Genus

Firmicutes/"Bacilli"/Bacillales/"Paenibacillaceae"/

Brevibacillus

Shida, Takagi, Kadowaki and Komagata 1996a, 942[VP]

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Bre.vi.ba.cil'lus. L. adj. *brevis* short; L. dim. n. *bacillus* small rod; N.L. masc. n. *Brevibacillus* short, small rod.

Gram-positive, Gram-variable, or Gram-negative, rod-shaped cells, 0.7–1.0 µm × 3.0–6.0 µm. Motile by means of peritrichous flagella. **Ellipsoidal spores are formed and swell the sporangia**. Most species grow on routine media such as nutrient agar and trypticase soy agar producing flat, smooth, yellowish-gray colonies. One species produces red pigment. **Most species are strictly aerobic, but one species is microaerophilic and one species is facultatively anaerobic**. Most species are catalase-positive. Oxidase reaction varies between species. Voges–Proskauer reaction is negative. Nitrate reduction and casein, gelatin, and starch hydrolysis varies between species. Growth is inhibited by 5% NaCl. Optimum growth occurs at pH 7.0. **Carbohydrates may be assimilated, but acid is produced weakly if at all from them by most species**. Some amino acids and organic acids may be used as carbon and energy sources. The major cellular fatty acids are $C_{15:0\ ante}$ and $C_{15:0\ iso}$.

DNA G+C content (*mol%*): 40.2–57.4.

Type species: **Brevibacillus brevis** (Migula 1900) Shida, Takagi, Kadowaki and Komagata 1996a, 943[VP] (*Bacillus brevis* Migula 1900, 583.).

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Number of validated species: 14

Further descriptive information

Phylogeny

Brevibacillus belongs to the family *Paenibacillaceae* and a phylogenetic tree covering the present species that are represented by their type strain is given in Figure 1 as a 16S rDNA sequence based neighbor-joining tree.

Differential characteristics for members of the genus *Brevibacillus* are given in Table 1. The rod-shaped cells of *Brevibacillus* species are usually round-ended, and occur

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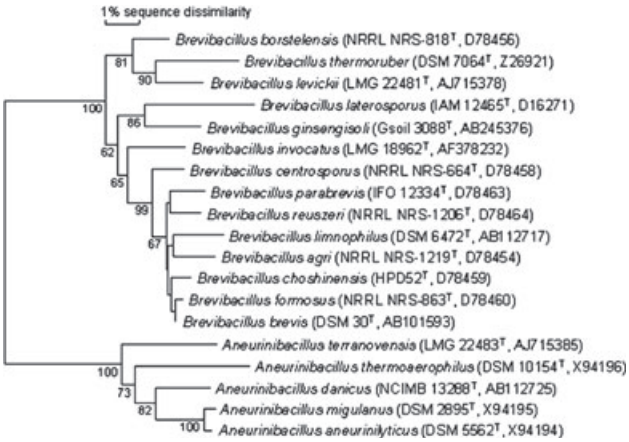
FIGURE 1. Phylogenetic neighbor-joining tree of type strains of *Brevibacillus* and *Aneurinibacillus* species based on 16S rDNA sequences. Bootstrap values are given at the branching points based on 1000 recalculations. Strain numbers with their respective EMBL accession numbers are given in parentheses.



singly, in pairs, and in chains. Cell diameters range from 0.7–1.0 µm and lengths from 3.0–6.0 µm, but the cells of a particular strain are usually quite regular in size, and individual species normally have dimensions within fairly narrow limits. Most of the species of *Brevibacillus* do not have distinctive sporangial morphologies; the spores are ellipsoidal, lie subterminally or perhaps terminally, and swell the sporangia slightly or moderately (Figure 2 and Figure 3). The notable exception is the unique sporangial morphology of *Brevibacillus laterosporus* which produces parasporal bodies (PBs) which laterally displace the spore in the sporangium (Figure 4), and which remain attached to the free spore (see below); the ellipsoidal spores of this species may lie centrally, paracentrally, or subterminally, and they characteristically swell the sporangia into spindle shapes.

Information on cell-wall composition is available for only two *Brevibacillus* species, *Brevibacillus brevis* and *Brevibacillus laterosporus*. They have the type of cross-linkage that is seen in the majority of *Bacillus* species for which it is known (see Table 2 in *Bacillus* section). A peptide bond is formed between the diamino acid in position 3 of one subunit and the d-Ala in position 4 of the neighboring peptide subunit so that no interpeptide bridge is involved. The diamino acid in most *Bacillus* species is *meso*-diaminopimelic acid (*meso*-DAP), and this cross-linkage is usually known as DAP-direct (Schleifer and Kandler, 1972).

