**Terriglobus albidus** sp. nov., a member of the family *Acidobacteriaceae* isolated from Namibian semiarid savannah soil

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A novel aerobic, chemo-organoheterotrophic bacterium, strain Ac_26_B10T, was isolated from a semiarid savannah soil collected in northern Namibia (Mashare, Kavango region). Based on analysis of its nearly full-length 16S rRNA gene sequence, the isolate belongs to the genus *Terriglobus* (family *Acidobacteriaceae*, order *Acidobacteriales*, class *Acidobacteria* and shares 98.3 and 96.9 % 16S rRNA gene sequence similarity with its closest relatives, *Terriglobus tenax* DRP 35T and *T. aquaticus* O3SUJ4T. Cells were Gram-negative, coccoid to rod-shaped, non-motile and divided by binary fission. Strain Ac_26_B10T showed weak catalase activity and, in contrast to the other described species of the genus *Terriglobus*, was oxidase-positive. Compared with the already established species of the genus *Terriglobus*, the novel strain used a larger range of sugars and sugar alcohols for growth, lacked α-mannosidase activity and exhibited a higher temperature optimum of growth. DNA–DNA hybridization studies with its closest phylogenetic relative, *T. tenax* DSM 28898T, confirmed that strain Ac_26_B10T represents a distinct genomospecies. Its most abundant fatty acids were iso-C_{15 : 0}, summed feature 3 (C_{16 : 1ω7c} and/or C_{16 : 1ω6c}) and C_{16 : 0}. Dominant polar lipids were phosphatidylethanolamine and diphosphatidylglycerol. The predominant menaquinone was MK-8; minor amounts of MK-7 and MK-8(H2) were also recorded. The G+C content of the genomic DNA was 58.5 mol%. On the basis of our polyphasic analysis, Ac_26_B10T represents a novel species of the genus *Terriglobus*, for which the name *Terriglobus albidus* sp. nov. is proposed. The type strain is Ac_26_B10T (=DSM 26559T = LMG 27984T).

Members of the phylum *Acidobacteria* are widespread across a large variety of habitats such as acid mine drainages (Diaby et al., 2007; Tan et al., 2007), caves (Meisinger et al., 2009), hot springs (Hobel et al., 2005), wastewater (Narihiro et al., 2009) and plant roots (Lee et al., 2008), and represent one of the most abundant bacterial groups, particularly in soil environments (Jones et al., 2009; Foesel et al., 2014). The phylogenetic and metabolic diversity of the phylum is comparable to that found in the phylum *Proteobacteria* (Hugenholtz et al., 1998). Although 26 different subdivisions have been recognized within the phylum *Acidobacteria* by 16S rRNA gene-based molecular analyses, only representatives of subdivisions 1, 3, 4, 8, 10 and 23 have been described taxonomically so far. Class *Acidobacteria* Cavalier-Smith 2002, which is taxonomically equivalent to subdivision 1 (Barns et al., 2007), harbours the largest number of described species, which are classified into the seven genera *Acidobacterium* (Kishimoto et al., 1991), *Terriglobus* (Eichorst et al., 2007), *Edaphobacter* (Koch et al., 2008), *Granulicella* (Pankratov & Dedysy, 2010), *Acidicapsa* (Kulichkova et al., 2012), *Bryocella* (Dedysy et al., 2012) and *Telmato bacter* (Pankratov et al., 2012). Two additional taxa have been proposed, the genus ‘*Acidipila*’ (Okamura et al., 2011) and the candidate species ‘*Candidatus* Koribacter versatilis’ Ellin345 (Joseph et al., 2003; Davis et al., 2005). The genus *Terriglobus* comprises four aerobic, chemo-organoheterotrophic species. The type strains of the three species *Terriglobus roseus* (Eichorst et al., 2007), *T. saanensis* (Männistö et al., 2011) and *T. tenax* (Whang et al., 2014) were isolated from soils, while the type strain of *Terriglobus aquaticus* was isolated from freshwater (Baik et al., 2013). In the
present study, a novel representative of the genus Terriglobus was obtained from a Namibian semiarid savannah soil. Characterization of strain Ac_26_B10T revealed that it represents a novel species within this genus. 

