Taxonomic Note

Redefining *Paracoccus denitrificans* and *Paracoccus pantotrophus* and the case for a reassessment of the strains held by international culture collections

Donovan P. Kelly,[1] Jean P. Euzéby,[2] Celia F. Goodhew[3] and Ann P. Wood[4]

[1]Department of Biological Sciences, University of Warwick, Coventry CV4 7AL, UK

[2]École Nationale Vétérinaire, 23 chemin des Capelles, B.P. 87614, 31076 Toulouse cedex 3, France

[3]Veterinary Biomedical Sciences, Royal (Dick) School of Veterinary Studies, Summerhall, Edinburgh EH9 1QH, UK

[4]Department of Microbiology, King's College London Dental Institute at Guy's, King's College and St Thomas' Hospitals, Floor 28 Guy's Tower, Guy's Campus, London SE1 9RT, UK

Correspondence
Donovan P. Kelly
D.P.Kelly@warwick.ac.uk

An outline of the current taxonomic diversity of the genus *Paracoccus* is presented. A definitive summary is given of the valid type strains of *Paracoccus denitrificans* and *Paracoccus pantotrophus* and of culture collection strains that can be assigned to these species. The case is established for a critical reassessment of the *P. denitrificans* strains held by international culture collections, to ensure that they are assigned to the correct species.

The genus *Paracoccus* was created in 1969 (Davis *et al.*, 1969) with *Paracoccus denitrificans* as the type species. The type strain ATCC 17741^T was originally isolated from soil by Martinus Beijerinck, using enrichment culture on tartrate and nitrate, and called '*Micrococcus denitrificans*' (Beijerinck & Minkman, 1910). In the original paper, no further description was given of the species, and the organism was not archived by the Delft collection (as LMD 22.21^T, now known as NCCB 22021^T) until 1922. No description of '*M. denitrificans*' appeared in early editions of *Bergey's Manual of Determinative Bacteriology* (e.g. the first edition of 1923 or the fifth edition of 1939). '*M. denitrificans*' was cited in the sixth edition, but only as one of a number of species 'listed here chiefly for their historical interest' (Breed *et al.*, 1948), and the first full description of '*M. denitrificans*' appeared only in the seventh edition (Breed *et al.*, 1957). For many years, *P. denitrificans* remained the only authentic species of *Paracoccus*, with the result that biotypes actually differing from each other at the species level were assigned to this species (Baj, 2000; Dobson & Franzmann, 1996; Kelly *et al.*, 2000; Jordan *et al.*, 1997; Nokhal & Schlegel, 1983; Van Verseveld & Stouthamer, 1992). An example was *Thiosphaera pantotropha* (strain GB17^T = ATCC 35512^T), which was transferred to *P. denitrificans* on the basis of showing 100 % 16S rRNA gene sequence identity to a supposed example of the type strain of *P. denitrificans* (LMG 4218; Ludwig *et al.*, 1993; Robertson & Kuenen, 1983). Moreover, another putative example of the type strain of *P. denitrificans* (DSM 65) showed 85 % DNA–DNA hybridization with *T. pantotropha* GB17^T. Subsequently, additional species of *Paracoccus* were described, with 14 being recognized by Kelly *et al.* (2000), and 24 are now recognized in the literature (Table 1), although not all these names are validly published.

The identity of a number of strains of *P. denitrificans* held in culture collections was first questioned by Goodhew *et al.* (1996), who showed by analysis of protein profiles and *c*-type cytochromes that some strains of [*P. denitrificans*] were likely to be of a different species. These included a supposed derivative of the type strain held in the Ghent collection (LMG 4218), the original *T. pantotropha* isolate (GB17^T) and DSM 65. Goodhew *et al.* (1996) were the first to suggest that a separate species, with GB17^T as the type strain, might be necessary to describe some of the extant strains of *P. denitrificans*. A comprehensive study by Rainey *et al.* (1999), using 16S rRNA gene sequence comparisons and DNA–DNA hybridization among culture collection strains of *P. denitrificans*, confirmed the findings of Goodhew *et al.* (1996) and confirmed the creation of a novel species, *Paracoccus pantotrophus*, with the former *T. pantotropha* strain GB17^T as the type strain. The definitive study of Rainey *et al.* (1999) resulted in numerous other culture collection strains previously regarded as representative of *P. denitrificans*, including LMG 4218, being redesignated strains of *P. pantotrophus* (Table 2).

