Pantoea gaviniae sp. nov. and Pantoea calida sp. nov., isolated from infant formula and an infant formula production environment

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Five Gram-negative, facultatively anaerobic, non-spore-forming, coccoid rod-shaped bacterial isolates were obtained from infant formula and an infant formula production environment and were investigated by use of a polyphasic taxonomic study. Biochemical tests and partial rpoB gene sequence analysis of the five isolates revealed that they formed two distinct groups in the family Enterobacteriaceae, closely related to several species of the genera Pantoea and Erwinia, which indicated a phylogenetic position within the genus Pantoea or the genus Erwinia. Multilocus sequence analysis of concatenated partial atpD, gyrB, infB and rpoB gene sequences of two of the isolates suggested that they represented two novel species of the genus Pantoea, phylogenetically related most closely to Pantoea septica. The five isolates had general characteristics consistent with those of the genus Pantoea, and DNA–DNA hybridizations between two representatives and the type strains of their phylogenetically closest relatives based on comparative 16S rRNA gene sequence analysis showed that the isolates represented two novel genospecies. These two genospecies could be differentiated from each other based on fermentation of galacturonate, sorbitol and potassium 5-ketogluconate. They could be differentiated from phylogenetically related Pantoea species based on their ability to ferment lactose and to utilize β-gentiobiose and raffinose, their inability to ferment or utilize α-arabitol, and their inability to produce indole. On the basis of the results obtained, the five isolates are considered to represent two novel species of the genus Pantoea, for which the names Pantoea gaviniae sp. nov. (type strain A18/07T =LMG 25382T =DSM 22758T) and Pantoea calida sp. nov. (type strain 1400/07T =LMG 25383T =DSM 22759T) are proposed.

Over the past few years, the family Enterobacteriaceae has gained in importance for the food industry, especially for infant formula processing plants. During a recent study by us, 470 Enterobacteriaceae isolates from raw ingredients, environmental samples and products of an infant formula processing plant were investigated by biochemical tests (API ID32E) and rpoB gene sequence analysis. This technique has proven to be useful for species identification and classification in the family Enterobacteriaceae (Mollet et al., 1997; Drancourt et al., 2001; Case et al., 2007; Stephan et al., 2007, 2008). Of these 470 isolates, 65 could not be identified to species level (Popp et al., 2009). The present study deals with the further characterization of five of these isolates and shows that they represent two novel species of the genus Pantoea.

The five isolates were obtained from powdered infant formula (1400/07T, A11/07, A18/07T) and an infant formula production environment (484/07, 1378/07) by using the following approach. After enrichment of the samples by incubation for 24 h at 37 °C in buffered peptone water, 0.1 ml was transferred to 9 ml Enterobacteriaceae
enrichment broth (Becton Dickinson) and incubated for a further 24 h at 37 °C. The culture obtained was then plated on violet red bile glucose agar (Becton Dickinson), incubated for 24 h at 37 °C and the five isolates were recovered as typical red colonies.

Gram staining was done according to standard protocols. Preliminary characterization based on API ID32E analysis (bioMérieux) was performed according to the manufacturer’s instructions. The results suggested that the five strains represented Pantoea spp. 1, Pantoea spp. 3 and Serratia plymuthica, but with low levels of confidence. In a next step, partial rpoB gene sequences were determined following the procedure described by Mollet et al. (1997). Comparison of partial rpoB gene sequences of the new isolates amongst each other suggested that they formed two distinct groups, with 1400/07T, A11/07, 484/07 and 1378/07 showing 99–100 % similarity, and isolate A18/07T showing 97 % similarity to the other four isolates. Additional phenotypic tests (API 20E and API 50CHE; bioMérieux) were then performed, and the same two groups could be delineated based on the fermentation of galacturonate, sorbitol and potassium 5-ketogluconate, and the utilization of citrate within 24 h (positive for isolates 1400/07T, A11/07, 484/07 and 1378/07; negative for A18/07T).

