Telluria mixta (*Pseudomonas mixta* Bowman, Sly, and Hayward 1988) gen. nov., comb. nov., and *Telluria chitinolytica* sp. nov., Soil-Dwelling Organisms Which Actively Degrade Polysaccharides†

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Pseudomonas mixta (type strain, ACM 1762 [=ATCC 49108], an actively dextranolytic species that possesses both lateral and polar flagella, was compared with the strictly aerobic, rod-shaped, chitinolytic bacterium "*Pseudomonas chitinolytica*" ACM 3522^T (= CNCM I-804) (T = type strain), which has a similar flagellation pattern, by performing phenotypic characterization and DNA-DNA hybridization studies and by analyzing DNA base compositions and 16S rRNA sequences. Our results indicated that "*P. chitinolytica*" ACM 3522^T was phenotypically and genotypically distinct from *P. mixta* and other phenotypically analogous *Pseudomonas* spp., *Xanthomonas maltophilia*, and other aerobic chitin degraders. The 16S rRNA sequences of strains ACM 1762^T and ACM 3522^T were found to be very similar (97%) to each other and indicated that these organisms are proteobacteria that belong to the β subclass. The strains were deeply branched in the β subclass and were distinct from other pseudomonads, including *Pseudomonas cepacia*, and from *Comamonas testosteroni*. On the basis of phenotypic, genotypic, and phylogenetic evidence, it is proposed that *P. mixta* and "*P. chitinolytica*" ACM 3522^T represent two distinct species in a new genus called *Telluria*. Thus, the genus *Telluria* gen. nov. contains *Telluria mixta* comb. nov. and *Telluria chitinolytica* sp. nov., which are strictly aerobic, rod-shaped, soil-dwelling bacteria that are active polysaccharide degraders.

The interest in using bacteria as a means of combating postharvest deterioration of sugar cane in Queensland, Australia, during the 1970s resulted in studies focused on an actively dextranolytic pseudomonad, strain ACM 733 (= UQM 733 = ATCC 49107), which was isolated from a sugar cane rhizosphere (16). The dextranases and other carbohydrate-degrading enzymes produced by this organism have been studied extensively (4, 5, 16). A partial phenotypic characterization of strain ACM 733 was subsequently performed (1), and the results suggested that this bacterium is a novel organism. A more extensive phenotypic analysis and DNA-DNA hybridization studies placed strain ACM 733 and other phenotypically similar soil isolates in the species *Pseudomonas mixta* (2). This species was phenotypically similar to members of *Pseudomonas* rRNA homology group II (15).

P. mixta strains are strictly aerobic, rod-shaped bacteria that possess both polar and lateral flagella when they are grown on solid agar media and have the ability to degrade several polysaccharides, including dextran, starch, inulin, pectate, and xylan. A few strains also attack alginate and xanthan gum, but chitinolytic or cellulolytic activity was not observed (2). Later, a chitinolytic, aerobic, rod-shaped bacterium designated "*Pseudomonas chitinolytica*" 20M^T (T = type strain) which had bionematicidal potential (18) was isolated from soil in Israel. This strain also was subsequently found to form polar and lateral flagella when it was grown on solid media. In this paper, we provide evidence that strain 20M^T is closely related to *P. mixta*, and on the basis of

phylogenetic data we propose that both species should be assigned to a new genus, the genus *Telluria*.

MATERIALS AND METHODS

Strains. The following strains were used in this study: "*P. chitinolytica*" 20M^T (= ACM 3522^T = CNCM I-804^T), *Pseudomonas cepacia* ACM 1771^T (= ATCC 25416^T), *Pseudomonas gladioli* pv. *gladioli* ACM 1770^T (= ATCC 10248^T), *P. mixta* ACM 1762^T (= UQM 1762^T = ATCC 49108^T), *Pseudomonas solanacearum* ACM 1648 (biotype III; from A. C. Hayward), and *Xanthomonas maltophilia* ACM 497^T (= ATCC 13637^T).