A high-throughput cultivation approach was used to enrich and isolate strain Ac_26_B10. It originates from a Kalahari sandy fallow soil with a slightly acidic pH (pH 6.2 and 5.2 measured in distilled water and in 2 mM CaCl2, respectively) that was collected in spring 2011 in Mashare (Kavango region, Namibia; 17° 55′ 00.2″ S 20° 06′ 18.7″ E). An aliquot of the soil sample was suspended in MES (10 mM, pH 6.0) and the total bacterial cell number was determined after staining with SYBR Green I (Life Technologies). Liquid cultures were set up in sterile 96-well microtitre plates containing 180 µl soil solution equivalent (SSE)/Cmix medium buffered at pH 6.0 (MES) per well (see supplementary methods, available in the online Supplementary Material), and each well was inoculated with 20 µl soil suspension containing approximately 100 bacterial cells. After 6 weeks of incubation at 20 °C in the dark as static cultures, bacterial growth was detected by turbidity (Huber et al., 2014). All growth-positive wells were screened for the presence of acidobacteria by group-specific diagnostic PCR using the primer pair Acido31f (Barns et al., 1999) and 907r (Lane, 1991). Acidobacterium-positive cultures were further streaked on SSE/Cmix medium solidified with 1.5 % (w/v) agar. Unless otherwise noted, strain Ac_26_B10T was grown under oxic conditions at 25 °C using SSE/HD 1 : 10 medium (DSMZ medium 1426; http://www.dsmz.de) buffered at pH 5.5 (MES) for inoculation or sample preparation.

Phenotypic characterization followed procedures outlined previously (Foesel et al., 2013; Huber et al., 2014). Cells of strain Ac_26_B10T stained Gram-negative, were non-motile, coccoid to rod-shaped, 1.1–2.5 μm long and 0.7–0.9 μm wide, and divided by binary fission (Table 1 and Fig. S1). Capsules and endospores were not observed after staining the cells with Indian ink and malachite green, respectively. After 1 week of growth on solid SSE/HD 1 : 10 medium, small white colonies (~1 mm in diameter) appeared that were round, smooth, convex and opaque.

Strain Ac_26_B10T was aerobic, chemo-organoheterotrophic and unable to reduce nitrate or to ferment glucose. It showed a weak response in the catalase test and a positive response in the cytochrome-c oxidase test. These properties distinguish the novel isolate from all other members of the genus Terriglobus, which are catalase-positive and oxidase-negative (Table 1). Ranges and optima of temperature and pH for growth were determined under oxic conditions in liquid SSE/HD 1 : 10 medium as described before (Huber et al., 2014). Depending on the pH, MES, HEPES, HEPPS or CHES (from Sigma-Aldrich or Appli- chem; 10 mM each) were used as buffers. Growth was determined by measuring the OD660. Optimal growth was defined as ≥75 % of the highest growth rate achieved. Strain Ac_26_B10T was able to grow between 10.1 and 42.5 °C, with a temperature optimum of 28.6–37.2 °C. It showed a temperature range comparable to that of T. tenax DRP 35T, but wider than those of the type strains of the other three species of the genus Terriglobus (Table 1). Growth was observed between pH 3.9 and 9.8 and was optimal between pH 4.7 and 7.3. However, initial growth was already observed at pH 3.2. As a result of bacterial growth, pH values above 8.0 dropped to nearly neutral values at the end of the experiment (Fig. S2). Nevertheless, strain Ac_26_B10T tolerated a wider initial pH range than the other representatives of the genus Terriglobus and was even able to grow at alkaline initial pH (Table 1). Doubling time under optimal conditions was 6.1 h, and thus Ac_26_B10T grows a little faster than T. roseus KBS 63T (10–15 h; Eichorst et al., 2007).

For physiological tests, commercial miniaturized API 20NE and API ZYM galleries (bioMérieux) were initially used, following the instructions of the manufacturer. Tests were examined after 48 h (API 20NE) and 4 h (API ZYM) of incubation. Strain Ac_26_B10T, like all other members of the genus Terriglobus, showed positive results for β-galactosidase and hydrolysis of aesculin, but tested negative for the reduction of nitrate, fermentation of glucose, indole production, hydrolysis of gelatin and the arginine dihydrolase test. Among exoenzymic activities, strain Ac_26_B10T showed a preference towards phosphate esters (alkaline and acid phosphatases and naphthol-AS-BI-phosphohydrolase) and glycosides (α-fucosidase, α-galactosidase, β-galactosidase, β-glucosidase and β-glucuronidase), like other members of the genus Terriglobus. However, unlike the described species, strain Ac_26_B10T showed no activity for α-mannosidase. The specific enzymic activities of strain Ac_26_B10T are further detailed in Table 1 and in the species description.