In the present study, the phylogenetic position of these isolates based on partial rpoB gene sequences was investigated, as a multilocus sequence analysis (MLSA) scheme for the genus Pantoea according to partial atpD, gyrB, infB and rpoB gene sequences was recently reported (Brady et al., 2008). By using the software package BioNumerics (Applied Maths), the rpoB gene sequences of the new isolates were compared with those of reference strains of recognized Pantoea species and related taxa (Brady et al., 2008) or a newly determined sequence (Erwinia aphidicola LMG 24877T). Phylogenetic trees were reconstructed by using the neighbour-joining (Saitou & Nei, 1987; see Supplementary Fig. S1 in IJSEM Online), maximum-parsimony and maximum-likelihood (Felsenstein, 1985) methods. The robustness of the branches was evaluated by bootstrap resamplings of the data (Felsenstein, 1985; Supplementary Fig. S1). The maximum-parsimony and maximum-likelihood trees showed basically the same topology as the neighbour-joining tree and the maximum-likelihood tree by Brady et al. (2008) (data not shown). MLSA revealed that isolates A18/07T and 1400/07T represented two novel species of the genus Pantoea, phylogenetically closely related to Pantoea septica (Brady et al., 2010). The two isolates were therefore characterized further.

The 16S rRNA genes of isolates A18/07T and 1400/07T were amplified and sequenced as described by Franz et al. (2006), by using the primers listed by Coenye et al. (1999). Almost-complete 16S rRNA gene sequences comprising 1494 nt (A18/07T) and 1495 nt (1400/07T) were obtained, and compared with almost-complete 16S rRNA gene sequences of reference strains of species of the genus Pantoea and related taxa (Brady et al., 2008) or of newly determined sequences (i.e. Erwinia aphidicola LMG 24877T and Erwinia toletana LMG 24162T). Pairwise similarities were calculated with the BioNumerics software package by using an open gap penalty of 100 % and a unit gap penalty of 0 %. A phylogenetic tree was reconstructed by using the neighbour-joining method (Saitou & Nei, 1987), and the robustness of the branches was evaluated by bootstrap resamplings of the data (Felsenstein, 1985; Fig. 2). Isolates A18/07T and 1400/07T showed highest levels of 16S rRNA gene sequence similarity with Pantoea deleyi LMG 24200T (98.0 and 97.9 %, respectively), Pantoea conspiciua LMG 24534 (97.9 and 98.0 %), Pantoea breneri LMG 5343 (97.8 and 97.9 %), Pantoea cyripedii ICMP 1591T (97.8 and 97.7 %), Erwinia toletana LMG 24162T (97.8 and 98.0 %), Erwinia tasmaniensis Et1/99T (97.7 % each), P. septica LMG 5345 (97.7 and 97.5 %), Pantoea MLSA group G LMG 24248 (97.7 % each), Pantoea vagans LMG 24199T (97.7 and 97.9 %), Pantoea agglomerans NCTC 9381T (97.6 and 97.8 %), Pantoea eucalypti LMG 24197T (97.6 % each), Pantoea anasthila LMG 2558T (97.5 and 97.7 %), Pantoea ananatis ATCC 33244T (97.5 and 97.4 %), Pantoea dispersa LMG 2603T (97.4 and 97.8 %), Erwinia aphidicola LMG

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Fig. 1. Neighbour-joining dendrogram based on concatenated partial atpD, gyrB, infB and rpoB gene sequences of strains 1400/07\(^T\) and A18/07\(^T\) and related taxa within the family Enterobacteriaceae. The reference strains of MLSA groups reported by Brady et al. (2008) are indicated with a superscript R. Numbers at nodes are bootstrap values (percentages of 500 replicates). Bar, 0.1 substitutions per nucleotide position.
24877T (97.4 % each), Erwinia persicina LMG 11254T (97.2 and 97.3 %), Enterobacter cowanii CIP 107300T (97.1 and 97.4 %), Pantoea eucrina LMG 2781 (97.1 and 97.0 %) and Pantoea stewartii subsp. stewartii LMG 2715T (97.0 and 97.2 %). The level of 16S rRNA gene sequence similarity between isolates 1400/07T and A18/07T was 99.6 %. Levels of 16S rRNA gene sequence similarity were below the range of 98.7–99 % recommended for delimiting species (Stackebrandt & Ebers, 2006), suggesting again that the isolates represented novel species within the family Enterobacteriaceae.

As the branches representing the different genera of the Enterobacteriaceae are not monophyletic and are not supported by high bootstrap values, and as highest levels of similarity with the new isolates are found with reference strains of different genera, it can be concluded that for the Enterobacteriaceae, the similarity values obtained reflect a high level of homoplasy in the 16S rRNA gene sequences.

