

Verrucosipora fiedleri sp. nov., an actinomycete isolated from a fjord sediment which synthesizes proximicins

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Abstract A novel filamentous actinobacterial organism, designated strain MG-37^T, was isolated from a Norwegian fjord sediment and examined using a polyphasic taxonomic approach. The organism was determined to have chemotaxonomic and morphological properties consistent with its classification in the genus *Verrucosipora* and formed a distinct phyletic line in the *Verrucosipora* 16S rRNA gene tree. It was most closely related to *Verrucosipora maris* DSM 45365^T (99.5 % 16S rRNA gene similarity) and *Verrucosipora gifhornensis* DSM 44337^T (99.4 % 16S rRNA gene similarity) but was distinguished from these strains based on low levels of DNA:DNA relatedness (~56 and ~50 %, respectively). It was readily delineated from all of the type strains of *Verrucosipora*

species based on a combination of phenotypic properties. Isolate MG-37^T (=NCIMB 14794^T = NRRL-B-24892^T) should therefore be classified as the type strain of a novel species of *Verrucosipora* for which the name *Verrucosipora fiedleri* is proposed.

Keywords *Verrucosipora fiedleri* · Polyphasic taxonomy · Marine sediment · Actinomycetes

Introduction

The genus *Verrucosipora* forms a distinct branch in the *Micromonosporaceae* 16S rRNA gene tree and can be distinguished from other genera classified in this family by using chemotaxonomic and morphological features (Goodfellow et al. 2012; Stackebrandt 2012) and genus-specific primers (Xie et al. 2011). The taxon currently encompasses six validly named species, *Verrucosipora gifhornensis* (Rheims et al. 1998), the type species, *Verrucosipora lutea* (Liao et al. 2009), *Verrucosipora maris* (Goodfellow et al. 2012), *V. quiiae* (Xi et al. 2012), *V. sediminis* (Dai et al. 2010) and *V. wenchangensis* (Xie et al. 2012), the members of which can be separated using a combination of genotypic and phenotypic procedures (Goodfellow et al. 2012; Xie et al. 2011; Xie et al. 2012). The type strains of these species were isolated from a peat bog (*V. gifhornensis*), mangrove soils (*V. lutea*, *V. quiiae* and *V. wenchangensis*) and deep-sea sediments (*V. maris* and *V. sediminis*).

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Verrucosipora strains are the focus of considerable interest as they are the source of new bioactive compounds, as shown by the discovery of the diterpene gifhornenolones A and B from *V. gifhornensis* (Shirai et al. 2010), the polycyclic polyketide abyssomicins A to H (Bister et al. 2004; Riedlinger et al. 2004; Keller et al. 2007a, b) from *V. maris* (Goodfellow et al. 2012) and the aminofuran proximicins A–C from *Verrucosipora* strain MG-37 (Fiedler et al. 2008). Proximicin A was detected in parallel from the type strain of *V. maris* (Schneider et al. 2008). The characteristic structural element of the proximicins is 4-amino-furan-2 carboxylic acid, a previously unknown γ -amino acid. Proximicins show weak antibacterial activity but have a strong cytostatic effect on various human tumour cell lines (Fiedler et al. 2008). The whole genome sequence of *V. maris* AB-18-032^T contains around 23 biosynthetic gene clusters that encode for the production of known or predicted secondary metabolites (Roh et al. 2011).

Partial characterization of strain MG-37 showed that it had chemotaxonomic and morphological properties characteristic of the genus *Verrucosipora* and was most closely related to the type strain of *V. gifhornensis*. However, it could be distinguished from the latter using a few phenotypic properties (Fiedler et al. 2008). The aim of the present study was to build upon these initial results by comparing isolate MG-37 with the type strains of *Verrucosipora* species in a polyphasic taxonomic analysis. The resultant dataset showed that the isolate represents a new centre of taxonomic variation in the genus for which the name *Verrucosipora fiedleri* sp. nov. is proposed. It is significant that at the time of the discovery of abyssomicin C (Bister et al. 2004) only one other member of the genus *Verrucosipora* had been described. Subsequently, the greater diversity within this genus has been revealed, as the characterization of strain MG-37^T further demonstrates.