Strain Ac_26_B10T was found to be unable to use any carbon source provided in the API 20NE test, which might be because of either the high concentration of nutrients provided in this commercial kit or its inability to use the provided substrates. Therefore, individual carbon substrates used for growth were analysed in duplicate cultures using SSE (pH 5.5) as the basal medium containing 10 mM MES and 1 ml trace element solution SL-10 and 1 ml vitamin solution per litre (supplementary methods). The final concentration of each substrate was described previously (Huber et al., 2014). Substrates were scored as supporting growth when a final OD660 (mean of parallel incubations) exceeded the control value (without the addition of substrate) by 1.5-fold. Of 108 single carbon substrates tested, strain Ac_26_B10T grew on 27 (Table 1). Strain Ac_26_B10T, like all other members of the genus Terriglobus, had a preference for simple sugars. In addition, strain Ac_26_B10T could utilize complex protein substrates such as Casamino acids, casein hydrolysate and yeast extract (Table 1).
Table 1. Differential characteristics of strain Ac_26_B10⁷ and type strains of other species of the genus Terriglobus

Strains: 1, Ac_26_B10⁷; 2, T. aquaticus 03SUJ4⁸; 3, T. roseus KBS 63⁹; 4, T. saanensis SP1PR4⁹; 5, T. tenax DRP 35⁹. Data for reference strains were taken from the literature (Eichorst et al., 2007; Männisto et al., 2011; Baik et al., 2013; Whang et al., 2014), as they were characterized under growth conditions comparable to those used in this study for strain Ac_26_B10⁷. +, Positive; −, negative; W, weakly positive; NA, no data available. Strain Ac_26_B10⁷, like the type strains of all other species of the genus Terriglobus, showed positive results for β-galactosidase, hydrolysis of aesculin, alkaline and acid phosphatases, naphthol-AS-BI-phosphohydrolase, β-glucosidase, α-galactosidase, β-galactosidase, β-glucuronidase and α-fucosidase, while they tested negative for the reduction of nitrate, fermentation of glucose, indole production, hydrolysis of gelatin and the arginine dihydrolase test.

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The capacity of the strain to degrade complex polymers was assayed on solid basal SSE medium (supplementary methods) amended with 0.005 % (w/v) yeast extract and the respective substrates by staining after bacterial growth with aqueous solutions of appropriate dyes. The polymers tested (and dyes) were starch (Lugol’s iodine) (Cowan, 1974), cellulose (Teather & Wood, 1982; Wood & Bhat, 1988), CM-cellulose (Teather & Wood, 1982; Wood & Bhat, 1988), xylan (Teather & Wood, 1982; Scheirlinck et al., 1990) and chitin (Thiagarajan et al., 2011) (all Congo red), pectin (ruthenium red) (Cruickshank & Wade, 1980; Gainvors et al., 1994) and lignin (solution of ferric chloride/potassium ferric cyanide) (Sundman & Nase, 1971; Tekere et al., 2001). To test for laccase activity, ABTS [2,2′-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid)] was used (Tekere et al., 2001; Soden et al., 2002).

Strain Ac_26_B10T hydrolysed only starch, and showed weak laccase activity.

The almost full-length 16S rRNA gene (1461 nt) of strain Ac_26_B10T was amplified and sequenced following the methodology detailed in the supplementary methods. Reference 16S rRNA gene sequences used in this study were obtained from the public All-Species Living Tree Project of the Silva database (Muñoz et al., 2011). Strain Ac_26_B10T was identified as a member of subdivision 1 of the phylum Acidobacteria. According to the EzTaxon-e database (Kim et al., 2012), the closest type strains to Ac_26_B10T were T. tenax DRP35T and T. aquaticus O3SUJ4T, sharing 98.3 and 96.9 % 16S rRNA gene sequence similarity, respectively. The different phylogenetic trees obtained with the neighbour-joining, maximum-parsimony and maximum-likelihood algorithms are depicted in Figs 1 and S3. These results confirmed the
phylogenetic affiliation of strain Ac_26_B10T with the genus Terriglobus. In all phylogenetic trees, the genus Terriglobus emerged as a well-defined clade. Strain Ac_26_B10T formed a separate lineage with T. tenax, distinct from the clade formed by T. aquaticus, T. roseus and T. saanensis. This arrangement was supported by high bootstrap values. Sister clades of the genus Terriglobus are the genera Edaphobacter, Granulicella and Bryocella.