DNA–DNA hybridizations were performed between isolates A18/07T and 1400/07T and the type strains of their phylogenetically closest relatives based on comparative 16S
rRNA gene sequence analysis. DNA for DNA–DNA hybridizations was prepared according to the method of Wilson (1987), with minor modifications (Cleenwerck et al., 2002), and hybridizations were carried out at 45 °C by using a modification (Goris et al., 1998; Cleenwerck et al., 2002) of the microplate method described by Ezaki et al. (1989). Levels of DNA–DNA relatedness reported are the means (±sd) of a minimum of seven hybridizations. Reciprocal reactions (i.e. A × B and B × A) were performed and the variation between them was within the limits of this method (Goris et al., 1998). The level of DNA–DNA relatedness between isolates 1400/07T and A18/07T was 59±4%. Levels of less than 25% were found between isolate 1400/07T and selected reference strains: P. deleyi LMG 24200T (14±5%), P. conspicae LMG 24534T (15±1%), P. breneri LMG 5343T (15±6%), P. cypripedii LMG 2657T (14±5%), Erwinia toletana LMG 24162T (16±14%), Erwinia tasmaniensis LMG 25318T (15±4%), P. septica LMG 5345T (23±4%), P. vagans LMG 24199T (15±4%), P. agglomerans LMG 1286T (18±1%), P. eucalipti LMG 24197T (14±3%), P. ananatis LMG 2665T (14±0%), P. dispersa LMG 2603T (18±13%), P. eucrina LMG 2781T (15±7%) and P. stewartii subsp. stewartii LMG 2715T (8±6%). These values are below the 70% generally accepted for species delineation (Wayne et al., 1987), demonstrating that the two isolates represented two novel genospecies.

The DNA G+C content of isolates A18/07T and 1400/07T was determined from DNA prepared in the frame of the DNA–DNA hybridization experiments, according to the HPLC method described by Mesbah et al. (1989). The values (means of three independent analyses of the same DNA sample) for A18/07T and 1400/07T were 58.4 and 57.4 mol%, respectively. These values are consistent with the DNA G+C contents of other members of the genus Pantoea (Gavini et al., 1989; Mergaert et al., 1993; Brady et al., 2009, 2010).

The phenotypic characteristics of the five new isolates were compared with those of strains of the genus Pantoea by using various biochemical tests (API ID32E, API 20E, API 50CHE and Biotype 100 with Biotype Medium 1; bioMérieux) performed according to the manufacturer’s instructions. The phenotypic characteristics of the five isolates were in accordance with the emended description of the genus Pantoea (Brady et al., 2010); however, the new isolates could be differentiated from phylogenetically related Pantoea species by their ability to ferment lactose and utilize β-gentiobiose and raffinose, their inability to ferment and utilize D-arabitol, and their inability to produce indole (Table 1). The two genospecies themselves could be differentiated, as previously mentioned, based on fermentation of galacturonate, sorbitol and potassium 5-ketogluconate (Table 1). Details of the physiological and

### Table 1. Differential phenotypic characteristics between Pantoea gaviniae sp. nov. and Pantoea calida sp. nov. and species of the genus Pantoea

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For taxa 3–7, indole production and fermentation data are from the present study and carbon source utilization data are from Brady et al. (2010); data for taxa 8–10 from Brady et al. (2009); data for taxa 12 and 13 from Gavini et al. (1989); data for taxa 14–16 from Mergaert et al. (1993). Fermentation data (API 50CHE) were recorded after 48 h. Data for carbon source utilization tests (Biotype 100) were recorded after 4 days. –, 0–10% positive; (–), 10–20% positive; V, 20–80% positive; (+), 80–90% positive; (+), 90–100% positive; ND, no data available.
biochemical characteristics of the novel species are given in the descriptions below.

The results of this polyphasic taxonomic study support the recognition of two novel species of the genus *Pantoea*, for which the names *Pantoea gaviniae* sp. nov. and *Pantoea calida* sp. nov. are proposed.

**Description of Pantoea gaviniae sp. nov.**

*Pantoea gaviniae* (g.a.vi.ni.a.e. N.L. fem. gen. n. gaviniae of Gavini, in honour of Françoise Gavini, a French microbiologist who first described the genus *Pantoea*).