Isolation. Strain 20M^T was isolated by using the procedure described below (18). Natural sandy loam soil from Bet Dagan, Israel, containing 14.8% clay, 38.4% silt, 37.7% fine sand, 9.1% coarse sand, and 0.8% organic matter (pH 7.4) was placed into 50-ml pots and mixed with 1% (wt/wt) natural crustacean shells (previously dried and milled to a powder). The pots were kept moist and maintained in a glasshouse at 27 to 29°C for up to 45 days. Portions (10 g) of soil were suspended in 90-ml volumes of sterile water in 250-ml flasks, which were shaken vigorously for 30 min on a rotary shaker. The resulting suspensions (0.1-ml portions) were appropriately diluted and spread onto agar plates containing 0.2% (wt/vol) colloidal chitin as the sole carbon source and mineral salts. Colonies producing a halo of chitin degradation were isolated. Strain 20M^T has been deposited in the Australian Collection of Microorganisms (Department of Microbiology, The University of Queensland) as strain ACM 3522^T and in the Pasteur Institute, Paris, France, as strain CNCM I-804^T.

Media and cultivation conditions. *Pseudomonas* strains were routinely cultivated on chitin or sucrose-peptone agar (9) at 28°C. Sucrose-peptone agar was used as the basal

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† I. Chet and Y. Spiegel dedicate this paper to the memory of the late Eli Cohn, our dear colleague and friend.

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medium for tests that did not require a defined medium and contained (per liter) 20 g of sucrose, 5 g of Bacto-Peptide (Difco), 0.25 g of $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.5 g of KH_2PO_4 , and, if needed, 15 g of Bacto-Agar (Difco). The chitin medium used for maintenance of strain ACM 3522^T contained (per liter) 15 g of a chitin suspension (14), 0.5 g of yeast extract, 1 g of $(\text{NH}_4)_2\text{SO}_4$, 0.3 g of $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 1.36 g of KH_2PO_4 , and 15 g of Bacto-Agar.

Phenotypic and genotypic characterization. The procedures used for phenotypic analysis have been described previously (2). DNA was extracted from cells as described previously (17). The DNA base composition was determined by thermal denaturation, using a Gilford model 2600 spectrophotometer equipped with a thermoprogrammer. The G+C content was calculated by the point of inflection temperature (T_i) procedure (17). For DNA-DNA studies, DNA held in a ice bath was sheared by using a model 250 Sonifier (Branson, Danbury, Conn.) for 15 s at maximum power and was dialyzed overnight at 4°C in 2× SSC (1× SSC is 0.15 M NaCl plus 0.015 M trisodium citrate, pH 7.0). The optical renaturation rate procedure of Huss et al. (10) was used to determine DNA homology values.

Quinone analysis. Quinones were extracted and analyzed by reverse thin-layer chromatography (12). Authentic standards (ubiquinones 6, 7, 9, and 10) were obtained from Sigma Chemical Co., St. Louis, Mo. Quinone extracted from *P. cepacia* ACM 1771^T was used as the ubiquinone 8 standard (3).

16S rRNA analysis. Bulk RNAs were extracted from strains ACM 3522^T and ACM 1762^T and were analyzed by using a modification (19) of the reverse transcriptase (13) and terminal transferase (6) procedures. Sequences were aligned with the sequences of various reference proteobacteria (8) (C. R. Woese, Illinois Ribosome Data Project, Department of Microbiology, University of Illinois, Urbana). Pairwise evolutionary distances (expressed as the estimated number of changes per 100 nucleotides) were computed from percentages of similarity by using the correction of Jukes and Cantor (11). Phylogenetic trees were constructed from the distance matrices by the algorithm of De Soete (7).

Nucleotide sequence accession numbers. The sequences of strains ACM 1762^T and ACM 3522^T have been deposited in the EMBL Data Library, Heidelberg, Germany, under accession numbers X65589 and X65590, respectively.

RESULTS

Phenotypic characterization. “*P. chitinolytica*” ACM 3522^T was found to be a polarly flagellated, gram-negative, rod-shaped organism (Fig. 1) that has several of the salient traits of *P. mixta*, including the development of mixed flagellation when the organism is grown on solid agar media; prominent accumulation of poly-β-hydroxybutyrate; a highly cartilaginous or elastic colony consistency; sensitivity to NaCl (no growth at NaCl concentrations higher than 1.5%); a lack of growth on media containing high levels of nitrogenous carbon (e.g., nutrient agar); an ability to grow well at 42°C; and a predilection for carbohydrates and tricarboxylic cycle intermediates as sources of carbon and energy. “*P. chitinolytica*” ACM 3522^T could be differentiated from *P. mixta* in several ways (Table 1); strain ACM 3522^T was slightly less biochemically versatile than *P. mixta*. The spectrum of polysaccharide degradation by strain ACM 3522^T was markedly different from the spectrum of polysaccharide degradation by *P. mixta*; the former was not able to hydrolyze dextran or pectate, although it hydrolyzed chitin.

