Modestobacter versicolor sp. nov., an actinobacterium from biological soil crusts that produces melanins under oligotrophy, with emended descriptions of the genus *Modestobacter* and *Modestobacter multiseptatus* Mevs *et al.* 2000

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A novel isolate, CP153-2^T, was obtained from topsoil biological crusts in the Colorado Plateau (USA). Colonies were black in colour due to melanin-like pigments when grown on oligotrophic medium, but not when grown on copiotrophic medium. Induction of melanogenesis was independent of growth phase or illumination conditions, including exposure to UVB and UVA radiation, but exposure to UVB could enhance total pigment production and growth under low nitrogen prevented its synthesis. This mode of regulation was previously unknown among melanin-producing bacteria. Polyphasic characterization of the strain revealed that cells were short, straight to curved or irregular rods that developed into pairs and formed multiseptate short filaments, with rare bud-like cells. Short rods were typically motile by means of flagella; multicellular structures tended to be sessile. Cells stained Gram-positive, grew at 4–30 °C and had a narrow range of pH tolerance (pH 5–9). The major fatty acids were iso-C_{15:0}, iso-C_{16:0}, anteiso-C_{15:0} and C_{18:1}; MK-9(H₄) was the major respiratory quinone. Its peptidoglycan contained *meso*-diaminopimelic acid. Based on 16S rRNA gene sequence similarity data, its closest relative (98.1 % similarity) was *Modestobacter multiseptatus* DSM 44406^T, which is similar morphologically. Based on the above characteristics, strain CP153-2^T was also assigned to the genus *Modestobacter*. However, CP153-2^T had a relatedness of only 49.9 % in whole-genome reassociation comparisons with the type strain of *M. multiseptatus* and thus formally represents a novel species, for which the name *Modestobacter versicolor* sp. nov. is proposed. Additional evidence in support of a novel species comes from phenotypic and chemotaxonomic characteristics. Strain CP153-2^T (=ATCC BAA-1040^T =DSM 16678^T) is the type strain of *M. versicolor*.

The description of microbial diversity in arid soils has received relatively little attention compared with that in mesic or agricultural soils, even though arid and semi-arid lands comprise around 30 % of the Earth's terrestrial surface. Biological soil crusts (BSCs) that develop in the topmost layers of otherwise bare soils are one of the most conspicuous and widespread microbial communities of the arid zone. BSCs are important components of the soil system as they not only stabilize the soil against erosion (Belnap & Gardner, 1993), but also import nutrients such as carbon and nitrogen (Belnap, 2002; Belnap & Lange, 2001; Johnson *et al.*, 2005). Their community composition

always includes some oxygenic phototrophs (often cyanobacteria, but also eukaryotic green algae), which are commonly free-living, but also often occur as lichen symbionts. An array of heterotrophic bacteria, archaea and fungi accompanies the primary producers (Garcia-Pichel, 2002). Recent cultivation-independent surveys have revealed that actinobacteria are one of the most important groups of heterotrophs in soil crusts (Reddy & Garcia-Pichel, 2006; Nagy *et al.*, 2005). North American BSCs have been surveyed using molecular cultivation-independent methods (Garcia-Pichel *et al.*, 2001; Smith *et al.*, 2004; Nagy *et al.*, 2005; Reddy & Garcia-Pichel, 2006) and novel bacteria and fungi have been isolated (Reddy & Garcia-Pichel, 2005; Reddy *et al.*, 2006; Reddy & Garcia-Pichel, 2007; Bates *et al.*, 2006). Many isolates from these crusts are pigmented and it would seem that pigment synthesis is a common strategy among many crust inhabitants, and not

Abbreviations: BSC, biological soil crust; *m*-DAP, *meso*-diaminopimelic acid; OPA, *o*-phthalaldehyde.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain CP153-2^T is AJ871304.

only among phototrophs. Here, the isolation and characterization of yet another pigmented bacterium, strain CP153-2^T, is reported. This strain presents the previously unreported ability to regulate pigment production depending on external nutrient conditions. Polyphasic taxonomic characterization of this strain is presented and it is proposed that it represents a novel species of the genus *Modestobacter*. This genus belongs to the actinobacterial family *Geodermatophilaceae* (Normand, 2006), which contains species that are typical inhabitants of exposed surfaces such as monuments and natural stones (e.g. *Blastococcus* species; Urzì *et al.*, 2004) or surface soils (e.g. *Geodermatophilus* species; Luedemann, 1968). Most are pigmented, either pink to red or brown to black, a character that is most likely related to photoprotection, although direct evidence for this is lacking.