Colonies of *Brevibacillus* species are usually smooth, moist, and glossy. Their elevations are flat to slightly raised, consistencies are butyrous, and shapes vary from round to irregular (Figure 5 and Figure 6). Diameters commonly range from 1–3 mm, but sizes up to 8 mm may occur. Colony color commonly ranges from buff or creamy-gray to off-white. *Brevibacillus thermoruber* produces spreading colonies and a red, nondiffusible pigment.

Brevibacillus species are heterotrophic and neutrophilic and will grow well on routine media such as nutrient agar or trypticase soy agar. Growth may be enhanced by the addition of a small amount of yeast extract. Most strains will grow on blood agar. They will use some amino acids, carbohydrates, and organic acids as sole sources of carbon and energy (see Table 3). Utilization of carbohydrates may be accompanied by the production of small amounts of acid, and utilization of amino acids and organic acids may be accompanied by the production of small amounts of alkali, but, these generally are not easily detected by the routine test methods, and some characters may prove to be inconsistent when retested. Growth temperatures vary considerably, and the descriptions of the individual species should be consulted.

Habitats

Most *Brevibacillus* strains have been isolated from the natural environment, particularly soils, where they appear to be saprophytes, but there have been some isolations from human clinical specimens and from human illness, and *Brevibacillus laterosporus* has long been associated with insect pathogenicity. As with *Bacillus*, the spores of these organisms may readily survive distribution from these natural environments to a wide variety of other habitats, and some strains have been found as contaminants in foods and pharmaceutical products. For more information on endospores in the environment, see the chapter on *Bacillus*. *Brevibacillus* species may be isolated following heat treatment of specimens in order to select for endospores. Although the presence of their spores in a given environment does not necessarily indicate that the organisms are metabolically active there, repeated and independent isolations from such a habitat make it reasonable to assume that vegetative *Brevibacillus* cells are, or have been, active there. Isolates identified as *Bacillus brevis* prior to the allocation of many strains bearing this name into the new and revived species *Brevibacillus agri*, *Brevibacillus borstelensis*, *Brevibacillus centrosporus*, *Brevibacillus choshinensis*, *Brevibacillus formosus*, *Brevibacillus* (now *Aneurinibacillus*) *migulanus*, *Brevibacillus parabrevis*, *Brevibacillus reuszeri*, *Aneurinibacillus danicus*, and strains assigned to *Bacillus brevis* by authors unaware that these nomenclatural changes had been proposed (between 1995 and 2004), may or may not be authentic strains of this species or even members of the

TABLE 1. Characteristics differentiating the species of the genus *Brevibacillus*[a,b]