FIG. 1. Electron micrograph of *T. chitinolytica* ACM 3522^T, showing the polar flagellum.

Other biochemical differences included a lack of urease and β-galactosidase activities in ACM 3522^T, while the lipolytic activity (lecithinase and lipase activities) of strain ACM 3522^T was more extensive than that of *P. mixta* strains. The carbon source utilization spectrum of strain ACM 3522^T (36 of 118 compounds were utilized) was less extensive than that of *P. mixta* (57 of 118 compounds were utilized). Aromatic compounds were not utilized by strain ACM 3522^T.

Genotypic characterization and quinone content. The DNA of “*P. chitinolytica*” ACM 3522^T had a G+C content of 72 mol%. This value was slightly higher than the values obtained for 23 strains of *P. mixta* (range, 67 to 70 mol%; average, 69 mol%) (2). DNA-DNA hybridization studies showed that strain ACM 3522^T was genetically distinct from *P. mixta* ACM 1762^T (14% DNA homology), *P. gladioli* pv. *gladioli* ACM 1770^T (13%), *P. cepacia* ACM 1771^T (13%), and *X. maltophilia* ACM 497^T (22%). The quinone contents of strain ACM 3522^T and *P. mixta* ACM 1762^T appeared to be identical and were similar to those of *P. cepacia*; ubiquinone 8 predominated, and a barely detectable amount of ubiquinone 9 was also present.

Phylogenetic analysis. The unambiguously alignable regions between nucleotide positions 2 and 1476 (*Escherichia coli* equivalents) of the 16S rRNAs (13) of strains ACM 3522^T and ACM 1762^T were compared with the same region of various representatives of the β subclass of the *Proteobacteria*. It was found that strains ACM 3522^T and ACM 1762^T were closely related and exhibited 3.6% divergence in their sequences. The sequences were relatively distinct from those of other members of the β subclass, including *P. cepacia* and *Comamonas testosteroni* (>11% sequence divergence). The closest relatives detected were members of the genera *Nitrosomonas* and *Nitrosolobus* (Table 2 and Fig. 2).

DISCUSSION

It was originally suspected that *P. mixta* and “*P. chitinolytica*” might be related to members of *Pseudomonas* rRNA homology group II (2, 15), especially *P. cepacia* and *P. gladioli*. This conclusion was based on the limited number of phenotypic criteria which help distinguish the various *Pseudomonas* rRNA homology groups from each other and from other phenotypically related bacteria. In the case of

TABLE 1. Phenotypic characteristics that distinguish the species of *Telluria* gen. nov.

Characteristic ^a	<i>T. mixta</i> (23 strains) ^b	<i>T. chitinolytica</i> ACM 3522 ^T
Yellow pigmentation	— ^c	+
Nitrate reduced to nitrite	d	—
Urease and β -galactosidase activities	+	—
Lecithinase activity (egg yolk)	—	+
Hydrolysis of:		
Chitin and tributyrin	—	+
Dextran, pectate (pH 5 to 8.3), and Tween 20	+	—
Growth at 45°C	—	+
Utilization of:		
DL-Arabinose, lactose, dextran, butyrate, DL-glycerate, glycolate, benzoate, <i>p</i> -hydroxybenzoate, DL-serine, DL-threonine, L-arginine, L-citrulline, L-ornithine, and L-phenylalanine	+	—
Glycerol and acetamide	—	+
L-Tyrosine, poly- β -hydroxybutyrate, heptanoate, caprylate, mannitol, phenol, <i>m</i> -hydroxybenzoate, benzoyl-formate, DL-mandelate, and quinate	d	—
L-Histidine	d	+
G+C content (mol%) ^d	67–70	72