Strain CP153-2^T was isolated from a BSC sample collected from the Colorado Plateau (38° 38.557' N 109° 38.910' W), USA. Crusted topsoil samples were suspended in Ringer's solution and plated on oligotrophic BG11-PGY plates (10 % strength BG11 mineral medium, 0.025 % peptone, 0.025 % yeast extract, 0.025 % glucose, 1.5 % agar). BG11 mineral medium contains (l⁻¹): NaNO₃ (1.5 g), K₂HPO₄·3H₂O (40 mg), MgSO₄·7H₂O (75 mg), CaCl₂·2H₂O (36 mg), citric acid (6 mg), ferric ammonium citrate (6 mg), EDTA (1 mg), Na₂CO₃ (20 mg) and trace element solution (1 ml; Reddy & Garcia-Pichel, 2005). For experiments using exposure to solar radiation, light sources used were GE fluorescent tubes (40 W soft white for visible, 20 W black light fluorescent tubes for UVA and 15 W sun-tanning tubes for UVB). White light and UVA sources were continuous, whereas UVB radiation was under a regime of 4 h daily. Direct solar exposure was obtained on a south-facing window ledge using liquid cultures in pure quartz test tubes. Morphology was studied using light microscopy and TEM as described previously (Reddy *et al.*, 2006). Growth and biochemical characteristics, carbon assimilation and the sensitivity of the cultures to different antibiotics were determined by previously described methods (Reddy & Garcia-Pichel, 2005; Reddy *et al.*, 2006).

For quantitative analysis of whole-cell fatty acids, cells of CP153-2^T were grown on tryptic soy agar medium at 25 °C, scraped off, suspended in 1 ml 15 % methanolic HCl and incubated at 85 °C for 2 h. Water and n-hexane (1 ml each) were added to the suspension, which was then cooled to room temperature and vortexed. The upper, n-hexane layer containing fatty acid methyl esters was evaporated and redissolved in 50 µl n-hexane; samples (3 µl) were analysed by GC-MS. Lipids were extracted and analysed by one-dimensional TLC using a pre-coated silica gel plate as described previously (Suresh *et al.*, 2004). Cells of CP153-2^T were grown on BG11-10 × PGY or BG11-PGY agar media, the former being 10-fold more concentrated in peptone, glucose and yeast extract than the latter, and UV-visible spectra were recorded *in vivo* as described by Reddy *et al.* (2006). Peptidoglycan was prepared according to the

method of Komagata & Suzuki (1987). Quantitative analysis of peptidoglycan amino acids was performed by the OPA (*o*-phthalaldehyde) method (G. S. N. Reddy and F. Garcia-Pichel, unpublished). Approximately 7 µl hydrolysed peptidoglycan in borate buffer was mixed with 1 µl OPA reagent (74.6 mM OPA and 94.2 mM mercaptopropionic acid prepared in methanol and 0.4 M sodium borate, pH 10.5) in the injection loop and immediately analysed on a C₁₈ reversed-phase HPLC column. The individual amino acids were eluted with 100 % solvent A (20 mM sodium acetate, pH 7.2, containing 3 % tetrahydrofuran and 0.018 % triethylamine) for 17 min and then with a gradient of solvent A to 60 % solvent B (20 mM sodium acetate, pH 7.2, plus 40 % each of acetonitrile and methanol) for 10 min. The flow rate used was 0.45 ml min⁻¹. Eluted amino acids were detected by a fluorescence detector set at excitation and emission wavelengths of 340 and 450 nm, respectively. Isoprenoid quinones were extracted according to the method of Collins *et al.* (1977) and separated by HPLC using the isocratic solvent system methanol/isopropylether (3:1), and identified by MS (Tamaoka *et al.*, 1983; Tamaoka, 1986).