Cells are Gram-negative rods that are facultatively anaerobic and motile. Cells are 1.0 µm wide by 2.0–3.0 µm long and occur singly or in pairs. After 24 h of aerobic incubation at 37 °C on trypticase soy agar (TSA) medium, colonies are non-pigmented and convex. Oxidase-negative and catalase-positive. Colonies grow well at 10 °C but poorly at 7 °C (within 3 days). They grow poorly at 41.5 °C and no growth occurs at 44 °C. Positive for β-glucosidase, β-galactosidase, x-galactosidase, aesculin hydrolysis and the Voges-Proskauer Test, but negative for ornithine decarboxylase, arginine dihydrolase, lysine decarboxylase, urease, lipase, β-glucuronidase, N-acetyl-β-glucosaminidase, α-glucosidase, α-maltosidase, l- aspartic acid arylamidase, tryptophan deaminase and gelatinase, and indole and H₂S production. Acid is produced under anaerobic conditions from the following compounds within 48 h: glycerol, L-arabinose, D-ribose, D-xylene, D-galactose, D-glucose, D-fructose, D-mannose, L-rhamnose, inositol, D-mannitol, N-acetylglucosamine, arbutin, salicin, cellulose, lactose, maltose, melibiose, sucrose, trehalose, raffinose, β-gentiobiose, potassium gluconate and potassium 2-ketogluconate. No acid is produced from erthyritol, D-arabinose, L-xylene, adonitol, methyl β-D-xylopyranoside, L-sorbosone, dulcitol, D-sorbitol, methyl α-D-mannopiranose, methyl α-D-glucopyranoside, amygdalin, inulin, melezitose, starch, glycerin, xylitol, turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, D-arbutin, L-arabitol, potassium 5-ketogluconate or galacturonic acid. Positive for utilization of α-D-glucose, β-D-fructose, D-galactose, trehalose, D-mannose, α-melibiose, sucrose, raffinose, maltotriose, maltose, α-lactose, lactulose, 1-0-methyl β-D-galactopyranoside, 1-0-methyl α-D-galactopyranoside, cellulose, β-gentiobiose, 1-0-methyl β-D-glucopyranoside, aesculin, D-ribose, L-arabinose, D-xylene, L-L-rhamnose, glycerol, myo-inositol, D-mannitol, D-sorbitol, D-saccharate, mucate, L-malate, cis-cisatate, trans-ateatate, citrate, D-glucuronate, D-galacturonate, 2-keto-D-gluconate, 5-keto-D-gluconate, N-acetyl-D-glucosamine, D-glucosone, Dl-lactate, succinate, fumarate, DL-glucate, D-glucosamine, L-aspartate, L-glutamate, L-proline, D-alanine, L-alanine, L-serine and α-ketoglutarate within 4 days. The following compounds are not utilized as sole carbon sources within 4 days: L-sorbosone, palatinose, α-L-fucose, melezitose, D-arabinose, L-arabitol, xylitol, dulcitol, D-tagatose, maltose, trehalose, adonitol, hydroxyquinoline-β-glucuronide, D-lyxose, i-erythritol, 1-0-methyl α-D-glucopyranoside, 3-0-methyl D-glucopyranoside, L-tartrate, D-tartrate, meso-tartrate, D-malate, tricarballylate, L-tryptophan, phenylacetate, proline, catechuate, p-hydroxybenzoate, quinate, gentisate, m-hydroxybenzoate, benzoate, 3-phenylpropionate, m-coumarate, trigonelline, betaine, putrescine, α-amino butyrate, histamine, caprate, caprylate, L-histidine, glutarate, 5-aminovalerate, ethanolamine, tryptamine, itaconate, 3-hydroxybutyrate, malonate, propionate and 1-tyrosine. The DNA G+C content of the type strain is 58.4 mol%.

The type strain, A18/07T (=LMG 25382T =DSM 22758T), was isolated from powdered infant formula.

**Description of Pantoea calida sp. nov.**

*Pantoea calida* (cal.i.da. L. fem. adj. calida warm, hot, reflecting its ability to grow at 44 °C).

