NOTE

Re-evaluation of the status of the genus *Oerskovia*, reclassification of *Promicromonospora enterophila* (Jäger *et al.* 1983) as *Oerskovia enterophila* comb. nov. and description of *Oerskovia jenensis* sp. nov. and *Oerskovia paurometabola* sp. nov.

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Phylogenetic analysis of *Promicromonospora enterophila* indicates that this taxon clusters with *Cellulomonas* species, adjacent to *Cellulomonas turbata* (basonym *Oerskovia turbata*). 16S rDNA analysis, DNA–DNA reassociation, ribotyping, peptidoglycan analysis and determination of phenotypic properties of various strains of *P. enterophila* and *C. turbata* reveal that they form a cluster that can be distinguished unambiguously from other *Cellulomonas* species by morphology, amino acid composition of the cell wall and 16S rDNA signatures. As a result of this polyphasic study, it appears taxonomically reasonable to re-establish the genus *Oerskovia* for *C. turbata* and to reclassify *P. enterophila* as *Oerskovia enterophila* comb. nov.; two novel species, *Oerskovia jenensis* sp. nov. (type strain DSM 46000^T = CIP 100330^T) and *Oerskovia paurometabola* sp. nov. (type strain DSM 14281^T = LMG 20385^T), are also proposed.

Keywords: *Oerskovia*, *Cellulomonas*, *Oerskovia enterophila* comb. nov., *Oerskovia jenensis* sp. nov., *Oerskovia paurometabola* sp. nov.

The observation of sessile spore-like elements located singly on the substrate hyphae was the morphological criterion for the accommodation of non-motile strains isolated from millipede faeces in the genus *Promicromonospora* as *Promicromonospora enterophila* (Jäger *et al.*, 1983). However, the occurrence of real spores and the taxonomic significance of the observed structures seem to be doubtful, since the spore-like elements were killed by heating at 80 °C and could be detected in only 6 of 54 strains, but not in the type strain (Stackebrandt & Prauser, 1991). Because of their physiological properties (Jäger *et al.*, 1983) and phage susceptibility (Prauser, 1986), the close relationship between *P. enterophila* and *Oerskovia turbata* was noted by Prauser (1986). This was confirmed by phylogenetic analysis showing the type strains of the two species to

be close phylogenetic neighbours (99.6% sequence similarity). *P. enterophila* did not group with the type species of *Promicromonospora*, *Promicromonospora citrea*, or with *Promicromonospora sukumoe* (Takahashi *et al.*, 1987) which, together with *Cellulosimicrobium cellulans* (Schumann *et al.*, 2001), form a distinct line of descent within the suborder *Micrococcineae*. On the basis of phylogenetic evidence, the genera *Oerskovia* and *Cellulomonas* were united (Stackebrandt *et al.*, 1982), leading to the reclassification of *O. turbata* as *Cellulomonas turbata* and of *Oerskovia xanthineolytica*, together with other, mainly cellulolytic strains, as *Cellulomonas cellulans* (Stackebrandt & Keddle, 1986), later reclassified as *Cellulosimicrobium cellulans* (Schumann *et al.*, 2001). Even at the time of unification, however, it was evident that *Cellulomonas turbata* differed from all other *Cellulomonas* species in terms of (i) susceptibility to *Oerskovia* phages (Prauser, 1986), (ii) amino acid composition of the peptidoglycan (see below) and

The EMBL accession numbers for the 16S rDNA sequences of *Oerskovia jenensis* DSM 46000^T, DSM 46001 and DSM 46097 and *Oerskovia paurometabola* DSM 14281^T are AJ314848–AJ314851, respectively.

Fig. 1. Consensus tree (Felsenstein, 1993) of almost complete 16S rDNA sequences of strains of *Cellulomonas*, *Promicromonospora* and some related genera of the suborder *Micrococcineae*, order *Actinomycetales*, class *Actinobacteria*. Numbers within the dendrogram indicate the percentages of occurrence of the branching order in 100 bootstrapped trees (only values of 70 % and above are shown).