DNA from CP153-2^T and *Modestobacter multiseptatus* DSM 44406^T was isolated according to the method described by Marmur (1961) and hybridization was carried out spectrophotometrically as described by De Ley *et al.* (1970). The DNA G + C content (mol%) was determined as described previously (Reddy *et al.*, 2000). The variation between the experiments was less than 2 %. The 16S rRNA gene was amplified by PCR and sequenced as described previously (Reddy & Garcia-Pichel, 2005; Reddy *et al.*, 2000). It was aligned with closely related sequences belonging to the family *Geodermatophilaceae* using CLUSTAL W (Thompson *et al.*, 1994). Pairwise evolutionary distances were computed using the program DNADIST with the two-parameter model as developed by Kimura (1980). Phylogenetic trees were constructed using four different tree-making algorithms (neighbour-joining, maximum evolution, UPGMA and DNAPARS) using the MEGA3 software package (Kumar *et al.*, 2004). Bootstrap analysis was performed using 1000 replicate datasets in order to assess stability among the clades recovered in the phylogenetic tree.

The nature and regulation of pigments in the novel isolate

During initial plating on oligotrophic medium and after 15 days incubation at room temperature in the dark, dark-brown- to black-coloured colonies were clearly visible. When a dark-brown colony was re-plated on copiotrophic medium (10-fold concentrated PGY in BG11) for purification, the dark-brown pigmentation disappeared and pink colonies grew instead. After clonal purification, pink colonies re-plated on oligotrophic medium regained their dark-brown coloration. Colonies of this strain, CP153-2^T, in pure culture could be repeatedly and consistently

induced to switch pigmentation from pink to dark brown according to the strength of the complex medium (Fig. 1). Upon closer inspection of the temporal dynamics of colour change, both in liquid culture and on agar plates, it became obvious that the availability of copious carbon sources resulted in pink to colourless growth. In oligotrophic complex medium, cells were initially colourless to pink, but rapidly turned dark within 2–4 days of inoculation and while still growing exponentially. In copiotrophic medium, cells remained colourless or pink for all of the exponential and early stationary phases, with colour change occurring only very late in the stationary phase (beyond 2 weeks). Because generation times under both media were not significantly different (around 6.4 h in rich medium and averaging 6.6 h in oligotrophic medium), the induction of dark-brown pigment synthesis cannot be deemed a 'starvation' response. Differences in growth rate per se did not influence pigment production. The production of dark pigment was also suppressed during active growth in nitrogen-poor media (minimal medium supplemented with glucose and a single 2.5 mM nitrogen source, i.e. ammonium, nitrate, glycine, tyrosine or tryptophan). Pigment production was also suppressed under diazotrophic growth. Exposure of CP153-2^T to solar radiation was not necessary for pigment production, since growth in the dark resulted clearly in dark-pigmented cells. However, exposure of cells to the UV region of the spectrum (either UVA or UVB) resulted in a noticeable enhancement of pigment production over cells grown in the dark or under white visible light, if grown in oligotrophic medium. However, exposure to either UVB or UVA alone was not sufficient to induce a colour change, as demonstrated by the fact that cells grown in copiotrophic medium under either UVA or UVB remained pink during exponential growth. Direct exposure to full summer radiation prevented growth of CP153-2^T. These results imply that an interaction between metabolic and photobiological cues regulates dark pigment production in this isolate.

Fig. 1. Colonies of strain CP153-2^T grown on rich (left) and oligotrophic (right) media. Melanin production is obvious in the low-carbon medium, but incipient production can be seen in the centre of the colonies growing on rich medium. Both plates were incubated for 5 days under UVB irradiation (see text for details).