The most recent taxonomic treatment of the genus *Paracoccus* (Van Spanning *et al.*, 2005) recognizes the establishment of *P. pantotrophus*, but unfortunately perpetuates the incorrect assignment of a number of its strains to

Table 1. Currently reported species of *Paracoccus* and their type strains and 16S rRNA gene sequence accession numbers

The originally designated type strains of *P. denitrificans* and *P. pantotrophus* are shown, together with examples of the type strains held in other culture collections. To avoid confusion, only these strains are identified in the text as type strains by a superscript T. The type species of the genus is *P. denitrificans*. Primary publications describing the species can be accessed through the nucleotide database of the GenBank website (http://www.ncbi.nlm.nih.gov).

Species	Type strain/proposed type strain	16S rRNA gene sequence accession number(s)
P. denitrificans	ATCC 17741^T, NCCB 22021^T*, DSM 413^T	Y16927, Y16928, Y16929
P. pantotrophus	ATCC 35512^T, NCCB 82005^T†, DSM 2944^T	Y16933, X69159, AJ288159
P. versutus	ATCC 25364^T, DSM 582^T	Y16932, Y16931
P. aminophilus	JCM 7686^T	D42239
P. aminovorans	JCM 7685^T	D32240
P. alcaliphilus	JCM 7364^T	D32238
P. thiocyanatus	IAM 12816^T	D32242
P. solventivorans	DSM 6637^T	Y07705
P. kocurii	JCM 7684^T	D32241
P. marcusii	DSM 11574^T	Y12703
P. alkenifer	DSM 11593^T	Y13827
P. carotinifaciens	IFO 16121^T	AB006899
P. methylutens	VKM B-2164^T	AF250334
P. kondratievae	VKM B-2222^T (strain GB^T)	AF250332
P. haeundensis	KCCM 10460^T	AY189743
P. koreensis	KCTC 12238^T	AB187584
P. sereniphilus	DSM 14827^T	AJ428275
P. yeei	ATCC BAA-599^T	AY014173
P. zeaxanthifaciens	ATCC 21588^T	AF461158
'*P. thiophilus*'	Strain AS001	AJ294414
'*P. bengalensis*'	Strain JJJ, LMG 22700‡	AJ864469
'*P. kawasakiensis*'	Strain AS-8	AB041770
'*P. homiensis*'	Strain DD-R11	DQ342239
'*P. ferrooxidans*'	NCCB 100066	AY954687

*Formerly LMD 22.21^T.
†*Thiosphaera pantotropha* strain GB17^T as used by Ludwig *et al.* (1993). Previously known as LMD 82.5^T.
‡Reported by Ghosh *et al.* (2006).

P. denitrificans. Microbiologists using this chapter of the second edition of *Bergey's Manual of Systematic Bacteriology* (Van Spanning *et al.*, 2005) to assist in taxonomic assignments should note a number of amendments, which are listed below. These are provided in the spirit of the request made by Bergey *et al.* (1923) in the first edition of *Bergey's Manual of Determinative Bacteriology* that 'the assistance of all bacteriologists is earnestly solicited in the correction of possible errors in the text'.

1. The entry for *P. denitrificans* cites the type strain as being represented by ATCC 17741, DSM 65, DSM 413, LMD 22.21 and LMG 4218. Of these, DSM 65 and LMG 4218 are strains of *P. pantotrophus*. LMD 22.21 is now known as NCCB 22021.