Materials and methods

Strains and cultural conditions

Strain MG-37^T was recovered from sediment collected from the Raune Fjord, Norway (N60°15.398, E5°08237) at a depth of 250 metres, as described previously (Fiedler et al. 2008). The organism was isolated on a starch-casein agar plate (Küster and Williams 1964), supplemented with cycloheximide and nystatin (each at 50 $\mu\text{g ml}^{-1}$),

that had been inoculated with a suspension of the sediment sample and then incubated at 30 °C for 14 days. The isolate and the type strains of *Verrucosipora* species were maintained on yeast extract- malt extract agar (ISP medium 2; Shirling and Gottlieb 1966) at 28 °C and as suspensions of hyphal fragments in glycerol (20 %, v/v) at –20 and –80 °C. Biomass for the molecular systematic and most of the chemosystematic studies carried out on the isolate and *V. gifhornensis* DSM 44337^T was prepared as described earlier (Goodfellow et al. 2012), as was the biomass of *V. maris* DSM 45365^T needed for the DNA:DNA relatedness study. Biomass for the fatty acid analysis performed on strain MG-37^T was harvested from Tryptic Soy Broth (Difco) which had been incubated at 28 °C for 7 days.

PCR amplification using genus-specific primers

Isolate MG-37^T and the type strains of *Verrucosipora* species were examined for their ability to generate diagnostic amplification products when probed with the genus-specific 16S rRNA primers S-G-Verr-0195-a-S-20 and S-G-Verr-1152-a-A-18 as described by Xie et al. (2011), albeit with the annealing temperature adjusted to 64 °C.

16S rRNA gene sequencing analyses

Isolation of chromosomal DNA, PCR amplification and direct sequencing of PCR products of isolate MG-37^T were carried out as described by Kim et al. (2002). The resultant almost complete 16S rRNA gene sequence (1,429 nucleotides [nt]) was aligned manually with corresponding gene sequences of the type strains of *Verrucosipora* species and the type strains of the type species of representative genera classified in the family *Micromonosporaceae*, retrieved from the DDBJ/EMBL/GenBank databases, using the PHYDIT program (<http://plaza.snu.ac.kr/~jchun/phydit/>). Phylogenetic trees were inferred using the maximum-likelihood (Felsenstein 1981), maximum-parsimony (Kluge and Farris 1969) and neighbour-joining (Saitou and Nei 1987) tree-making algorithms from the PHYLIP package (Felsenstein 1993).

Chemotaxonomy and morphology

The isolate was examined for chemotaxonomic and morphological properties characteristic of the genus

Verrucospora (Goodfellow et al. 2012; Stackebrandt 2012). The arrangement of hyphae and spores were examined on an oatmeal agar (ISP medium 3; Shirling and Gottlieb 1966) plate which had been incubated at 28 °C for 2 weeks. Spore morphology and ornamentation were observed by scanning gold-coated dehydrated specimens taken from the oatmeal agar plate, using a scanning electron microscope (Cambridge Stereoscan 240 instrument), as described by O'Donnell et al. (1993). Cultural properties were determined using ISP media (Shirling and Gottlieb 1966) after incubation at 28 °C for 14 days. Standard procedures were used to determine the isomers of diaminopimelic acid (A_2pm) (Staneck and Roberts 1974), the acyl type of murein (Uchida et al. 1999), menaquinones (Minnikin et al. 1984), sugars (Schaal 1985), polar lipids (Minnikin et al. 1984) and the presence of mycolic acids (Minnikin et al. 1975), in all cases using appropriate controls. Fatty acids of the strain were methylated, determined by gas chromatography (Hewlett Packard 6890) and analysed using the standard Sherlock Microbial Identification (MIDI) system and the ACTINO version 5 database (Sasser 1990). The DNA base composition of the isolate was determined after Gonzalez and Saiz-Jimenez (2002).

DNA:DNA pairing

The DNA:DNA relatedness values (ΔT_m) between isolate MG-37^T, *V. maris* AB-18-032^T and *V. giffhornensis* DSM 44337^T, its nearest phylogenetic neighbours, were determined using a fluorimetric method (Gonzalez and Saiz-Jimenez 2005). The optimum temperature for renaturation (T_m) was calculated using $Tor-0.51$ (GC %) + 47. The melting temperature (T_m) at which 50 % of the initial double stranded DNA denatured into single-stranded DNA for isolate MG-37^T genomic DNA and the isolate MG-37^T/*V. maris* AB-18-032^T and MG-37^T/*V. giffhornensis* DSM 44337^T hybrid DNA preparations were compared and the differences (ΔT_m) calculated.