The pigment from dark-brown-coloured colonies was insoluble in water, phosphate buffer and alkali and it did not diffuse on agar plates. It was also insoluble in methanol, hot DMSO, acetone and hexane, even after sonication. The scatter-corrected *in vivo* absorption spectrum of whole cells was flat and otherwise featureless across the visible range (Fig. 2). All of these characteristics imply that the brown pigment is a eumelanin (Kollias, 1995). The pink pigmentation from colonies grown on copiotrophic medium, which was particularly obvious on plates, was not extractable with ethanol or acetone, but could be extracted with methanol after sonication and showed an absorption spectrum with maxima at 450, 480 and 510 nm in the visible range and, thus, it is probably a carotenoid. This pigment was absent in cells grown in oligotrophic and nitrogen-poor media and was not merely masked by the brown pigment. When grown on copiotrophic solid media, colonies would eventually turn a brownish colour at the centre (Fig. 1), most likely due to localized carbon limitation brought about by an insufficient diffusional supply of carbon.

Many bacteria can synthesize a variety of allegedly photoprotective pigments, many of which are directly regulated by exposure to visible light or UV (Garcia-Pichel, 1998). In some cases, biosynthesis can be influenced by nutrient conditions, such as in members of the genus *Streptomyces*, where synthesis of a variety of pigments is notoriously dependent on the conditions in the medium (Kämpfer, 2006). In some melanin-producing isolates of the proteobacterial genus *Marinobacter*, melanogenesis

Fig. 2. *In vivo* absorption spectrum of whole cells of strain CP153-2^T suspended in 50 % glycerol containing 0.04 % sodium thioglycollate to suppress light scatter during exponential growth under oligotrophy (thick line, rather featureless) and copiotrophy (thin line, with carotenoid-like features).

starts only in the late exponential phase of growth (Solano & Sánchez-Amat, 1999) and in members of *Weeksella* (*Bacteroidetes*), a melanin-like diffusible pigment is only synthesized upon growth on tyrosine agar (Hugo *et al.*, 2006). However, the type of pigment regulation shown by strain CP153-2^T is unparalleled among bacteria. Melanins, like other microbial sunscreens, act by intercepting photons before they create excited molecular states or oxygen radicals and are thus passive photoprotectants (García-Pichel *et al.*, 1993). Our results indicate that the switch to melanogenesis is caused by low availability of carbon during growth, if sufficient nitrogen is available, and not just by growth rate, since no switch occurs at the transition to stationary phase or soon thereafter and the growth rates in rich medium do not differ from those in oligotrophic medium. Synthesis may be controlled by general regulators, such as the starvation-response-specific *rpoS* of *Escherichia coli* (Rockabrand *et al.*, 1998).

Polyphasic taxonomy of CP153-2^T

Cells of strain CP153-2^T are Gram-positive, motile, short, small rods (straight, lightly curved, irregular or even tapering), often developing into multiseptate cells, occurring singly or in pairs, sometimes remaining aggregated and only rarely forming filaments longer than several cells (Fig. 3). Single rods can be 0.5–1.0 µm wide and 1.0–3.0 µm long. Short filaments are up to 7.0 µm long.

Fig. 3. (a) Phase-contrast optical photomicrograph of strain CP153-2^T showing aggregation, single cells varying in morphology from simple to irregular rods and short multiseptate cells. (b–d) Negatively stained TEM photomicrographs of strain CP153-2^T showing detail of transversal multiseptation and tapering (b) as well as single, very small rods (c, d). Flagella are also visible (arrow in c). Bars, 4 µm (a), 1 µm (b) and 0.5 µm (c, d).