^a The following tests were positive for both *T. mixta* and *T. chitinolytica*: oxidative reaction in Hayward's oxidation-fermentation test; catalase; oxidase; poly- β -hydroxybutyrate accumulation; growth at 42°C; hydrolysis of starch, xylan, gelatin, casein, Tween 40, Tween 60, Tween 80, DNA, and esculin; gluconate oxidation; phosphatase; arylsulfatase; growth on King A and King B media (very poor to poor growth) and glucose-nitrate medium (good growth); tolerance to 0.5% NaCl (very poor to poor growth only); and utilization of D-xylose, L-rhamnose, D-fructose, D-galactose, D-glucose, D-mannose, D-melezitose, maltose sucrose, cellobiose, trehalose, inulin, starch, xylan, gluconate, 2-ketogluconate, glucuronate, galacturonate, mucate, saccharate, β -hydroxybutyrate, malonate, succinate, DL-lactate, fumarate, DL-malate, pyruvate, L-(+)-tartaric acid, citrate, D-alanine, L-alanine, L-aspartate, and L-glutamate as sole sources of carbon and energy. The following tests were negative for both *T. mixta* and *T. chitinolytica*: arginine dihydrolase; hydrogen autotrophy; denitrification; growth at 4°C; hydrolysis of cellulose, xanthan gum, and alginate; hydrogen sulfide production; levan production from sucrose; tolerance to >1.5% NaCl, 0.03% cetrimide, and 0.0075% KCN; growth on MacConkey agar; fluorescent pigment production; hemolysis of sheep blood; and utilization of D-ribose, acetate, propionate, isobutyrate, valerate, isovalerate, caproate, pelargonate, caprate, oxalate, glutarate, adipate, pimelate, suberate, azelate, sebacate, maleate, D-(–)-tartaric acid, meso-tartrate, citraconate, itaconate, mesaconate, levulinic acid, ethanol, propanol, butanol, 1,2-ethanediol, 1,3-propanediol, 2,3-butanediol, adonitol, meso-erythritol, meso-inositol, sorbitol, anthranilate, *p*-aminobenzoate, benzylamine, sarcosine, betaine, β -alanine, DL-2-aminobutyrate, DL-4-aminobutyrate, DL-2-aminovalerate, DL-5-aminovalerate, L-valine, L-proline, L-hydroxyproline, L-glutamine, L-lysine, L-tryptophan, L-methionine, L-cysteine, putrescine, spermine, ethanolamine, histamine, α -amylamine, tryptamine, and pantothenate as sole sources of carbon and energy.

^b Data from reference 2.

^c +, present in 90 to 100% of the strains; d, present in 11 to 89% of the strains; —, present in 0 to 10% of the strains.

^d Determined by the *T_i* method.

rRNA homology group II species such as *P. cepacia*, these phenotypic characteristics include *ortho* cleavage of protocatechuate; growth at 42°C; lack of arginine dihydrolase and denitrification activity; strong poly- β -hydroxybutyrate accumulation; and a G+C content greater than 65 mol% (15). The results of a phylogenetic analysis (in which 16S rRNA sequences were used) showed that *P. mixta* and "*P. chitinolytica*" ACM 3522^T were members of the β subclass, but despite their superficial phenotypic resemblance to *P. cepacia* and to *C. testosteroni*, they were phylogenetically dis-