Phenotypic tests

Isolate MG-37^T and the type strains of the *Verrucospora* species were examined, in duplicate, for a broad range of phenotypic tests, as described previously (Goodfellow et al. 2012). All of the media were incubated at 28 °C for 2–3 weeks, apart from the

temperature tests, following the addition of a standard inoculum equivalent to 2.5 on the McFarland scale (<http://www.microbial.org/wp-content/uploads/2011/07/MR13286.pdf>).

Results

16S rRNA gene sequencing and DNA:DNA relatedness studies

The 16S rRNA gene sequence strain MG-37^T (GenBank accession number JQ423921) was determined and used for phylogenetic analysis. It can be seen from Fig. 1 that isolate MG-37^T was recovered in the *Verrucospora* 16S rRNA gene clade, a result that is underpinned by all of the tree-making algorithms and by a 99 % bootstrap value. The isolate formed a subclade in the 16S rRNA gene tree together with the type strains of *V. giffhornensis* and *V. maris*, a relationship which was

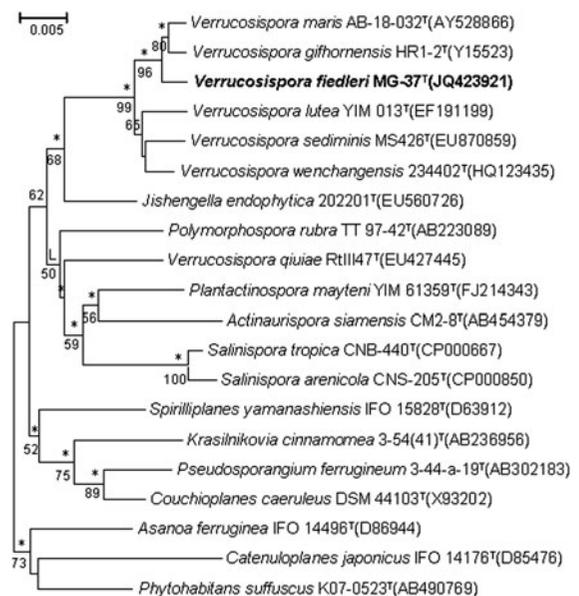


Fig. 1 Neighbour-joining tree based on nearly complete 16S rRNA gene sequences (1,414 nt) showing relationships between isolate MG-37^T and representatives of genera classified in the family *Micromonosporaceae*. Asterisks indicate branches of the tree that were also found using the maximum-likelihood and maximum-parsimony tree-making algorithms. The *L* indicates a node that was also recovered in the maximum-likelihood tree. The numbers at the nodes indicate levels of bootstrap support (%) based on a neighbour-joining analysis of 1,000 resampled datasets; only values at or above 50 % are given. *T* type strain, *Bar* 0.005 substitutions per nucleotide position

supported by all of the tree-making algorithms and by a 96 % bootstrap value. The organism shared its highest 16S rRNA gene similarity with *V. maris* DSM 45365^T, namely 99.5 %, a value which corresponded to seven nt differences at 1,414 locations (one nt difference was in variable region V1, two in variable region V2, one in variable region V6 and the other three nt in non-variable regions). The corresponding 16S rRNA gene similarity with *V. gifhornensis* DSM 44337^T was 99.4 %, which was equivalent to 8 nt differences at 1,406 sites (two nt differences were in variable region V1, three in variable region V2, one in the variable region V6, one in the variable region V9, and the final one in the non-variable region). The 16S rRNA similarities with the remaining *Verrucosipora* type strains fell within the range 96.1–99.0 %, values corresponding to between 56 and 14 nt differences respectively. The lowest similarity was shown against the type strain of *V. quiuae*, which fell outside the *Verrucosipora* clade (Fig. 1), an observation supported by all of the tree-making algorithms.

The ΔT_m between isolate MG-37^T genomic DNA and MG-37^T *V. maris* AB-18-032^T hybrid DNA, and MG-37^T *V. gifhornensis* DSM 44337^T hybrid DNA were 8.6 and 6.6 °C respectively (Fig. S1), results equivalent to DNA:DNA relatedness similarities of about 56 and 50 %, respectively (Gonzalez and Saiz-Jimenez 2005), values well below the 70 % cut-off point for the circumscription of bacterial species according to Wayne et al. (1987).