Septation is transversal (orthogonal to the long cellular axis) and apical cells may resemble buds. Motility is variable, most often seen in young cultures and single rods, with larger multiseptate cells being sessile. Flagellation is polar, with one to a few flagella per cell. Strain CP153-2^T is a non-spore-forming, aerobic chemoheterotroph that is capable of growing on relatively oligotrophic medium (PGY) and of aerobic diazotrophy. It is psychrotolerant, growing at 4–30 °C, but it is only narrowly tolerant of variations in pH, with fast growth occurring at pH 6–8 and survival or very slow growth at pH 5 and 9 (growth assessed at pH 4–12 at 1 unit intervals). Major fatty acids are iso-C_{16:0}, anteiso-C_{15:0}, iso-C_{15:0} and C_{18:1}; the major respiratory quinone is MK-9(H₄). The cell wall peptidoglycan contains *meso*-diaminopimelic acid (*m*-DAP) as the diamino acid. Based on the coincidence of many of these characteristics, strain CP153-2^T belongs to the genus *Modestobacter* (Mevs *et al.*, 2000). In addition, CP153-2^T could utilize adonitol, D-cellobiose, dulcitol, fumaric acid, D-glucose, glycerol, inositol, inulin, lactose, lactic acid, D-laevalulose, maltose, D-mannitol, D-mannose, D-melibiose, D-raffinose, L-rhamnose, D-ribose, sucrose, L-sorbose, trehalose, L-alanine, L-leucine, L-isoleucine, L-proline, L-threonine and L-valine, but not L-arabinose, acetate, citrate, dextran, ethanolamine, D-fructose, D-galactose, pyruvate, sucrose, succinate, D-sorbitol, D-xylose, L-arginine, L-aspartic acid, L-asparagine, L-cysteine, L-glycine, L-glutamine, L-glutamic acid, L-histidine, L-lysine, L-methionine, L-phenylalanine, L-serine, L-tryptophan, L-tyrosine, adenine, cytosine, guanine, thymidine, nicotinic acid or tartaric acid. Cells were sensitive to (per disc) aztreonam (30 µg), bacitracin (10 U), carbenicillin (100 µg), ciprofloxacin (5 µg), ceftriaxone (30 µg), cephalothin (30 µg), chloramphenicol (30 µg), doxycycline (30 µg), ethanbutol (50 µg), gentamicin (10 µg), novobiocin (30 µg), nitrofurantoin (150 µg), penicillin (10 U), polymyxin B (300 U), rifampicin (30 µg), streptomycin (10 µg), sulfisoxazole (300 µg), sulfthiazole (300 µg), tetracycline (30 µg), trimethoprim (5 µg) and vancomycin (30 µg), but resistant to colistin (10 µg) and erythromycin (2 µg).

The affiliation of CP153-2^T was further supported by a BLAST sequence similarity search based on virtually complete 16S rRNA gene sequences, which showed 98.1% similarity to the type strain of *M. multiseptatus*. Phylogenetic analysis based on all of the tree-making algorithms used clearly suggested that CP153-2^T is a member of the genus *Modestobacter*, forming a robust cluster with a bootstrap value of 100% (Fig. 4). However, DNA–DNA hybridization between CP153-2^T and *M. multiseptatus* DSM 44406^T, the type strain for the lone species in the genus, yielded a value of only 49.9%, firmly establishing the separate species status of strain CP153-2^T (Stackebrandt & Goebel, 1994). This was not surprising, because CP153-2^T presented morphological traits and physiological ranges for pH and temperature that differed from those reported for *M. multiseptatus* (Mevs *et al.*, 2000). Several biochemical characteristics, the enzyme profile and pigmentation and fatty acid composition were

Fig. 4. Neighbour-joining tree based on 16S rRNA gene sequences showing the phylogenetic relationship between strain CP153-2^T and other related reference micro-organisms of the family Geodermatophilaceae. Bootstrap values (expressed as percentages of 1000 replications) greater than 50 % are indicated at nodes. Bar, 0.01 substitutions per site.

also divergent (see Table 1). Thus, based on genetic and phenotypic criteria, it is proposed that CP153-2^T represents a novel species, *Modestobacter versicolor* sp. nov.