(iii) formation of mycelia. As already stated by Stackebrandt & Prauser (1991), 'The rationale for this union was based on an overestimation of phylogenetic relationships between members of these two genera while, at the same time, neglecting the presence of genus-specific chemotaxonomic properties'. In fact, the correlation between phylogenetic position and chemotaxonomic uniqueness among actinobacterial genera has been demonstrated in the past decade (Stackebrandt & Schumann, 2000) and indication of a novel genus with either approach is mutual.

This taxonomic study has been performed on seven strains deposited in the DSMZ as either *P. enterophila* or *Cellulomonas turbata*. Analysis of the almost complete 16S rDNA sequences (Rainey *et al.*, 1996) revealed the high degree of relatedness between these strains (> 98 % similarity). The phylogenetic position of these organisms within the radiation of *Cellulomonas* species and other representatives of the sub-

order *Micrococcineae*, determined by different treeing algorithms [distance matrix (De Soete, 1983; Felsenstein, 1993), neighbour-joining and maximum-parsimony (Felsenstein, 1993)] revealed that *Cellulomonas turbata* and its relatives (here defined as the *O. turbata* lineage) branched close to the root of *Cellulomonas* in most analyses. The consensus tree (Fig. 1), in which the order but not the length of branches is significant, displays the relative phylogenetic position of these organisms. Almost no branching point was supported by high bootstrap values. Members of the *O. turbata* lineage differed from all other cellulomonads by the presence of several signature 16S rDNA nucleotides (Table 1). All strains were characterized by MK-9(H₄) as predominant menaquinone and by a phospholipid pattern consisting of phosphatidylglycerol, diphosphatidylglycerol, phosphatidylinositol and three unidentified phospholipids. The main fatty acid components, determined according to Groth *et al.* (2001), were ai-C_{15:0}, C_{16:0}, ai-C_{17:0}, i-C_{15:0} and C_{14:0}.

Table 1. Signature nucleotides that define members of the *Oerskovia* and *Cellulomonas* lineages

16S rDNA position	Members of the <i>Oerskovia</i> lineage	Members of the <i>Cellulomonas</i> lineage*
18–917	X–G†	X–A†
139–224	A–U	U–A
146–176	G–U	G–C
185–192	C–G	R–Y
186–192	U–G	C–G, G–C
601–637	G–C	G–U
602–636	G–U	C–G
612–628	U–A	Y–G
614–626	A–U	G–C, C–G
1120–1153	U–A	C–G
1438–1463	G–U	G–C

* R, Purine (G, A); Y, pyrimidine (C, U).

† X, Position 18 not determined.

(Table 2). This composition is very similar to that found in *Cellulomonas* and *Cellulosimicrobium* species (Schumann *et al.*, 2001). Strains of *Cellulomonas turbata* are defined by a peptidoglycan structure in which the amino acid moiety of position 3 of the peptide side chain consists of lysine and the interpeptide bridge is composed of threonine and either D-aspartic acid (A4 α ; L-Lys $\leftarrow$ L-Thr $\leftarrow$ D-Asp, DSM 20577^T and DSM 43878) or D-glutamic acid (A4 α ; L-Lys $\leftarrow$ L-Thr $\leftarrow$ D-Glu, *Oerskovia jenensis* sp. nov. DSM 46000^T and DSM 46001, *Oerskovia paurometabola* sp. nov. DSM 14281^T, and *P. enterophila* DSM 43852^T and DSM 46097; Seidl *et al.*, 1980; this study). In contrast, strains of *Cellulomonas* possess L-ornithine at position 3 of the side chain and a single

dicarboxylic amino acid, either D-aspartic acid or D-glutamic acid, represents the interpeptide bridge.

Discrimination of the seven strains at a lower taxonomic level by DNA–DNA hybridization (Escara & Hutton, 1980; Huß *et al.*, 1983; Jahnke, 1992) revealed the presence of four clusters (Table 3). DNA reassociation values above 70%, indicative of members of the same genomospecies (Wayne *et al.*, 1987) were found for *Cellulomonas turbata* DSM 20577^T and DSM 43878 (cluster I, 97%) and for *O. jenensis* sp. nov. DSM 46000^T, DSM 46001 and DSM 46097 (cluster II, 85–97%). These groups, as well as *P. enterophila* DSM 43852^T (cluster III) and *O. paurometabola* sp. nov. DSM 14281^T (cluster IV), generally showed less than 70% similarity among each other. The same composition of groups emerged after ribotyping analysis (Allerberger & Fritschel, 1999; Bruce, 1996) using the restriction enzyme *Pst*I (Fig. 2). This enzyme failed to give distinct patterns with DNA from *Cellulomonas* strains, which can be characterized by *Pvu*II. *Eco*RI failed to reveal distinct patterns with strains of either genus.