Genus-specific primers

Isolate MG-37^T and all of the *Verrucosipora* type strains, apart from *V. quiuae* Rt11147^T, gave the expected ≈ 960 base pair amplification product with primers S-G-Verr-0195-a-S-20 and S-G-Verr-1152-a-A-18 (data not shown). Corresponding *in silico* testing with CLUSTAL X 1.81 showed that neither of the primers matched with the appropriate sections of the 16S rRNA gene of the *V. quiuae* strain, indicating that the V2 and V6 variable regions of this organism are different from those of the other tested strains.

Chemotaxonomic, cultural, morphological and phenotypic characteristics

Isolate MG-37^T was observed to form an extensively branched, orange substrate mycelium which carried

single, warty ornamented spores on long sporophores on oatmeal agar, as shown in Fig. 2. The isolate was determined to contain a mixture of *meso*- and hydroxyl

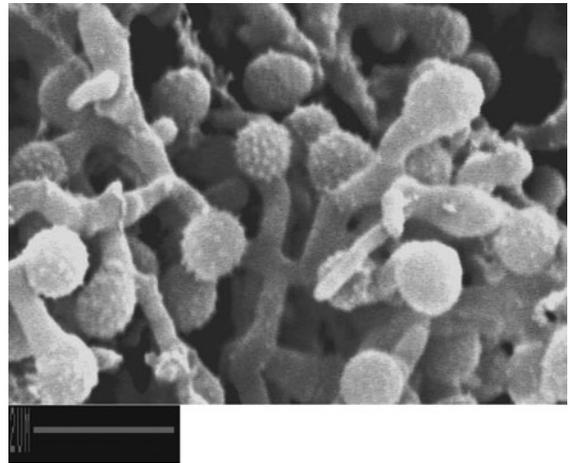


Fig. 2 Scanning electron micrograph of *Verrucosipora* isolate MG-37^T grown on oatmeal agar for 2 weeks at 28 °C showing single, ornamented spores borne on long sporophores. Scale bar 2 μ m

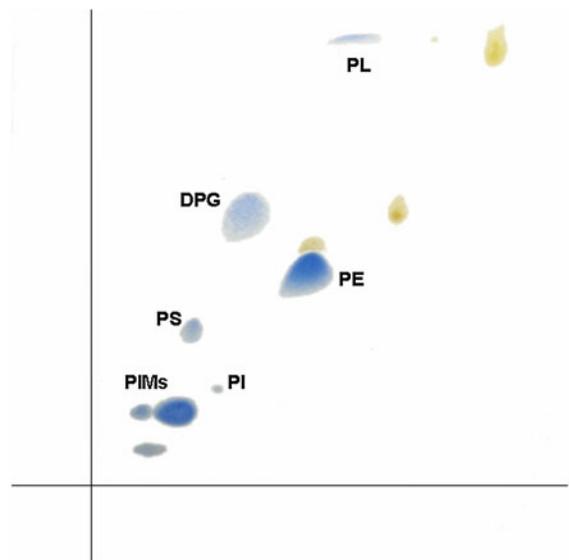


Fig. 3 Two-dimensional thin-layer chromatography of polar lipids of isolate MG-37^T stained with molybdenum blue spray (Sigma). Chloroform:methanol:water (32.5:12.5:2.0) was used in the first direction and chloroform:acetic acid:methanol:water (40:7.5:6:2) in the second direction. DPG diphosphatidylglycerol, PE phosphatidylethanolamine, PIMs phosphatidylinositol mannosides, PS phosphatidylserine, PI phosphatidylinositol, and PL unknown phospholipid

A₂pm in whole-organism hydrolysates; *N*-glycolyl muramic acid in the wall peptidoglycan; mannose and xylose as diagnostic sugars; MK-9 (H₄), MK-9 (H₆) and MK-10 (H₄) as predominant isoprenologues in a ratio of 27:10:2 (Fig. S2); diphosphatidylglycerol, phosphatidylethanolamine and phosphatidylinositol mannosides as major polar lipids (Fig. 3), and trace amounts of phosphatidylinositol, phosphatidylserine and an unknown polar lipid; but to lack mycolic acids. The cellular fatty acid profile was determined to consist of major amounts of *iso*-C_{16:0} (37.4 %) and C_{17:1} ω8c (24.9 %). The G + C content of the DNA was determined to be 72.0 mol % using the fluorimetric method (Fig. S3). In addition, like its closest phylogenetic neighbours, the isolate was observed to form light to dark coloured substrate mycelia with orange pigments on ISP media, and to grow

particularly well on tryptic- yeast extract and yeast extract-malt extract agars (Table 1).