Since the maximum 16S rRNA gene sequence similarity found between strain Ac_26_B10T and the type strain of T. tenax (98.3 %) was very close to or greater than the threshold values typically used for differentiation of prokaryotic species (98.7 %, Kim et al., 2014; 97.0 %, Stackebrandt & Goebel, 1994), we conducted DNA–DNA hybridizations to confirm the status of strain Ac_26_B10T as a representative of a novel species of the genus Terriglobus. The established protocol for DNA–DNA hybridization (De Ley et al., 1970) as modified by Huss et al. (1983) was used, employing a Cary 100 Bio UV/Vis spectrophotometer equipped with a Peltier-thermostatted 6 × 6 multicell changer and a temperature controller with in situ temperature probe (Varian). Cells of strain Ac_26_B10T and T. tenax DSM 28898T were disrupted in a Constant Systems TS 0.75 kW cell disruptor (IUL Instruments). The DNA was purified from the crude lysate by chromatography on hydroxypatite (Cashion et al., 1977). DNA–DNA hybridization experiments were done in duplicate in 2 × SSC at 69 °C. The resulting DNA–DNA hybridization values were 21.0 and 12.9 %, which are clearly below the threshold value of 70 % accepted for species delineation (Wayne et al., 1987). This result corroborates the conclusion that strain Ac_26_B10T represents a unique genomospecies.

The molar G + C content of genomic DNA was analysed by HPLC according to Tamaoka & Komagata (1984) and Mesbah et al. (1989). The genomic DNA G + C content of strain Ac_26_B10T was 58.5 mol%, within the range reported for other members of the genus Terriglobus (57.3–63.2 mol%; Eichorst et al., 2007; Männistö et al., 2011; Baik et al., 2013; Whang et al., 2014).

Fatty acids were extracted, saponified and methylated according to standard protocols and individual fatty acid methyl esters were identified using the Microbial Identification System using the TSBA40 library (MIDI Microbial Identification System; Sasser, 1990). The fatty acid profile included straight-chain, methyl- and hydroxyl-branched saturated and monounsaturated fatty acids. Similar to all other described members of the genus Terriglobus (Baik et al., 2013; Whang et al., 2014), the major fatty acids were iso-C_{15:0} (59.1 %), summed feature 3 (C_{16:1}ω7c and/or C_{16:1}ω6c 32.3 %) and C_{16:0} (3.9 %). Summed feature 3 of the MIDI system (C_{16:1}ω7c and/or C_{16:1}ω6c) represents C_{16:1}ω7c in this case, as proven for several species of subdivision 1 of the phyllum Acidobacteria via GC-MS (Männistö et al., 2011; Sinninghe Damsté et al., 2011) (Table S1).

The polar lipid composition of Ac_26_B10T was analysed by two-dimensional TLC (Bligh & Dyer, 1959; Tindall et al., 2007). The major polar lipids of the strain were phosphatidylethanolamine and diphosphatidylglycerol. In addition, minor amounts of an unidentified aminophospholipid, an unidentified glycolipid and an unidentified phospholipid were detected (Fig. S4). This profile is similar to those of other species of the genus Terriglobus such as T. aquaticus and T. tenax, where phosphatidylethanolamine constitutes the major polar lipid (Baik et al., 2013; Whang et al., 2014).

Isochiroen quinones were extracted from dried biomass with chloroform/methanol (2 : 1, v/v) (Collins & Jones, 1981) and analysed via HPLC (Tindall, 1990). The predominant respiratory quinone of strain Ac_26_B10T was MK-8. The strain also contained minor amounts of MK-7 and MK-8(H2). This is in agreement with the results obtained for T. aquaticus (Baik et al., 2013) and T. tenax (Whang et al., 2014), which also contain MK-8 as the predominant quinone.