As all strains of *Cellulomonas turbata* and *P. enterophila* possess a peptidoglycan type that differed from those found in other *Cellulomonas* strains, it is considered that this feature is taxonomically more significant for delineating genera than the statistically weak phylogenetic position of single *Cellulomonas* species that, in some treeing programs, branch deeply with the *O. turbata* lineage (e.g. *Cellulomonas hominis*, *Cellulomonas humilata*; not shown) and may falsely mirror the phylogenetic incoherence of the genus *Cellulomonas sensu stricto*. In light of chemotaxonomic and phylogenetic evidence, the taxonomic opinion to treat *Oerskovia*, a validly published name (Prauser *et al.*, 1970; Lechevalier & Lechevalier, 1986), as a synonym of *Cellulomonas* has been reconsidered. As a

Table 2. Fatty acid composition of *Cellulomonas turbata*, *P. enterophila*, *O. jenensis* sp. nov. and *O. paurometabola* sp. nov.

Values are percentages of total fatty acids.

Fatty acid	<i>Cellulomonas turbata</i>		<i>O. jenensis</i>			<i>P. enterophila</i> DSM 43852 ^T	<i>O. paurometabola</i> DSM 14281 ^T
	DSM 20577 ^T	DSM 43878	DSM 46000 ^T	DSM 46001	DSM 46097		
C14:0	7.95	5.76	8.08	8.60	6.89	7.00	4.38
C15:0	0.63	–	1.63	1.28	2.43	0.70	1.16
C16:0	19.45	10.55	14.70	14.57	12.78	17.42	10.55
C18:0	0.78	–	0.94	0.54	–	0.72	0.51
i-C14:0	1.14	1.10	–	0.80	1.25	1.78	0.46
i-C15:0	11.63	5.68	9.49	8.76	8.01	4.39	4.21
i-C16:0	6.61	6.46	1.97	3.67	4.69	7.52	3.11
i-C17:0	0.60	–	–	–	–	–	–
ai-C15:0	44.53	57.51	54.35	53.01	53.59	51.51	57.96
ai-C17:0	6.14	12.19	8.84	8.77	9.73	8.41	17.66
i-C15:1	0.54	0.75	–	–	0.63	0.55	–

Table 3. DNA–DNA reassociation values for *Cellulomonas turbata*, *P. enterophila*, *O. jenensis* sp. nov. and *O. paurometabola* sp. nov.

Mean percentages from two measurements are given. ND, Not determined.

Taxon	Cluster I		Cluster II			Cluster III	Cluster IV
	1	2	3	4	5	6	7
1. <i>Cellulomonas turbata</i> DSM 20577 ^T	100						
2. <i>Cellulomonas turbata</i> DSM 43878	97	100					
3. <i>O. jenensis</i> DSM 46000 ^T	57	ND	100				
4. <i>O. jenensis</i> DSM 46001	57	ND	94	100			
5. <i>O. jenensis</i> DSM 46097	64	67	97	85	100		
6. <i>P. enterophila</i> DSM 43852 ^T	55	ND	53	49	57	100	
7. <i>O. paurometabola</i> DSM 14281 ^T	58	65	64	67	75	59	100

Fig. 2. Riboprint pattern of strains of *Cellulomonas turbata* and *Promicromonospora enterophila* generated with *Pst*I. The relationship dendrogram was generated with the BioNumerics software (Applied Maths).

result, *Oerskovia* and *Oerskovia turbata* have been emended and *P. enterophila* reclassified as *Oerskovia enterophila* comb. nov. Emendations and description are given below.

