i>Promicromonospora enterophila</i>	<i>Promicromonospora citrea</i>	<i>Terrabacter tumescens</i>	<i>Joncsia denitrificans</i>
<i>Cellulomonas gelida</i>	97.2												
<i>Cellulomonas uda</i>	96.7	98.8											
<i>Cellulomonas biasotea</i>	96.5	96.4	96.5										
<i>Cellulomonas fimi</i>	96.5	96.4	96.5	99.7									
<i>Cellulomonas cellasea</i>	96.2	96.3	96.2	98.0	98.0								
<i>Cellulomonas fermentans</i>	95.1	94.8	95.0	95.6	95.6	95.9							
<i>Cellulomonas cellulans</i>	93.8	94.5	95.4	94.7	94.6	94.6	93.9						
<i>Cellulomonas turbata</i>	95.6	96.1	95.9	95.7	95.7	96.4	94.8	95.7					
<i>Promicromonospora enterophila</i>	95.9	96.4	96.2	95.6	95.5	96.2	95.1	95.4	99.6				
<i>Promicromonospora citrea</i>	93.0	94.3	94.1	93.3	93.3	92.5	92.4	95.6	93.9	93.6			
<i>Terrabacter tumescens</i>	92.8	93.8	93.7	94.2	94.1	94.4	94.1	93.9	94.8	94.6	92.2		
<i>Joncsia denitrificans</i>	90.5	91.2	91.3	91.5	91.6	91.8	90.4	91.6	91.5	91.2	91.4	90.9	
<i>Nocardioides simplex</i>	88.6	89.1	89.1	89.0	89.1	88.6	88.6	89.6	88.3	88.6	89.0	88.5	86.3

for a selection of species that define the arthrobacterial lineage in the order *Actinomycetales*. Binary similarity values were determined for members of the genera *Agromyces*, *Arthrobacter*, *Brachybacterium*, *Brevibacterium*, *Clavibacter*, *Curtobacterium*, *Dermabacter*, *Dermatophilus*, *Microbacterium*, *Micrococcus*, *Rathayibacter*, *Renibacterium*, *Rothia*, and *Terrabacter*, and a similarity matrix was generated (Table 1). The overall level of 16S rDNA similarity for members of this lineage was high; the 16S rDNA similarity values were greater than 89% (data not shown).

Interfamily relationships. When the sequence of *Nocardioideus simplex* was used as a reference to root the *Arthrobacter* lineage (4), distance matrix analyses of dissimilarity values revealed that the majority of the strains which we studied are members of the following four main clusters: the *Arthrobacter-Micrococcus* group (12), the family *Microbacteriaceae* (17), the *Cellulomonas* group, and the *Brevibacterium-Brachybacterium* group (Fig. 1). *Dermatophilus congolensis* branches as an individual lineage. The position of the two *Brevibacterium* species does not agree with the position described in a recent report (1) in which the authors found that members of this genus represent a distinct actinomycete line of descent that exhibits no specific affinity to the genus *Arthrobacter* and its relatives. Both of the distance matrix algorithms used in this study suggested that the genus *Brevibacterium*, together with *J. denitrificans*, *Dermabacter hominis*, and *Brachybacterium faecium*, branches within the radiation of the *Arthrobacter* lineage. Low bootstrap values, however, indicated that the proposal that the *Arthrobacter-Brevibacterium* lineage has a common origin is not supported by the results of a statistical analysis. The phylogenetic position of *J. denitrificans* outside the radiation of the family *Cellulomonadaceae* is not unexpected. The same situation was found in several analyses of rRNA catalogs which were based on a significantly smaller number of sequences (18, 26). In those cases *P. citrea* also branched outside the family (18). *J. denitrificans* has a significantly lower DNA G+C content (56 to 58 mol%) than the cellulomonads (70 to 76 mol%). However, placement of this species outside the radiation of the *Cellulomonadaceae* is probably not an artifact induced by its G+C composition because the G+C content of the rRNA gene of this species (56.6 mol%) is within the range of values

found for members of the cellulomonad lineage (54.9 to 58.3 mol%). In several chemotaxonomic properties, such as the amino acid composition of the peptidoglycan, the presence of teichoic acids (6), the menaquinone type, and the G+C composition of the DNA (18), *J. denitrificans* differs from members of the genera *Cellulomonas* and *Promicromonospora*, and these properties were not given due consideration in the original discussion concerning the allocation of the genus *Jonesia* to the family *Cellulomonadaceae* (26). Now that the phylogenetic relationship between the genus *Jonesia* and the *Cellulomonas-Promicromonospora* group cannot be confirmed, the rationale for keeping the genus *Jonesia* in this family has vanished.

On the basis of 16S rDNA similarity data, the closest (albeit distant) relatives of *J. denitrificans* are *Dermabacter hominis* and *Brachybacterium faecium*. While *Dermabacter hominis*, a gram-positive, asporogenous, rod-shaped bacterium (9), has been isolated from human skin, *Brachybacterium faecium* is a pleomorphic coryneform bacterium that has been isolated from poultry deep litter (2). These two taxa are chemotaxonomically similar in that they possess *meso*-diaminopimelic acid in the peptidoglycan, fully unsaturated menaquinones, and fatty acid and polar lipid profiles frequently found in members of the *Arthrobacter* lineage (8). The presence of unsaturated menaquinones is shared with *J. denitrificans* but is not exclusive to members of the lineage. Interestingly, a loose relationship between *J. denitrificans* and *Brachybacterium faecium* was observed in an early numerical taxonomic analysis (7). In contrast to the previously published amino acid compositions of peptidoglycans (2, 9), neither *Dermabacter hominis* nor *Brachybacterium faecium* contains a directly cross-linked type A1 γ murein, as found in other members of the genera *Brevibacterium* and *Dermatophilus*, but these organisms contain a type A4 γ murein. While in *Dermabacter hominis* the peptide subunits are cross-linked by a glutamyl-asparagyl dipeptide, a diglutamyl peptide has been detected in cells of *Brachybacterium faecium*; in both taxa the α -carboxyl group of D-glutamic acid is replaced by glycine. In a previous phylogenetic study (1), *Dermabacter hominis* occupied an individual subline of descent in the *Arthrobacter* lineage, exhibiting a branching point at the root of three members of the *Arthrobacter* group. Even though the recent increase in the number of sequences of