Comparison of the morphological, physiological, chemotaxonomic and phylogenetic characteristics of strain Ac_26_B10T with those of its closest phylogenetic neighbours supports the conclusion that the novel isolate represents a novel species of the genus Terriglobus, for which we propose the name Terriglobus albidus sp. nov.

**Description of Terriglobus albidus sp. nov.**

Terriglobus albidus (a’lbi’i dus. L. masc. adj. albidus white, referring to the colour of the colonies).

Cells are Gram-negative, coccolid to rod-shaped, 0.7–0.9 μm wide and 1.1–2.5 μm long, non-spore-forming, non-capsule-forming and non-motile. Divides by binary fission. Aerobic chemo-organoheterotroph, unable to reduce nitrate or to ferment glucose. Oxidase-positive and weakly catalase-positive. After 1 week of growth on solid SSE/HD 1 : 10 medium, colonies are round, smooth, convex, opaque and white. Growth is observed at 10.1–42.5 °C (optimum 28.6–37.2 °C) and pH 3.9–9.8 (optimum pH 4.7–7.3). Doubling time under optimal conditions is 6.1 h. Shows positive responses for hydrolysis of aesculin, β-galactosidase, alkaline and acid phosphatases, naphthol-AS-BI-phosphohydrolase, β-glucosidase, β-galactosidase, β-galactosidase, α-fucosidase and β-glucuronidase and weak responses for leucine and valine arylaminidases, esterase lipase C8, α-galactosidase and N-acetyl-β-glucosaminidase. In tests for indole production, urease activity, hydrolysis of gelatin, arginine dihydrolase, cystine arylaminidase, lipase C14, esterase C4, trypsin, α-chymotrypsin and α-mannosidase, it shows no activity. Uses as single carbon and energy sources L-arabinose, cellobiose, D-fructose, D-galactose, D-glucose, lactose, D-lyxose, maltose, D-mannose, melezitose, raffinose, L-rhamnose, sucrose, trehalose, xylose, N-acetylgalactosamine, D-adonitol, myo-inositol, aspartate, l-glutamate, hydroxyproline,
D-glucuronate, glycerol, Casamino acids, casein hydrolysate and yeast extract. Shows a weak response for utilization of succinate. Does not use D-erythrose, erythulose, L-fucose, D-arabitol, dulcitol, Lxyitol, D-mannitol, D-sorbitol, xylitol, L-alanine, L-arginine, L-asparagine, L-cysteine, L-glutamic acid, histidine, L-isoleucine, L-leucine, L-lysine, methionine, ornithine, phenylalanine, serine, L-proline, threonine, tryptophan, tyrosine, valine, isoleucine, valerate, benzoate, trimethoxybenzoate, butyrate, x-hydroxybutyrate, δ-hydroxybutyrate, γ-hydroxybutyrate, isobutyrate, caproate, caprylate, citrate, isocitrate, crotonate, formate, fumarate, oxogluconate, glucunonate, 2-oxoglutarate, glutarate, glycine, glutamate, heptanoic acid, isovalerate, laevulinate, lactate, malate, maleic acid, malonate, nocardic acid, oxaloacetate, propionate, protocatechuate, pyruvate, shikimate, tartrate, 2-oxoalurate, 2,3-butanediol, 2,3-butadiol, ethanol, ethylene glycol, methanol, propanol, 1,2-propanediol, fermented rumen extract, lamarin, Tween 80 or peptone. Hydrolyses starch and shows a weak response for laccase. The most abundant fatty acids are iso-C_{15:0}, summed feature 3 (C_{16:0} 10:7c and/or C_{16:0} 10:6c) and C_{16:0}. Major polar lipids are phosphatidylethanolamine and phosphatidylglycerol. Minor amounts of an unidentified aminophospholipid, an unidentified glycolipid and an unidentified phospholipid are also detected. The predominant menaquinone is MK-8. Minor amounts of MK-7 and MK-8(H_2) are detected.

The type strain is Ac_{26}B10^T (=DSM 26559^T=LMG 27984^T), isolated from a Kalahari sandy fallow soil in Mashare, Namibia (17°55'00.2" S 20°06'18.7" E). The DNA G+C content of the type strain is 58.5 mol%.

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