2. The entry for *P. denitrificans* cites the GenBank 16S rRNA gene sequence accession numbers for the 'type strain' as Y16927 (ATCC 17741), Y16935 (DSM 65), D13480 (IAM 12479), Y16928 (LMD 22.21, now known as NCCB 22021) and X69159 (LMG 4218). Of these, D13480, Y16935 and X69159 are sequences for *P. pantotrophus*, with X69159 also being 100 % identical to the sequence from the type strain of *P. pantotrophus* (LMD 82.5^T, now known as NCCB 82005^T; Ludwig *et al.*, 1993).

3. The entry for *P. pantotrophus* should be expanded to include DSM 65 and LMG 4218 as valid examples of the type strain and the accession number for the 16S rRNA gene sequence of the type strain (ATCC 35512^T) needs to be cited (Y16933).

4. There are inconsistencies between the tabulated and text information given by Van Spanning *et al.* (2005), resulting in uncertainty about some key properties of several species. It needs to be clear that *P. denitrificans*, *P. pantotrophus* and *Paracoccus versutus* can all grow chemolithoautotrophically with thiosulfate as the sole energy source (Kelly & Harrison, 1989; Kelly *et al.*, 2000; Robertson & Kuenen, 1983; Sijderius, 1946; Taylor & Hoare, 1969) and that *P. versutus* is capable of growth on methanol as the sole energy source

Table 2. Strains representing *P. denitrificans* and *P. pantotrophus*

See Table 1 for the authentic type strains of both species. Strains have been assigned to species on the basis of 16S rRNA gene sequences, DNA–DNA hybridization, cytochrome c_{550}, chromosome and megaplasmid content and the culture histories published by the holding culture collection (Auling *et al.*, 1980; Euzéby, 2006; Goodhew *et al.*, 1996; Kelly *et al.*, 2000; Ludwig *et al.*, 1993; Nokhal & Schlegel, 1983; Rainey *et al.*, 1999; Winterstein & Ludwig, 1998). 16S rRNA gene sequence accession numbers (where known) are given in parentheses.

P. denitrificans	*P. pantotrophus*
ATCC 19367 (Y16930)	LMG 4218 (X69159, Y16936)
ATCC 13543	DSM 65 (Y16935)
NBRC (formerly IFO) 13301*	IAM 12479 (Y17512)
NCIMB 8944	JCM 6892 (Y17511)
NCCB 97099 (strain PD 1222)†	DSM 11072 (U58015)
DSM 15418 (AY157621)	DSM 11073 (U58017)
DSM 415‡	DSM 11074 (U58016)
NCIMB 11627§‖	DSM 1403–1406
NCIMB 9722‖	DSM 6610, DSM 6392, DSM 12449
IMET 10380‖	CIP 106306¶
VKM B-1324§‖	CIP 71.11#
ICPB 3979‖	Strain TUT 1022 (AB098590)
	Strain JT 001 (AJ864466)
	NCCB 52044**
	LMD 92.63 (Y16934)††
	NCCB 91129‡‡

*Culture history: NCIB 8944 → ATCC 19367 → Kyoto → IFO 13301 → NBRC 13301.

†A derivative of DSM 413^T via PD 1001 (De Vries *et al.*, 1989). See Table 1. Its 16S rRNA gene sequence is available from the complete genome shotgun sequence: contig 62 (GI:69152905) at http://genome.ornl.gov/microbial/pden, which shows only one nucleotide difference from the sequences of ATCC 17741^T, NCCB 22021^T and DSM 413^T.

‡DSM 415 showed 100 % DNA–DNA relatedness with DSM 413^T (Auling *et al.*, 1980).

§Derived from ATCC 17741^T (see Table 1).

‖Confirmation by 16S rRNA sequencing is desirable.

¶The 16S rRNA gene sequence (1312 bp and 22 gaps) published at http://www.crbip.pasteur.fr shows 98·3 % identity to those of *P. pantotrophus* LMG 4218 and IAM 12479 (1311/1334 aligned nucleotides) and ATCC 35512^T (1294/1320 aligned nucleotides). Assuming that the 22 gaps in the CIP strain sequence match the nucleotides in the type strain sequence gives 100 % identity to the type strain.

#The CIP culture history of this strain indicates that it was derived from *P. pantotrophus* NCCB 52044 (formerly LMD 52.44).