Physiological properties and enzymic activities were tested using GP2 microplates of the Biolog and API Coryne identification system. Whereas *P. enterophila* DSM 43852^T utilized a broad range of Biolog compounds (76 of 95 substrates), strain DSM 14281^T reactions were mostly negative towards the Biolog substrate panel (28 of 95). Strains of *Cellulomonas turbata*, including strain DSM 20577^T, and *P. enterophila* DSM 46097 reacted similarly (44–61 of 95) and no single substrate could be identified that is characteristic of members of DNA and riboprint groups I and II. Differentiating phenotypic properties are displayed in Tables 4 and 5. Other physiological tests and determination of motility on semi-solid agar were performed according to the methods described by Gerhardt *et al.* (1981). The present study gives evidence for the re-evaluation of the status of *O. turbata*, for the reclassification of *P. enterophila* as a member of *Oerskovia*, and for the description of two novel species of this genus. At this point, an emendation of the genus

Cellulomonas (Bergey *et al.*, 1923; emend. Clark, 1952; emend. Stackebrandt *et al.*, 1982) appears premature. Despite the exclusion of *Cellulomonas turbata* from *Cellulomonas*, this genus appears incoherent with respect to peptidoglycan composition; it embraces *C. humilata* (Collins & Pascual, 2000), reported to contain lysine and ornithine in its peptidoglycan (Gledhill & Casida, 1969). However, in this study, *C. humilata* CCUG 35596^T had peptidoglycan type L-Orn ← D-Glu, like most *Cellulomonas* species. In contrast to other *Cellulomonas* strains, *Cellulomonas fermentans* (Bagnara *et al.*, 1985) and *C. humilata* (Gledhill & Casida, 1969) are described as catalase-negative and the latter species is characterized by negative nitrate reduction. It appears that, prior to an emendation of the genus, the physiological and molecular properties of the type strain of *C. humilata* should be re-determined.

Emended description of the genus *Oerskovia*

Emendation is based on the original generic description of Prauser *et al.* (1970), supplemented with results on peptidoglycan structure, cellular fatty acid and

Table 4. Differentiating phenotypic properties of *Cellulomonas turbata*, *P. enterophila*, *O. jenensis* sp. nov. and *O. paurometabola* sp. nov. (utilization determined by Biolog GP)

Cellulomonas turbata strains DSM 20577^T and DSM 43878 and *O. jenensis* strains DSM 46000^T, DSM 46001 and DSM 46097 gave identical results (except for α -D-lactose), as shown. All strains utilized the following substrates: β -cyclodextrin, dextrin, glycogen, Tween 40, *N*-acetylglucosamine, D-gluconic acid, α -D-glucose, maltose, maltotriose, mannose, ribose, salicin, sucrose, trehalose, turanose, D-xylose, methyl pyruvate, glycerol, adenosine, 2-deoxyadenosine, inosine, thymidine, uridine and adenosine 5'-monophosphate. The following substrates were not utilized by any *Oerskovia* strain: inulin, D-arabitol, melizitose, *p*-hydroxyphenylacetic acid, α -ketoglutaric acid, alaninamide, D-alanine, L-alanine, L-alanyl glycine, glucose 1-phosphate and glucose 6-phosphate.

Characteristic	<i>Cellulomonas turbata</i> (2 strains)	<i>O. jenensis</i> (3 strains)	<i>P. enterophila</i> DSM 43852 ^T	<i>O. paurometabola</i> DSM 14281 ^T
Peptidoglycan type	Lys←Thr←Asp	Lys←Thr←Glu	Lys←Thr←Glu	Lys←Thr←Glu
Motility	+	+	—	—
Utilization of:				
Mannan	+	+	+	—
α -Acetyl mannosamine	+	+	+	—
Amygdalin	+	+	+	—
Arbutin	+	+	+	—
Cellobiose	+	+	+	—
D-Fructose	+	+	+	—
DL-Fucose	—	—	+	—
D-Galactose	+	+	+	—
D-Galacturonic acid	—	—	+	—
Gentiobiose	+	+	+	—
<i>m</i> -Inositol	—	—	+	—
α -D-Lactose	+	—	+	—
D-Melibiose	+	+	+	—
Methyl α -D-galactoside	+	+	+	—
Sedoheptulosan	—	—	+	—
Stachyose	—	—	+	—
Acetic acid	+	+	+	—
α -Hydroxybutyric acid	—	—	+	—
γ -Hydroxybutyric acid	—	—	+	—
Lactamide	—	—	+	—
D-Lactic acid methyl ester	+	+	+	—
L-Lactic acid	+	+	+	—
D-Malic acid	—	—	+	—
L-Asparagine	—	—	+	—
Fructose 6-phosphate	—	—	+	—