The original genus description of *Modestobacter* by Mevs *et al.* (2000) contained many traits (e.g. growth ranges, utilization and hydrolysis of carbon compounds, etc.) that are, in the light of the description of this novel species, better circumscribed to the species level rather than to the genus level. It is to be expected that such low-rank characteristics will tend to vary as novel species are described. Emended descriptions of the genus *Modestobacter*, achieved by transferring low-rank characteristics to the species description, and *M. multiseptatus* are presented.

Emended description of the genus *Modestobacter* Mevs *et al.* 2000

Modestobacter (Mo.des.to.bac'ter. L. adj. *modestus* modest, humble; *bacter* the equivalent of Gr. neut. n. *baktron* a rod or staff; N.L. masc. n. *Modestobacter* a rod with modest growth requirements).

Gram-positive, non-spore-forming. Short rods or cocci with a tendency to remain aggregated and form short, multiseptate filaments. Aerobic heterotrophs able to grow in oligotrophic medium. Typically psychrotolerant. Major fatty acids include C_{18:1}, iso-C_{16:0} and anteiso-C_{17:0}. The major respiratory quinone is MK-9(H₄). The cell wall peptidoglycan contains *m*-DAP as diamino acid, with alanine, glutamate and *m*-DAP present in a 2:1:1 stoichiometry. The DNA G+C content is around 70 mol%. The type species is *Modestobacter multiseptatus*.

Emended description of *Modestobacter multiseptatus* Mevs *et al.* 2000

Modestobacter multiseptatus (mul.ti.sep.ta'tus. L. adj. *multus* -a -um much; L. adj. *septatus* fenced; N.L. masc.

adj. *multiseptatus* much fenced, with many cross-walls, multiseptate).

Colonies are irregularly shaped, shiny, beige to pinkish. Cells are Gram-positive short rods or cocci with a tendency to remain aggregated. Cells show cross and longitudinal wall growth and multiply by budding and swarmer formation. Cell sizes vary (1.0–2.8 × 1.0–3.0 µm), with a mean size of 1.7 × 1.6–1.9 µm. Slender buds may become motile. Aerobic heterotroph; can grow on oligotrophic medium PYGV or on DSMZ medium 65. Growth occurs between 0 and 28 °C. Can tolerate pH 3–12, with optimum growth at pH 7.5–8.5. Positive for catalase, cytochrome oxidase, phosphatase and amylase. Shows type II restriction endonuclease activity. H₂S is not formed from cystine or sulfate. Does not utilize fructose, xylose or trehalose, but can utilize D-glucose, D-galactose, lactose, sucrose, mannitol, succinate and malate. Utilization of maltose, mannose, melibiose, fucose, ribose, rhamnose, sorbitol and N-acetylglucosamine is variable. Adenine, hypoxanthine, xanthine, hippurate, cellulose, chitin, dextrin, xylan, arbutin and casein are not hydrolysed. Utilizes peptone or yeast extract as nitrogen source and reduces nitrate aerobically or anaerobically. The main respiratory quinone is MK-9(H₄); MK-8(H₄) and MK-9(H₆) are present in small amounts. Fatty acid, polar lipid and cell-wall peptidoglycan compositions are given in Table 1. Cell-wall sugars are composed of galactose, glucose and ribose.

The type strain is strain AA-826^T (=DSM 44406^T =CIP 106529^T =JCM 12207^T). The DNA G+C content of the type strain is 68–70 mol%.

Description of *Modestobacter versicolor* sp. nov.

Modestobacter versicolor (ver.si.co'lor. L. masc. adj. *versicolor* that changes its colour, of changeable colour, of various colours, particoloured).