Characteristic	*B. brevis*	*B. agri*	*B. borstelensis*	*B. centrosporus*	*B. choshinensis*	*B. formosus*	*B. ginsengisoli*	*B. invocatus*	*B. laterosporus*	*B. levickii*[c]	*B. limnophilus*	*B. parabrevis*	*B. reuszeri*	*B. thermoruber*[d]
Gram reaction	+/v	+	+	+	+	+	+	–	+/v/–	+	v	+/v	+	+
Anaerobic growth	–	–	–	–	–	–	+	–	+	–[e]	–	–	–	–
Growth at:														
20°C	d	+	+	+	+	+	+	+	+	+	+	+	+	–
50°C	–	–	+	–	–	–	–	–	d	+	–	d	–	+
55°C	–	–	–	–	–	–	–	–	–	d	–	–	–	+
NaCl tolerance:														
2%	d	+	–		–	–	+				w	d	+	
3%	–	–	–	–	–	–								–
4%							–							
5%									d		–	–		–
Hydrolysis of:														
Casein	+	+	+	–	–	+	+	–	+	d/w	–	+	–	+
Gelatin	+	+	+	–	–	+	+	–	+	+	–	+	–	+
ONPG	+	–	–	–	–	–	–	–	–			+	–	
Starch	–	–	–	–	–	–	–	–	–	w	–	–	–	+
Urea	–	–	–	–	–	–	+	–	–	–	–	–	–	+
Nitrate reduction	d	–	+	d	–	+	+	–	+	d	–	+	–	–
Acid from:[f]														
N-Acetylglucosamine	+	+	+	+	–	+		–	+	–	–	–	+	
D-Fructose	+	+	+	–	–	d		–	+	–	+	–	+	
D-Glucose	+	+	–	d	–	d		–	+	–	–	+	+	
Glycerol	+	+	D	d	–	+		–	+	–	+	+	–	
Maltose	+	+	–	–	–	–		–	+	–	–	+	–	
D-Mannitol	+	+	–	+	–	–		–	+	–	–	+	+	
D-Mannose	–	d	–	–	–	–		–	+	–		–	–	
Ribose	+	d	+	+	+	+		–	+	–	+	+	–	
D-Tagatose	–	–	+	–	–	d		–	–	–	–	–	–	
D-Trehalose	+	+	–	–	–	–		–	+	–	–	+	–	
D-Turanose	+	–	–	–	–	–		–	–	–	–	+	–	
Alkali from:[f]														
cis-Aconitate	+	d	–	+	–	+		–	–	d		+	–	
trans-Aconitate	–	d	–	–	–	–		–	–	d		–	–	
Aspartate	+	+	–	+	–	+		–	+	+		d	+	
Caprylate	–	–	–	d	–	–		–	–	d		–	+	
Citrate	+	d	–	+	d	–		–	–	d	–	+	+	
Fumarate	+	+	+	+	–	d		d	+	d		+	–	
D-Galacturonate	–	d	–	–	–	–		–	–	+		–	+	
D-Gluconate	+	+	–	d	d	–		–	–	+		–	–	
D-Glucuronate	–	–	–	–	–	–		–	–	d		–	+	
L-Glutamate	+	+	–	+	–	+		–	+	+		+	+	
DL-Lactate	+	+	–	+	–	–		d	–	d		+	+	
D-Malate	+	+	–	–	d	–		–	–	d		–	–	
L-Malate	+	+	d	+	+	d		–	–	+		+	+	
Malonate	+	+	+	+	d	–		–	–	+		d	+	
Mucate	–	–	–	–	–	–		d	–	+		d	–	
2-Oxoglutarate	+	+	+	+	+	+		+	+	+		+	+	
Propionate	+	d	+	+	+	d		–	–	d		d	+	
Quinate	–	–	–	–	–	–		–	–	+		+	–	
Succinate	+	+	+	+	–	+		–	–	+		+	+	
L-Tartrate	–	d	–	–	–	–		–	–	+		d	–	

[a]Symbols: +, >85% positive; d, results differ between strains (16–84% positive); –, 0–15% positive; +/v, positive or variable reaction within a strain; +/v/–, positive, variable or negative reaction within a strain; v, reaction varies within a strain; w, weak reaction; +/w, positive or weak positive reaction; d/w, results differ between strains, but positive reactions are weak; no entry indicates that no data are available.

[b]Data from Manachini et al. (1985), Goto et al. (2004), Heyndrickx et al. (1997), Allan et al. (2005), Albaser and Logan (unpublished results).

[c]Data for this species (other than growth temperature tests) were obtained by incubating at 40 °C, and (excepting acid and alkali production from carbon sources – see[f] below) were obtained at pH 5.5.

[d]Data for this species were obtained by incubating at 45 °C.

[e]*Brevibacillus levickii* is microaerophilic.

[f]Data for *Brevibacillus limnophilus* are from Goto et al. (2004); data for *Brevibacillus thermoruber* are from Manachini et al. (1985); data for *Brevibacillus levickii* are from Allan et al. (2005) and inoculum was at pH 7, although this is supra-optimal for this species. Data for all other species are from Albaser and Logan (unpublished results), and the method of testing is described in the section *Procedures for testing special characters.*

TABLE 2. Murein cross-linkage types found in *Bacillus* species and in former *Bacillus* species that have been transferred to other genera