**Previously known as LMD 52.44.

††LMD 92.63 is a variant of *P. pantotrophus* NCCB 82005^T (Baker *et al.*, 1997; Rainey *et al.*, 1999; Saunders *et al.*, 2000). This strain is currently being made available on its open catalogue by the NCCB.

‡‡Strain TP43, a Sox$^-$, Hox$^-$, Nitd$^-$ mutant of strain GB17^T (NCCB 82005^T; Chandra & Friedrich, 1986).

(Kelly & Wood, 1982; Kelly *et al.*, 2000; Taylor & Hoare, 1969). Moreover, the ability to grow on carbon disulfide is a property of *P. pantotrophus*, not yet shown also to apply to *P. denitrificans* (Jordan *et al.*, 1995, 1997; Rainey *et al.*, 1999).

Comparison of 16S rRNA gene sequences is routinely used to ensure the correct placement of strains of *Paracoccus* within the alpha-3 subgroup of the class *Alphaproteobacteria*. The class itself is delimited by the 16S rRNA relationships of its members (Kainth & Gupta, 2005) with DNA–DNA relatedness and structural and physiological properties being applied as supporting diagnostic features at the species level. It is notable that relatively few separate isolations of *P. denitrificans* have been reported since the first publication by Beijerinck & Minkman (1910): the valid strains in culture collections seem to have been derived either from the original isolate or from those isolated by Verhoeven *et al.* (1954) (DSM 413^T) and Vogt (1965) (DSM 415) and more recently by Ruff *et al.* (2003) (DSM 15418).

Inevitably, international culture collections do not always cite the correct type strains in their catalogues. As shown by Goodhew *et al.* (1996), the culture history of a strain as reported by a culture collection does not always correspond to the correct identity of that strain. For example, the culture history of the Ghent strain of *P. pantotrophus*, LMG 4218, was supposedly Beijerinck (1909) → LMD 22.21 (1922) → Van Niel → Stanier 381 → ATCC 17741^T → LMG 4218. As LMG 4218 is not an example of the type strain of *P. denitrificans*, it is clear that the culture archived by LMG was incorrect. Also in question is *P. denitrificans* strain NBRC 16712 (http://www.nbrc.nite.go.jp/e/index.html), whose accession history is given as Van Niel → Stanier 381 → ATCC 17741^T → IAM 12479 → IFO 16712^T → NBRC 16712^T, where IAM 12479 is now known to be an example of *P. pantotrophus*. NBRC 16712 is thus a strain for which 16S rRNA gene sequencing is desirable. In Table 2, we have listed those strains that are correctly assigned to *P. denitrificans* and those strains that can with reasonable certainty be designated *P. pantotrophus*. The lists are incomplete as some strains not included by us but listed as *P. denitrificans* in culture collections are probably derived from the original type culture (although their culture history is not necessarily clear). There is a case, however, for further study of any strains not yet subjected to 16S rRNA gene sequencing, in order to confirm their phylogenetic relationships.

An example of the kind of assessment we recommend has been provided to us by the DSMZ. Eleven strains catalogued by the DSMZ as *P. denitrificans* have been subjected to diagnostic sequencing of their 16S RNA genes (E. Stackebrandt and J. Swiderski, personal communications). Three of these, DSM 413^T, DSM 415 and DSM 15418, were confirmed to show 100 % sequence identity to each other and to the type strain ATCC 17741^T, but the remaining eight required reconsideration of their identity.