Colonies are dark brown on oligotrophic medium and pink to white on copiotrophic medium, 1–4 mm in diameter, convex, entire, smooth to rugose and slightly mucoid. Cells are short, small rods (straight, lightly curved, irregular or even tapering), often developing into multiseptate cells, occurring singly or in pairs, sometimes remaining aggregated and only rarely forming filaments longer than several cells (Fig. 3). Single rods are 0.5–1.0 × 1.0–3.0 µm. Short filaments are up to 7.0 µm long. Septation is transversal (orthogonal to the long cellular axis) and apical cells may resemble buds. Motility is variable, by means of polar flagellation. Growth is observed at 4–30 °C (but not at 37 °C) and pH 5–9, with optimum growth at 25 °C and pH 7. Produces copious melanins under oligotrophic conditions. Tolerates NaCl at concentrations less than 3 %. Cells are positive for catalase, β-galactosidase, phosphatase, urease and lipase, but negative for oxidase, gelatinase, arginine decarboxylase, lysine decarboxylase, ornithine decarboxylase and phenylalanine deaminase. Negative for methyl red, Voges–Proskauer and indole

Table 1. Metabolic, biochemical and chemotaxonomic traits that distinguish *Modestobacter versicolor* sp. nov. CP153-2^T from *M. multiseptatus* AA-826^T

Data for *M. multiseptatus* AA-826^T were taken from the original description (Mevs *et al.*, 2000).

Characteristic	<i>M. versicolor</i> CP153-2 ^T	<i>M. multiseptatus</i> AA-826 ^T
Temperature range (°C)	4–30	0–28
Temperature optimum (°C)	25	19–21
pH range	5–9	3–12
pH optimum	7	7.5–8.5
Oxidase	–	+
Lipase	+	–
Casein hydrolysis	+	–
Nitrate reduction	+	–
Starch hydrolysis	–	+
Utilization of:		
Arabinose	–	+
Acetate	–	+
Citrate	–	+
Galactose	–	+
Melibiose	+	–
Sorbitol	+	–
Trehalose	+	–
Inositol	+	–
Cellobiose	+	–
Fatty acid methyl esters (% of total)		
C _{13:0}	1.0	–
iso-C _{14:0}	–	1.9
C _{14:1}	0.9	2.6
C _{14:0}	0.9	3.4
iso-C _{15:0}	12.8	3.3
anteiso-C _{15:0}	15.4	7.8
C _{15:0}	1.8	2.1
iso-C _{16:0}	27.5	13.8
anteiso-C _{16:0}	3.4	–
C _{16:1}	5.5	6.2
C _{16:0}	4.8	7.9
C _{17:0}	0.4	–
iso-C _{17:0}	1.8	–
antesio-C _{17:0}	6.2	9.2
C _{17:1}	2.8	–
C _{18:1}	8.0	21.4
C _{18:0}	3.0	2.2
cyclo C _{19:0}	–	8.5
Unidentified fatty acids*	3.7	7.0
Quinones (% of total)		
MK-9(H ₄)	93.4	87
MK-9(H ₆)	–	2
MK-8(H ₄)	6.6	12
Peptidoglycan amino acids (molar ratio)		
Alanine	2.0	1.75
Glutamic acid	1.0	1.0
<i>m</i> -DAP	0.92	0.85
Glycine	0.3	0.66
Serine	0.5	0.56

Characteristic	<i>M. versicolor</i> CP153-2 ^T	<i>M. multiseptatus</i> AA-826 ^T
Arginine	0.2	0.33
Leucine	0.15	0.15
Presence of unknown lipids 1 and 2†	+	–
DNA G + C content (mol%)	73 ± 2.5	68–70

*The respective unidentified compounds are not necessarily identical.

†Both strains contain phosphatidylglycerol, diphosphatidylglycerol, phosphatidylethanolamine and phosphatidylinositol.

tests. Hydrolyses casein and aesculin, but not cellulose or starch. Reduces nitrate to nitrite. Does not produce H₂S gas and cannot grow on DNase or Simmons' citrate test plates. Utilizes a wide variety of sugars, low-molecular-mass organic acids and amino acids and all four nitrogenous bases. Dinitrogen fixer. Respiratory quinones and cell-wall peptidoglycan, fatty acid and polar lipid compositions are given in Table 1.

The type strain is CP153-2^T (=ATCC BAA-1040^T =DSM 16678^T), isolated from a biological soil crust. The DNA G + C content of the type strain is 73 ± 2.5 mol%.

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