FIG. 1. Distance matrix tree (3) showing the relationships of members of the *Arthrobacter* lineage in the subphylum containing the order *Actinomycetales*. The corrected dissimilarity values for members of the family *Cellulomonadaceae* and two reference organisms are shown in Table 1. Values for the other organisms have been published previously (11, 12, 17). The values indicate the percentages of occurrence in 300 bootstrapped trees; only values that are greater than 40% are shown. Bar = 5 nucleotide substitutions per 100 nucleotides.

members of this lineage from about 10 to about 50 (1, 11, 12, 17) allows much more precise measurement of relationships, a specific relationship between *Dermabacter hominis* and members of the *Arthrobacter*-*Micrococcus* group cannot be confirmed by results of this study.

Intrafamily relationships. When measured by the levels of similarity of the 16S rDNAs of the most unrelated members, the phylogenetic depth of the family *Cellulomonadaceae* is as great as the depth that separates the five genera that belong to the *Microbacteriaceae* and the four genera in the *Arthrobacter*-*Micrococcus* group. In these taxa, the traditionally defined gen-

era are not always clearly separated by a combination of phenotypic and chemotaxonomic properties, and their taxonomy is presently under revision (11, 17). Except for confirmation of the intermixing of *Cellulomonas* and *Oerskovia* species (22), the intrafamily relationships of the members of the *Cellulomonadaceae* which we observed were not expected. While in a previous phylogenetic analysis of members of the genera *Cellulomonas* and *Promicromonospora* based on the partial 16S rRNA sequences of five species, workers found that *P. citrea* groups outside the radiation of *Cellulomonas* species, the situation is different when almost all species of the genera *Cel-*

lulomonas and *Promicromonospora* are included. Type species *P. citrea* clusters with *Cellulomonas cellulans*, while *P. enterophila* is highly related to *Cellulomonas turbata* (level of sequence similarity, 99.4%). The close relationship between the latter two species has been noted previously (27), and DNA-DNA reassociation experiments will be required to determine whether these two taxa should be combined. Differences between members of the *Cellulomonas-Oerskovia* group and *Promicromonospora* species are mainly phenotypic. Unlike cellulomonads, *Cellulomonas (Oerskovia) turbata* and *Promicromonospora* species do not form branched rods but produce persistent or transient branching mycelia which fragment in older cultures. *Promicromonospora* species produce aerial mycelia (which have never been detected in *Cellulomonas [Oerskovia] turbata*), form motile elements, and are strictly aerobic (15, 27).

Unexpectedly, *T. tumescens* appears to share ancestry with the cellulomonads. In previous reports (4, 14), workers found that this species branched more deeply and close to the root of the *Arthrobacter* lineage. The difference between these reports and our findings may be due to the lengths of the 16S rDNA sequences compared. All previous investigations were based on a data set in which the 3'-terminal 200 nucleotides of the sequence were missing, while the data sets compared in this study included about 98% of the complete sequence.

Intragenetic structure of the genus *Cellulomonas*. The relationship among certain *Cellulomonas* species determined by 16S rDNA analysis is in good agreement with the results of DNA-DNA reassociation studies (22, 23). The species pair *Cellulomonas biazotea* and *Cellulomonas fimi* and the species pair *Cellulomonas gelida* and *Cellulomonas uda* exhibit high levels of 16S rDNA similarity (99.7 and 98.8%, respectively) and have significant phylogenetic relationships, as indicated by bootstrap values of 100 and 60%, respectively, and the corresponding levels of DNA similarity are high (55 and 45%, respectively). *Cellulomonas flavigena* and *Cellulomonas cellasea* are closely related to the *Cellulomonas gelida-Cellulomonas uda* group (bootstrap value, 85%) and the *Cellulomonas biazotea-Cellulomonas fimi* group (bootstrap value, 100%), respectively. *Cellulomonas cellulans* appears to be the most divergent species in the genus, as judged by the binary levels of 16S rDNA similarity with other *Cellulomonas* species (levels of similarity, 93.8 to 95.4%) and by its phylogenetic position. Fine-tuning of intragenetic relationships is not possible on the basis of low levels of DNA-DNA similarity (i.e., levels of similarity between 20 and 35%) (22, 23), and direct correlations between DNA reassociation values and 16S rDNA similarity values cannot be made. Phylogenetic separation of *Cellulomonas cellulans* from the other *Cellulomonas* species is consistent with differences in the amino acid compositions of the peptidoglycans of these organisms. *Cellulomonas cellulans*, which encompasses strains formerly classified as *Oerskovia xanthineolytica*, *Nocardia cellulans*, *Brevibacterium fermentans*, *Corynebacterium manihot*, and *Arthrobacter luteus*, has type A4 α peptidoglycan (L-Lys-D-Ser-D-Asp), while all other *Cellulomonas* species have type A4 β peptidoglycan (L-Orn-D-Asp or L-Orn-D-Glu). Comparative analyses of the chemotaxonomic and phenotypic properties of all members of the *Cellulomonas* group are needed for a future revision of the taxonomy of these organisms.

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