	Murein cross-linkage[a]	Reference
Bacillus		
B. subtilis	*meso*-DAP direct	Schleifer and Kandler (1972)
B. anthracis	(*meso*-DAP direct)	Schleifer and Kandler (1972)
B. aquimaris	*meso*-DAP[b]	Yoon et al. (2003a)
B. barbaricus	DAP[b]	Taubel et al. (2003)
B. badius	*meso*-DAP direct	Schleifer and Kandler (1972)
B. cereus	*meso*-DAP direct	Schleifer and Kandler (1972)
B. coagulans	*meso*-DAP direct	Schleifer and Kandler (1972)
B. fastidiosus	*meso*-DAP direct	Claus and Berkeley (1986)
B. firmus	(*meso*-DAP direct)	Schleifer and Kandler (1972)
B. funiculus	DAP[b]	Ajithkumar et al. (2002)
B. halophilus	*meso*-DAP direct	Ventosa et al. (1989)
B. hwajinpoensis	*meso*-DAP[b]	Yoon et al. (2004b)
B. horti	*meso*-DAP[b]	Yumoto et al. (1998)
B. indicus[c]	L-Orn-D-Asp	Suresh et al. (2004)
B. jeotgali	*meso*-DAP direct	Yoon et al. (2001a)
B. lentus	(*meso*-DAP direct)	Schleifer and Kandler (1972)
B. licheniformis	*meso*-DAP direct	Schleifer and Kandler (1972)
B. marisflavi	*meso*-DAP[b]	Yoon et al. (2003a)
B. megaterium	(*meso*-DAP direct)	Schleifer and Kandler (1972)
B. methanolicus	*meso*-DAP direct	Arfman et al. (1992)
B. mycoides	*meso*-DAP direct	Claus and Berkeley (1986)
B. oleronius	*meso*-DAP direct	Kuhnigk et al. (1995)
B. pumilus	*meso*-DAP direct	Schleifer and Kandler (1972)
B. schlegelii	*meso*-DAP direct	Krüger and Meyer (1984)
B. smithii	DAP[b]	Nakamura et al. (1988)
B. thermocloacae	*meso*-DAP direct	Demharter and Hensel (1989b)
B. thuringiensis	*meso*-DAP direct	Schleifer and Kandler (1972)
B. vietnamensis	*meso*-DAP[b]	Noguchi et al. (2004)
Alkaliphilic and alkalitolerant *Bacillus* species		
B. cohnii	L-Orn-D-Asp	Spanka and Fritze (1993)
B. halmapalus	No DAP	Nielsen et al. (1994)
Alkaliphilic species in 6th 16S rRNA group of Nielsen et al. (1994)		
B. horikoshii	No DAP	Nielsen et al. (1994)
Spherical-spored *Bacillus* species		
B. fusiformis[d]	L-Lys-D-Asp	Ahmed et al. (2007c)
B. insolitus	Orn-D-Glu	Stackebrandt et al. (1987)
B. neidei	L-Lys-D-Glu	Nakamura et al. (2002)

TABLE 2. (*Continued*)

	Murein cross-linkage[a]	Reference
B. psychrodurans	Orn-D-Glu	Abd El-Rahman et al. (2002)
B. psychrotolerans	Orn-D-Glu	Abd El-Rahman et al. (2002)
B. pycnus	L-Lys-D-Glu	Nakamura et al. (2002)
B. silvestris	L-Lys-D-Glu	Rheims et al. (1999)
B. sphaericus[d]	L-Lys-D-Asp	Schleifer and Kandler (1972)
Alkalibacillus		
A. haloalkaliphilus	*meso*-DAP direct	Fritze (1996b)
Brevibacillus		
Br. Brevis	*meso*-DAP direct	Schleifer and Kandler (1972)
Br. laterosporus	*meso*-DAP direct	Schleifer and Kandler (1972)
Geobacillus		
G. stearothermophilus	(*meso*-DAP direct)	Schleifer and Kandler (1972)
G. thermoleovorans	DAP[b]	Zarilla and Perry (1987)
G. pallidus	*meso*-DAP direct	Scholz et al. (1987)
Gracilibacillus		
Gr. dipsosauri	*meso*-DAP direct	Lawson et al. (1996)
Marinibacillus		
M. marinus	L-Lys-direct	Yoon et al. (2001b)
Paenibacillus		
P. polymyxa	(*meso*-DAP direct)	Schleifer and Kandler (1972)
P. alvei	*meso*-DAP direct	Schleifer and Kandler (1972)
P. amylolyticus[e]	(*meso*-DAP direct)	Schleifer and Kandler (1972)
P. lentimorbus	*meso*-DAP direct	Schleifer and Kandler (1972)
P. macerans	*meso*-DAP direct	Schleifer and Kandler (1972)
Sporolactobacillus		
S. laevolacticus	*meso*-DAP direct	Andersch et al. (1994)
Sporosarcina		
S. ureae	L-Lys-Gly-D-Glu	Stackebrandt et al. (1987)
S. globisporus	L-Lys-D-Glu	Stackebrandt et al. (1987)
S. psychrophilus	L-Lys-D-Glu	Stackebrandt et al. (1987)
S. pasteurii	L-Lys-D-Asp	Ranftl and Kandler (1973)
Ureibacillus		
U. thermosphaericus	L-Lys-D-Asp	Andersson et al. (1995)
Virgibacillus		
V. pantothenticus	*meso*-DAP direct	Schleifer and Kandler (1972)
V. halodenitrificans	*meso*-DAP direct	Denariaz et al. (1989)
V. marismortui	*meso*-DAP[b]	Arahal et al. (1999)
V. salexigens	*meso*-DAP[b]	Garabito et al. (1997)