TABLE 2. Similarity matrix^a

Organism	% of differences ^a													
	Alcaligenes eutrophus	Pseudomonas cepacia	Nitrosomonas europaea	Nitrosolobus multiiformis	Spirillum volutans	Alcaligenes faecalis	Iodobacter fluviatilis	Chromobacterium violaceum	Vitreoscilla stercoraria	Neisseria gonorrhoeae	Kingella kingae	Simonella muelleri	Eikenella corrodens	Kingella denitrificans
<i>Pseudomonas cepacia</i>	8.6													
<i>Nitrosomonas europaea</i>	11.8	14.0												
<i>Nitrosolobus multiiformis</i>	10.5	11.9	7.9											
<i>Spirillum volutans</i>	12.1	11.2	13.7	11.5										
<i>Alcaligenes faecalis</i>	11.5	11.3	13.7	11.7	12.7									
<i>Iodobacter fluviatilis</i>	12.6	11.2	14.3	12.6	13.2	11.7	9.5							
<i>Chromobacterium violaceum</i>	10.9	10.9	14.5	12.2	13.2	12.3								
<i>Vitreoscilla stercoraria</i>	13.0	12.6	15.3	14.0	11.8	12.5	11.1	8.8						
<i>Neisseria gonorrhoeae</i>	13.7	12.7	16.6	14.5	14.4	13.4	13.0	11.0	7.0					
<i>Kingella kingae</i>	13.1	12.5	16.3	14.4	13.1	12.7	12.2	10.3	7.1	6.2				
<i>Simonella muelleri</i>	13.7	14.0	17.1	15.0	13.7	12.1	12.0	11.1	7.3	7.0	6.2			
<i>Eikenella corrodens</i>	12.9	12.4	15.3	13.8	13.6	11.4	11.8	9.4	6.5	6.3	5.3	4.8		
<i>Kingella denitrificans</i>	13.1	12.9	16.3	14.2	13.1	11.9	12.1	9.6	7.4	5.6	4.6	5.4	2.8	
Strain ACM 3522 ^T	11.1	12.2	13.1	11.3	13.6	12.1	11.2	12.4	13.3	14.7	14.4	14.7	12.9	14.0
<i>Pseudomonas mixta</i> ACM 1762 ^T	11.2	11.6	12.9	10.6	12.9	11.5	11.1	11.8	12.8	14.5	14.9	14.5	12.8	14.1
<i>Comamonas testosteroni</i>	11.2	12.2	14.5	13.7	14.5	13.6	13.1	14.3	13.9	17.0	16.4	16.7	16.2	16.9
														13.3

^a Values were corrected for multiple base changes by the method of Jukes and Cantor (11).

FIG. 2. Phylogenetic tree of the β subclass of the *Proteobacteria*. The scale bar represents a 2% difference in nucleotide sequences, as determined by measuring the lengths of the horizontal lines connecting two species.

tinct. A common feature of all of these organisms is the predominance of ubiquinone 8 (3), which supports the hypothesis that they are related at a higher taxonomic level.

Phenotypically, *P. mixta* and "*P. chitinolytica*" ACM 3522^T could be differentiated from the species belonging to

Pseudomonas rRNA homology group II (also referred to as the *P. solanacearum* branch [21]) and other strictly aerobic, high-G+C-content, rod-shaped genera belonging to rRNA superfamily III (effectively the β subclass) in a number of ways, including formation of highly elastic or cartilaginous colonies upon isolation; very poor or no growth on media (such as nutrient agar) which contain a high level of nitrogenous carbon; formation of lateral flagella and a single polar flagellum when cultures are grown on solid media; and a propensity for the utilization of complex and simple carbohydrates (Table 3). Phylogenetic data provided good evidence that *P. mixta* and "*P. chitinolytica*" ACM 3522^T represent distinct species in a new genus. Thus, it is proposed that *P. mixta* and "*P. chitinolytica*" should be assigned to the genus *Telluria* as *Telluria mixta* gen. nov., comb. nov. and *Telluria chitinolytica* sp. nov., respectively.

Description of *Telluria* gen. nov. *Telluria* (Tel.lu'.ri.a. L. fem. n. *Tellus*, a Roman goddess of the earth, also the ground or earth; M. L. fem. n. *Telluria*, from the earth). Gram negative. Cells are straight rods that are 0.5 to 1.0 μ m wide and 2.0 to 3.0 μ m long. Occasionally filamentous cells up to 30 μ m long are formed, a tendency which increases in older cultures. The cells occur singly, in pairs, or in short chains. When cultures are grown in liquid media, a single polar flagellum is formed on each cell, while on solid media additional lateral flagella occur. Strongly accumulates poly- β -hydroxybutyrate. Strictly aerobic, growing only as a surface pellicle in static liquid cultures. Chemoheterotrophic. Incapable of gaining energy chemolithotrophically from hydrogen. Denitrification does not occur. Arginine dihydrolase is absent. Good growth occurs on media containing carbohy-

TABLE 3. Phenotypic characteristics that differentiate *T. mixta* and *T. chitinolytica* from other high-G+C-content, strictly oxidative aerobes belonging to the β subclass of the *Proteobacteria* (rRNA superfamily III)