physiological data (Stackebrandt *et al.*, 1982) and the results of Biolog (Table 4) and API Coryne (Table 5) tests. The emended description of *Oerskovia* by Lechevalier (1972) is not taken into account, as *Oerskovia xanthineolytica*, the description of which was the reason for the emendation, has been reclassified as a strain of *Cellulomonas cellulans* (Stackebrandt *et al.*, 1980), now classified as *Cellulomicrobium cellulans* (Schumann *et al.*, 2001). Has extensively branching vegetative hyphae (approx. 0.5 μ m in diameter), growing on the surface of and penetrating into the agar, which break up into motile rod-like elements. Growth appears bacteroid in smears. No aerial mycelium. Motile or non-motile. Gram-positive, catalase-positive, oxidase-positive. Aerobic to facultatively anaerobic; strictly aerobic strains may occur. Major fatty acids are ai-C_{15:0} and

C_{16:0}; i-C_{15:0}, C_{14:0} and ai-C_{17:0} occur in smaller amounts. Major isoprenoid quinone is MK-9(H₄). Diamino acid of peptidoglycan peptide side chain is L-lysine; the interpeptide bridge consists of either L-Thr←D-Asp or L-Thr←D-Glu. Muramic acid residues are acetylated. Major polar lipids are phosphatidylglycerol, diphosphatidylglycerol and phosphatidylinositol. The G+C content of the DNA of the type species is 70.5–75.0 mol %. Widely distributed in soil. The type species is *Oerskovia turbata*.

Emended description of *Oerskovia turbata* (Prauser *et al.* 1970)

In addition to the physiological properties given in the original description by Prauser *et al.* (1970), strains of this species are characterized by the physiological

Table 5. Differentiating phenotypic properties of *Cellulomonas turbata*, *P. enterophila*, *O. jenensis* sp. nov. and *O. paurometabola* sp. nov. as determined by API Coryne tests

All strains were positive in the following reactions: oxidase, catalase, nitrate reduction, pyrazinamidase, α -glucosidase, *N*-acetyl- β -glucosidase, β -glucosidase and fermentation of glucose, ribose, xylose, maltose and sucrose. All strains were negative in the following reactions: pyrrolidonyl arylamidase, β -glucuronidase and fermentation of mannitol and lactose. +, Positive reaction; –, negative reaction; (+), weak reaction.

Characteristic	<i>Cellulomonas turbata</i>		<i>O. jenensis</i>			<i>P. enterophila</i> DSM 43852 ^T	<i>O. paurometabola</i> DSM 14281 ^T
	DSM 20577 ^T	DSM 43878	DSM 46000 ^T	DSM 46001	DSM 46097		
Pyrazinamidase	–	–	–	–	–	+	–
β -Galactosidase	+	+	(+)	(+)	(+)	+	–
Urease	–	–	–	–	+	+	+
Gelatin hydrolysis	+	+	–	–	–	–	–
Glycogen fermentation	(+)	–	+	+	+	+	+

reactions indicated in Tables 4 and 5. Colonies on trypticase/soy/yeast extract agar (medium 92, DSMZ Catalogue of Strains) are lemon yellow and 0.2–0.4 mm in diameter at 28 °C after 2 days. The type strain is aerobic to facultatively anaerobic. Peptidoglycan type is L-Lys ← L-Thr ← D-Asp.

Description of *Oerskovia enterophila* (Jäger *et al.* 1983) comb. nov.

Basonym: *Promicromonospora enterophila* (Jäger *et al.* 1983).