The 16S rRNA gene sequences of DSM 1403, DSM 1404, DSM 1405, DSM 1406, DSM 6610 and DSM 6392 were identical to each other and showed 100 % identity to that of *P. pantotrophus* LMG 4218 (and hence 100 % identity to strains ATCC 35512^T, DSM 65, NCCB 82005^T, JCM 6892 and IAM 12479). DSM 1403, DSM 1405 and DSM 1406 showed 81–98 % DNA–DNA hybridization with DSM 1404, but all four showed a mean of only about 55 % hybridization with two reference strains of *P. denitrificans* (Stanier 381 and DSM 413^T; Auling *et al.*, 1980). Unlike *P. denitrificans*, the type strain of *P. pantotrophus* cannot use methanol as a carbon and energy source (Mox$^-$), although it can mutate spontaneously to a Mox$^+$ phenotype (Robertson & Kuenen, 1983; Egert *et al.*, 1993). In common with wild-type *P. pantotrophus*, DSM 1403, DSM 1404 and DSM 1405 could not grow on methanol, although DSM 1406 was Mox$^+$ (Nokhal & Schlegel, 1983). Strains DSM 1403, DSM 1404, DSM 1405, DSM 1406, DSM 6610 and DSM 6392 must therefore be reassigned to *P. pantotrophus*.

Strain DSM 1407 was previously found not to cluster with DSM 1403, DSM 1404, DSM 1405, DSM 1406 and DSM 1408 in the computer-based analysis of their properties, and it was also unable to grow on methanol (Nokhal & Schlegel, 1983). DSM 1407 was found by the DSMZ to show 16S rRNA gene sequence identity of 100 % to *Paracoccus* sp. strain WB1 (GenBank accession no. AF526892) and 98·4 % to *P. denitrificans* ATCC 17741^T, but only 96·2 % 16S rRNA gene sequence identity to *P. pantotrophus* ATCC 35512^T. A BLASTN analysis of the sequence from *Paracoccus* sp. strain WB1 showed it to be most similar to 12 strains of *P. pantotrophus* (with 98·3 % identity to the type strain), with 97·1–97·8 % identity to strains of *P. denitrificans*, *P. versutus*, '*Paracoccus thiophilus*' and '*Paracoccus bengalensis*'. DNA–DNA hybridization analysis by Auling *et al.* (1980) found strain DSM 1407 to show only 53–61 % relatedness with *P. pantotrophus* DSM 1404 and two reference strains of *P. denitrificans*. Strain DSM 1407 can thus not be assigned to either *P. pantotrophus* or *P. denitrificans* on the basis of the data currently available and may represent a novel species.

Strain DSM 1408 (strain N11 of Nokhal & Schlegel, 1983) proved more problematic, as its 16S rRNA gene sequence showed highest identities to those of *Paracoccus* sp. strain R-24616 (100 %; GenBank accession no. AM084041) and *Paracoccus alcaliphilus* JCM 7364^T (98·2 %; D32238). The sequence from strain R-24616 showed only 97·5–97·6 % identity to those of *P. alcaliphilus* JCM 7364^T, *P. denitrificans* ATCC 17741^T and *Paracoccus aminophilus* ATCC 49673^T (GenBank accession no. AY014176). Strain DSM 1408 is thus unlikely to be a strain of *P. denitrificans* and is also unlikely to belong to either *P. alcaliphilus* or *P. aminophilus*, as neither of these can denitrify (Urakami *et al.*, 1989, 1990) and the pH range for growth of DSM 1408 is pH 6·0–8·0, compared with pH 7·0–9·5 for *P. alcaliphilus* (Urakami *et al.*, 1989). Like *P. pantotrophus* and *P. aminophilus*, DSM 1408 cannot grow on methanol (Nokhal & Schlegel, 1983; Urakami *et al.*, 1990). It seems that DSM 1408 cannot be assigned unequivocally to any currently recognized species of *Paracoccus*, and it was also found to be different from DSM 1403, DSM 1404, DSM 1405, DSM 1406 and DSM 1407 in the systematic analysis of Nokhal & Schlegel (1983). With strains R-24615, R-24616, R-24617 and R-25058 (based on the 16S rRNA gene sequences available from GenBank), DSM 1408 appears to represent a novel clade within the genus, clearly meriting further study.

It has been our aim in this note to clarify the taxonomic status of the numerous culture collection strains of two key species of *Paracoccus* that have been used for many years in fundamental biochemical studies and as reference species in the identification of new isolates of *Paracoccus*. It is important to the integrity of taxonomy that any confusion about the identity of strains of the type species should be clarified.

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