It can be seen from Table 2 that isolate MG-37^T can be distinguished readily from all of the type strains of *Verrucosispora* species by a broad range of phenotypic properties. All of the organisms can degrade adenine, gelatin and xanthine; grow on dextran, D-fucose, D-maltose, D-mannose, D-melezitose, D-sucrose, D-trehalose and xylitol as sole carbon sources; use gelatin, L-leucine, DL-methionine, L-ornithine, DL-phenylalanine, L-proline, L-threonine, L-tyrosine and urea as sole carbon and nitrogen sources; L-aspartic acid and L-histidine as sole nitrogen sources; and grow at 20 and 37 °C, from pH 7.0–9.0 and in the presence of novobiocin (8 µg ml⁻¹). In contrast, none of the strains can degrade casein or hypoxanthine; use *meso*-inositol as a sole carbon source; L-glutamic acid or L-norvaline as carbon and nitrogen

Table 1 Growth and cultural characteristics of isolate MG-37^T and the type strains of the most closely related *Verrucosispora* species after incubation at 28 °C for 14 days

Medium	Strains		
	Isolate MG-37 ^T	<i>V. gifhornensis</i> ^a DSM 44337 ^T	<i>V. maris</i> ^a DSM 45365 ^T
Glycerol-asparagine agar (ISP medium 5)			
Growth	+	++	++
Colour of substrate mycelium	Light orange	Light orange	Light orange
Inorganic salts-starch agar (ISP medium 4)			
Growth	+++	++	+++
Colour of substrate mycelium	Orange	Light orange	Orange
Oatmeal agar (ISP medium 3)			
Growth	+++	++	+++
Colour of substrate mycelium	Orange	Orange	Orange
Peptone-yeast extract agar (ISP medium 6)			
Growth	++	+	+
Colour of substrate mycelium	Orange	Orange	Orange
Tryptic-yeast extract-iron agar (ISP medium 1)			
Growth	+++	+++	+++
Colour of substrate mycelium	Orange	Orange	Dark orange brown
Tyrosine agar (ISP medium 7)			
Growth	++	++	+
Colour of substrate mycelium	Orange	Orange	Orange
Yeast extract-malt extract agar (ISP medium 2)			
Growth	+++	+++	+++
Colour of substrate mycelium	Dark orange	Orange	Orange

None of the strains formed aerial hyphae or produced diffusible pigments

Key +++ abundant growth; ++ moderate growth; + poor growth

^a Data taken from Goodfellow et al. (2012)

Table 2 Phenotypic properties which distinguish isolate MG-37^T from the type strains of *Verrucosispora* species

Characteristic	Isolate MG-37 ^T	<i>V. gifhornensis</i> DSM 44337 ^T	<i>V. lutea</i> YIM 013 ^T	<i>V. maris</i> DSM 45365 ^T	<i>V. sediminis</i> MS 426 ^T	<i>V. qiuiiae</i> RIII47 ^T	<i>V. wenchangensis</i> 234402 ^T
Spore arrangement	Single	Single, pairs, clusters ^a	Single, pairs, clusters ^a	Single, clusters+	Single, clusters ^a	Single ^a	Single ^a
Spore ornamentation	Warty	Warty turning to hairy with increasing age	Smooth ^a	Warty ^a	Warty ^a	Warty ^a	Warty ^b
Biochemical tests							
Aesculin hydrolysis	-	+	-	-	-	-	-
Allantoin hydrolysis	+	+	+	+	+	-	-
Arbutin hydrolysis	-	+	-	+	+	-	-
H ₂ S production	-	-	+	-	+	-	+
Nitrate reduction	-	-	+	-	+	-	+
Urea hydrolysis	+	+	-	-	-	-	+
Degradation tests							
Elastin	+	-	+	-	-	-	+
Guanine	-	+	-	+	+	-	+
Starch	-	+	-	+	+	+	-
L-Tyrosine	+	+	-	+	+	-	+
Xylan	-	-	-	-	+	+	+
Growth on sole carbon sources							
Adonitol, D-arabitol	-	-	+	+	+	-	+
Amygdalin	-	+	-	+	-	+	+
L-Arabinose	-	+	+	-	-	-	-
Arbutin	-	+	-	+	+	+	-
Erythritol, maltotriose	-	+	-	+	-	-	-
Cellobiose, ribose	-	-	+	-	+	-	-
Dulcitol	-	+	+	+	-	-	-
Ethanol	+	+	-	+	-	-	-
Fructose	-	-	+	-	-	+	+
L-Fucose	+	-	+	+	+	+	+
Glycerol	+	-	+	+	+	-	+
Galactose, rhamnose	-	-	+	-	+	+	+
Mannitol	-	-	+	+	+	+	-
Melibiose, turanose	+	-	+	+	+	-	+