Characteristic ^a	<i>Telluria</i> gen. nov.	<i>Pseudomonas solanacearum</i> branch	<i>Comamonas</i>	<i>Acidovorax</i>	<i>Hydrogenophaga</i>	<i>Variovorax paradoxus</i>	<i>Xylophilus</i>
Flagellation							
Mixed (1 polar and >1 lateral)	+ ^b	—	—	—	—	—	—
Polar (≥ 1)	+	+	—	+	+	—	+
Peritrichous	—	—	—	—	—	+	—
Bipolar tufts	—	—	+	—	—	—	—
Hydrogen autotrophy	—	—	—	d	+	d	—
Hydrolysis of starch	+	D	—	—	—	—	d
Growth on nutrient agar	—	+	+	+	+	+	—
Tolerance to 1.5% NaCl	—	+	+	+	+	+	—
Utilization of:							
Lactose	D	—	—	—	—	—	—
Maltose	+	— ^c	—	—	—	—	—
Inulin	+	—	—	—	—	—	—
Acetate	—	+	+	+	+	+	—
Propionate	—	+	+	d	d	d	—
Isobutyrate	—	+ ^d	+	d	—	d	ND
Valerate	—	+ ^d	+	+	—	d	—
meso-Inositol	—	+ ^e	d	—	+	d	ND
β -Alanine	—	+	d	d	—	d	ND
DL-4-Aminobutyrate	—	+	d	+	—	+	—
L-Proline	—	+	+	+	+	+	ND
Occurrence ^f	S	S, FW, CS, IP	S, FW, CS	S, FW, CS	S, FW	S, FW	IP
G+C content (mol%)	67–72	64–69	60–69	62–66	65–69	67–69	68–69

^a Data from references 15 and 20 through 24.

^b +, present in 90 to 100% of the strains; d, present in 11 to 89% of the strains; —, present in 0 to 10% of the strains; D, varies among species; ND, no data.

^c Positive in *Pseudomonas mallei* and *Pseudomonas pseudomallei*.

^d Negative in *Pseudomonas mallei*.

^e Negative in *Pseudomonas pickettii*.

^f S, soil; FW, fresh water; CS, clinical samples; IP, infected plants (phytopathogenic).

drates and an inorganic or organic combined nitrogen source. Much poorer growth occurs on media lacking carbohydrates. NaCl sensitive; completely inhibited by NaCl concentrations greater than 1.5%, and only poor growth occurs at an NaCl concentration of 0.5%. Actively utilizes complex polysaccharides, including starch and xylan, as well as other polysaccharides which vary among the species. Cellulose is not hydrolyzed. Hydrolyzes gelatin, casein, DNA, esculin, and Tween 40, Tween 60, and Tween 80. Produces phosphatase and arylsulfatase. Grows well at temperatures between 20 and 45°C and optimally at 30 to 35°C; optimal growth occurs at pH 7.0. The major quinone is ubiquinone 8. The DNA base composition varies between 67 and 72 mol% G+C (as determined by the T_i method). The only known habitat is soil, particularly the rhizosphere. The type species is *Telluria mixta* (formerly *Pseudomonas mixta*). The genus *Telluria* is a member of the β subclass of the *Proteobacteria* and is not closely related phylogenetically to other taxa.

Description of *Telluria mixta* (Bowman, Sly, and Hayward 1988) comb. nov. The description of *Telluria mixta* (mix'ta. L. adj. *mixtus*, mixed; M. L. fem. adj. *mixta*, mixed, referring to mixed flagellation) is the same as that given above for the genus; additional biochemical and nutritional characteristics are shown in Table 1. *T. mixta* strains have been isolated from various soils in Queensland, Australia (2). The average G+C content of the DNA of the species is 69 mol% (as determined by the T_i method). The type strain is strain ACM 1762 (= UQM 1762 = ATCC 49108).

Description of *Telluria chitinolytica* sp. nov. The description of *Telluria chitinolytica* (chi.tin.o.lyt'i.ca. chem. term *chitin*, chitin, a polysaccharide; Gr. adj. *lytos*, soluble; M. L. fem. adj. *chitinolytica*, dissolving chitin) is the same as that given above for the genus; additional biochemical and nutritional characteristics are shown in Table 1. *T. chitinolytica* is monotypic, and type strain ACM 3522 (= CNCM I-804) was isolated from a loamy soil from Bet Dagan, Israel (18). The G+C content of the DNA of strain ACM 3522^T is 72 mol% (as determined by the T_i method).

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