The description is based on data reported by Jäger *et al.* (1983) supplemented with results on peptidoglycan structure, cellular fatty acids and DNA base composition obtained in this study. Gram-positive, not acid-fast, facultatively anaerobic organism with branching vegetative hyphae. Aerial mycelium absent. Substrate hyphae fragment into non-motile bacillary and coccoid or spore-like elements. In general, colonies are glistening, soft, pasty and cream-yellow in colour. On trypticase/soy/yeast extract agar (medium 92, DSMZ Catalogue of Strains), colonies are 0.3–0.5 mm in diameter at 28 °C after 2 days. On starch/yeast extract media, rough, wrinkled, dull colony variants may also occur. Water-soluble diffusible pigments and melanins are not produced. Glucose is metabolized both oxidatively and fermentatively. Dextrin, fructose, galactose, lactose, maltose, mannose, sucrose, salicin, trehalose and xylose are utilized. Adonitol, dulcitol, inositol, inulin, mannitol, melibiose, melezitose, raffinose, rhamnose, sorbitol and sorbose are not utilized. Cellulose is not attacked. Indole and Voges–Proskauer tests are negative. Tween 80, ribonucleic acid, tyrosine, xanthine and hypoxanthine are not hydrolysed. Reaction for β -glucosidase (aesculin) is positive in the API Coryne substrate panel, but negative according to Jäger *et al.* (1983). Additional positive and negative reactions are listed in Tables 4 and 5. Susceptible to cephalosporin (10 µg), pristina-

mycin (10 µg), spiramycin (30 µg) and vancomycin (50 µg), but resistant to nalidixic acid (30 µg), nitrofurantoin (300 µg) and nystatin (100 IU). Growth occurs at pH 3.0, in 5% (w/v) NaCl and at 32 °C. Peptidoglycan is of the A4 α type, variation L-Lys ← L-Thr ← D-Glu. Cell wall sugars are rhamnose, mannose and fucose. The G+C content of the DNA is 71 mol%. Isolated from fresh faecal pellets of *Chromatolius projectus* Verh. (Diplopoda, Myriapoda). The type strain is DSM 43852^T (= ATCC 35307^T = JCM 7350^T).

Description of *Oerskovia jenensis* sp. nov.

Oerskovia jenensis (je.nen'sis. N.L. adj. *jenensis* pertaining to Jena, Germany).

Gram-positive, not acid-fast, facultatively anaerobic organism with branching vegetative hyphae. Aerial mycelium absent. Substrate hyphae fragment into motile bacillary and coccoid or spore-like elements. On trypticase/soy/yeast extract agar (medium 92, DSMZ Catalogue of Strains), colonies are cream-yellow, 0.2–0.4 or 0.5–0.7 mm in diameter at 28 °C after 2 days. Aerial mycelium absent. Water-soluble diffusible pigments and melanins are not produced. Glucose is metabolized both oxidatively and facultatively fermentatively. Positive and negative reactions are listed in Tables 4 and 5. Peptidoglycan is of the A4 α type, variation L-Lys ← L-Thr ← D-Glu. Isolated from soil, spruce-forest, Carpathian Mountains. Type strain is DSM 46000^T (= CIP 100330^T).

Description of *Oerskovia paurometabola* sp. nov.

Oerskovia paurometabola (pau.ro.me.ta'bo.la. Gr. adj. *paurus* little; Gr. adj. *metabolus* changeable; N.L. fem. adj. *paurometabola* producing little change).

Gram-positive, not acid-fast, facultatively anaerobic organism with branching vegetative hyphae. Aerial

mycelium absent. On trypticase/soy/yeast extract agar (medium 92, DSMZ Catalogue of Strains), colonies are cream-yellow, 0.5–0.6 mm in diameter at 28 °C after 2 days. Aerial mycelium absent. Substrate hyphae fragment into non-motile bacillary and coccoid or spore-like elements. Water-soluble diffusible pigments and melanins are not produced. Glucose is metabolized both oxidatively and facultatively fermentatively. Positive and negative reactions are listed in Tables 4 and 5. Peptidoglycan is of the A4 α type, variation L-Lys $\leftarrow$ L-Thr $\leftarrow$ D-Glu. Isolated from soil, leafy wood, Carpathian Mountains. Type strain is DSM 14281^T (= LMG 20385^T).

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