Table 2 continued

Characteristic	Isolate MG-37 ^T	<i>V. giffhornensis</i> DSM 44337 ^T	<i>V. latea</i> YIM 013 ^T	<i>V. marts</i> DSM 45365 ^T	<i>V. sedimintis</i> MS 426 ^T	<i>V. quatae</i> R11147 ^T	<i>V. wenchangensis</i> 234402 ^T
α-Methyl-D-glucoside	-	+	+	+	+	+	-
Raffinose	+	+	-	-	+	-	+
Salicin	+	-	-	-	+	+	+
Sorbitol	-	-	+	-	+	+	+
Xylose	+	+	-	+	+	+	-
Growth on sole nitrogen sources							
L-Alanine	+	-	-	+	+	+	+
L-Arginine	+	-	+	+	+	+	+
L-Glutamic acid	-	+	-	-	-	+	-
L-Methionine	+	+	-	+	+	+	-
L-Phenylalanine	+	-	-	+	+	+	-
L-Serine	-	+	-	-	-	-	-
L-Valine	+	+	-	+	+	+	-
Growth on sole carbon and nitrogen sources							
Acetamide	+	+	-	+	-	+	-
L-Asparagine	+	+	+	+	-	+	+
L-Cysteine	+	+	-	+	-	+	-
Glycine	+	+	-	+	+	+	-
L-Histidine	+	+	+	+	-	+	+
L-Isoleucine	+	+	-	+	-	+	-
Sensitivity to antibiotics (µg ml):							
Ampicillin (8)	+	+	-	+	-	-	-
Chloramphenicol (8)	+	+	-	+	-	-	-
Cephaloridine (4)	+	+	+	+	-	-	-
Ciprofloxacin (4)	+	+	+	+	-	-	+
Clindamycin (8), Lincomycin (8)s	-	-	+	+	+	+	-
Erythromycin (10)	+	+	+	+	+	-	-
Gentamicin (8)	-	-	+	-	-	-	+
Oxytetracycline (16)	-	-	-	-	+	-	-
Rifampicin (16)	+	+	+	+	-	-	-
Tolerance tests							
Growth in presence of 5 % w/v NaCl	-	+	-	+	+	+	+

Table 2 continued

Characteristic	Isolate MG-37 ^T	<i>V. giffhornensis</i> DSM 44337 ^T	<i>V. lutea</i> YIM 013 ^T	<i>V. maris</i> DSM 45365 ^T	<i>V. sediminitis</i> MS 426 ^T	<i>V. quiaie</i> R11147 ^T	<i>V. wenchangensis</i> 234402 ^T
pH range for growth	7–10	7–9	7–10	7–10	7–10	7–10	7–10
Temperature range for growth	20–45 °C	20–40 °C	20–45 °C	20–37 °C	20–45 °C	20–45 °C	20–37 °C
DNA G + C content ml %	72.0	72.0 ^f /70.0 ^d	69.3 ^e	69.5 ^g /70.9 ^f	66.8 ^g	72.0 ^h	69.2 ⁱ

Key + positive, – negative, ND not determined

^a These data were taken from Rheims et al. (1998); Liao et al. (2009); Goodfellow et al. (2012); Dai et al. (2010); Xi et al. (2012); Xie et al. (2012), respectively

^b Unpublished data (Kui Hong, unpublished data)