Cells are Gram-negative coccoid rods that are facultatively anaerobic and motile. Cells are 1.0 µm wide by 1.5–2.0 µm long and occur singly or in pairs. After 24 h of aerobic incubation at 37 °C on TSA medium, colonies are non-pigmented and convex. Oxidase-negative and catalase-positive. Colonies grow poorly at 10 °C (within 3 days) but well at 44 °C. Positive for β-glucosidase, β-galactosidase, aesculin hydrolysis and the Voges-Proskauer test, but negative for ornithine decarboxylase, arginine dihydrolase, lysine decarboxylase, urease, lipase, β-glucuronidase, α-maltosidase, L-aspartic acid arylamidase, tryptophan deaminase and gelatinase, and indole and H₂S production. Acid is produced under anaerobic conditions from the following compounds within 48 h: glycerol, L-arabinose, D-ribose, L-xylene, D-galactose, D-glucose, D-fructose, D-mannose, L-rhamnose, inositol, D-mannitol, D-sorbitol, N-acetylglucosamine, arbutin, salicin, cellulose, maltose, lactose, melibiose, sucrose, trehalose, raffinose, β-gentiobiose, potassium gluconate, potassium 2-ketogluconate, potassium 5-ketogluconate and galacturonic acid. No acid is produced from erthyritol, D-arabinose, L-xylene, adonitol, methyl β-D-xylopyranoside, L-sorbosone, dulcitol, D-sorbitol, methyl α-D-mannopiranose, methyl α-D-glucopyranoside, amygdalin, inulin, melezitose, starch, glycerin, xylitol, turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, D-arbutin, L-arabitol, potassium 5-ketogluconate or galacturonate. Positive for utilization of α-D-glucose, β-D-fructose, D-galactose, trehalose, D-mannose, α-melibiose, sucrose, raffinose, maltotriose, maltose, α-lactose, lactulose, 1-0-methyl β-D-galactopyranoside, 1-0-methyl α-D-galactopyranoside, cellulose, β-gentiobiose, 1-0-methyl β-D-glucopyranoside, aesculin, D-ribose, L-arabinose, D-xylene, L-L-rhamnose, glycerol, myo-inositol, D-mannitol, D-sorbitol, D-saccharate, mucate, L-malate, cis-cisatate, trans-ateatate, citrate, D-glucuronate, D-galacturonate, 2-keto-D-gluconate, 5-keto-D-gluconate, N-acetyl-D-glucosamine, D-glucosone, Dl-lactate, succinate, fumarate, DL-glucate, D-glucosamine, L-aspartate, L-glutamate, L-proline, D-alanine, L-alanine, L-serine and α-ketoglutarate within 4 days. The following compounds are not utilized as sole carbon sources within 4 days: L-sorbosone, palatinose, α-L-fucose, melezitose, D-arabinose, L-arabitol, xylitol, dulcitol, D-tagatose, maltose, trehalose, adonitol, hydroxyquinoline-β-glucuronide, D-lyxose, i-erythritol, 1-0-methyl α-D-glucopyranoside, 3-0-methyl D-glucopyranoside, L-tartrate, D-tartrate, meso-tartrate, D-malate, tricarballylate, L-tryptophan, phenylacetate, proline, catechuate, p-hydroxybenzoate, quinate, gentisate, m-hydroxybenzoate, benzoate, 3-phenylpropionate, m-coumarate, trigonelline, betaine, putrescine, α-amino butyrate, histamine, caprate, caprylate, L-histidine, glutarate, 5-aminovalerate, ethanolamine, tryptamine, itaconate, 3-hydroxybutyrate, malonate, propionate and 1-tyrosine. The DNA G+C content of the type strain is 58.4 mol%.
i-erythritol, L-0-methyl D-glucopyranoside, 3-O-methyl D-glucopyranoside, L-tartrate, D-tartrate, meso-tartrate, D-malate, tricarballylate, L-triptophan, phenylaceta
tate, protocatechuic acid, p-hydroxybenzoate, quinate, gentisate, m-hydroxybenzoate, benzoate, 3-phenylpropionate, m-coumarate, trigonelline, betaine, putrescine, 4-amino
butyrate, histamine, caprate, caprylate, L-histidine, glutarate, 5-amino
valerate, ethanolamine, tryptamine, itaconate, 3-hydroxybutyrate, malonate, propionate and L-tyrosine. The DNA G+C content of the type strain is 57.4 mol%.

The type strain, 1400/07T (=LMG 25383T =DSM 22759T), was isolated from powdered infant formula. A11/07, 484/07 and 1378/07 are additional strains of the species.

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References