^c Determined by fluorimetry and thermal denaturation (Goodfellow et al. 2012)

^d Determined by HPLC (Rheims et al. 1998)

^e Determined by HPLC (Liao et al. 2009)

^f Determined by whole genome sequencing (Roh et al. 2011)

^g Determined by spectrophotometric method (Dai et al. 2010)

^h Determined by a modified fluorimetric microwell plate method (Xi et al. 2012)

ⁱ Determined by using melting profiles in microplates (Xie et al. 2012)

sources; grow at 10 °C, at pH 6.0 or in the presence of imipenem (8 µg ml⁻¹), neomycin (8 µg ml⁻¹), streptomycin (54 µg ml⁻¹), tetracycline (8 µg ml⁻¹), tylosin (8 µg ml⁻¹) or vancomycin (2 µg ml⁻¹).

Discussion

The results of the present study confirm and extend those reported by Fiedler et al. (2008) in showing that the proximicin-producing strain MG-37^T has chemotaxonomic, molecular and morphological properties consistent with its classification in the genus *Verrucosispora* (Rheims et al. 1998; Goodfellow et al. 2012; Stackebrandt 2012). However, the detection of a high proportion of C_{17:1} ω8c in strain MG 37^T was unexpected although relatively high proportions of this fatty acid and correspondingly lower proportions of C_{17:1} ω9c have also been detected in the type strains of *V. lutea* and *V. quiaie* (Liao et al. 2009; Xi et al. 2012). Nevertheless the genotypic and phenotypic data show that the organism can be delineated readily from the type strains of *Verrucosispora* species, notably from its nearest phylogenetic neighbours, *V. giffhornensis* DSM 44337^T and *V. maris* DSM 45365^T. It is, therefore, proposed that strain MG-37^T be recognised as a new *Verrucosispora* species, *Verrucosispora fiedleri* sp. nov. Further comparative studies are needed to determine the taxonomic status of *V. quiaie* as the type and only representative of this organism falls outside the *Verrucosispora* gene clade and does not give the genus-specific amplification product with the *Verrucosispora*-specific primers.

Description of *Verrucosispora fiedleri*

Verrucosispora fiedleri (fi. ed. le' ri. N.L. gen. masc. *fiedleri*, after Hans-Peter Fiedler in recognition of his contributions to the search and discovery of new antibiotics from actinomycetes).

The description is based on data taken from this and an earlier study (Fiedler et al. 2008). Aerobic, Gram-positive, non-acid-fast actinomycete which forms an extensively branched light to dark orange pigmented substrate mycelium on ISP media. Neither aerial hyphae nor spore vesicles are formed. Single, non-motile, spores with warty surfaces are borne on long sporophores on oatmeal agar. Grows at 20 and 45 °C, from pH 7–10, and in the presence of up to 2.5 %, w/v NaCl. Additional

phenotypic properties are cited in the text and in Table 2. The peptidoglycan is rich in *meso*- and hydroxyl-diaminopimelic acid and contains *N*-glycolated muramic acid. Mannose and xylose are the characteristic sugars in whole-organism hydrolysates and a tetrahydrogenated menaquinone with nine isoprene units is the major isoprenologue. The cellular fatty acid profile contains major proportions of *iso*-C_{16:0} and C_{17:1} ω8c; lower proportions of *iso*-C_{15:0}, anteiso-C_{15:0}, anteiso-C_{17:0}, C_{17:0}, 10-methyl C_{17:0} and trace amounts (<2.0 %) of *iso*-C_{14:0}, C_{15:1B}, *iso*-C_{16:H}, *iso*-C_{16:H}, C_{16:1 cis 9}, C_{16:0}, 9-methyl C_{16:0}, anteiso C_{17:1}, *iso*-C_{17:0}, *iso*-C_{18:0} C_{18:1 cis 9}, C_{18:0}, 10-methyl C_{18:0}, C_{19:0} plus trace amounts of summed components. The phospholipid pattern contains diphosphatidylglycerol, phosphatidylethanolamine and phosphatidylinositol mannosides as major components. The G + C content of the DNA is 72.0 %. Produces proximicins A, B and C.

The type strain, MG-37^T (NCIMB 14794^T = NRRL B-24892^T), was isolated from a sediment sample collected from the Raune Fjord in Norway.

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