[a]Data in parentheses were not obtained from the type strain of the species.
[b]Configuration not determined.
[c]This neutrophilic species is closely related to the alkaliphilic species *Bacillus cohnii* and *Bacillus halmapalus*.
[d]Ahmed et al. (2007c) proposed the transfer of these species to the new genus *Lysinibacillus*.
[e]The strain analyzed by Schleifer and Kandler (1972) as *Bacillus circulans* (ATCC 9966) has been reallocated to *Paenibacillus amylolyticus*.

FIGURE 2. Photomicrograph of type strain of *Brevibacillus brevis* viewed by phase-contrast microscopy, showing ellipsoidal, subterminal spores that usually swell the sporangia. Bar = 2 µm. Photomicrograph prepared by N.A. Logan.

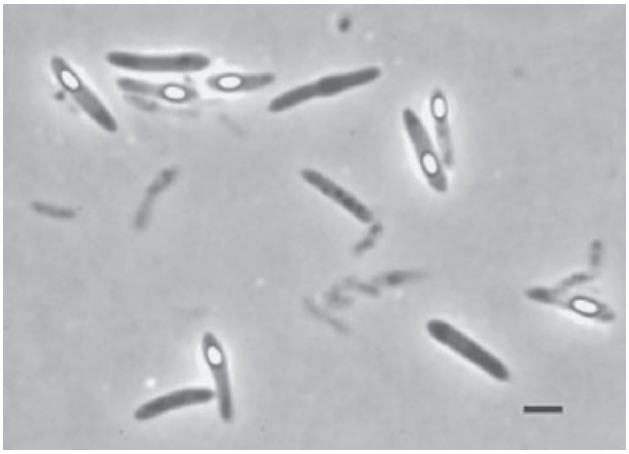
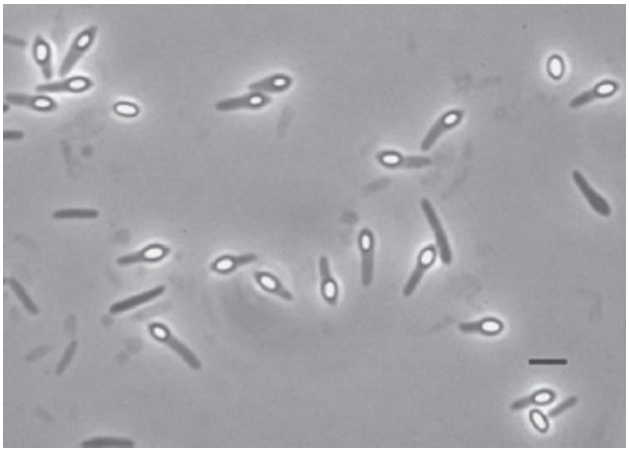


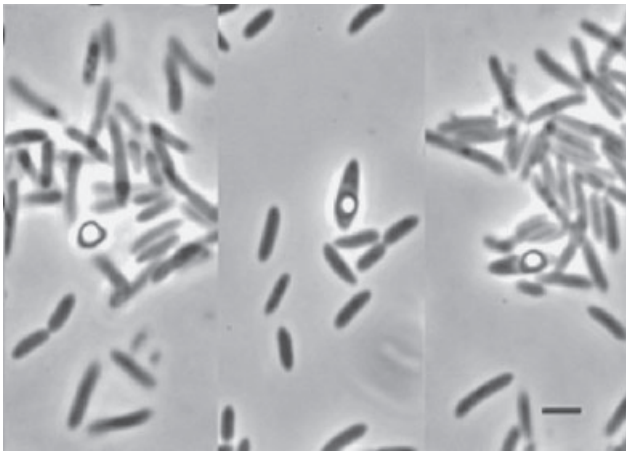
FIGURE 3. Photomicrograph of type strain of *Brevibacillus levickii* viewed by phase-contrast microscopy, showing ellipsoidal, subterminal and terminal spores in swollen sporangia. Bar = 2 µm. Photomicrograph prepared by N.A. Logan.



genus. This should be borne in mind when reading the accounts of habitats in which strains have been found. Isolations of strains identified as *Bacillus brevis* have been reported from tannery processing (Birbir and Ilgaz, 1996), black crusts on open-air stone monuments in Italy (Turtura et al., 2000), and soil contaminated with hexachlorocyclohexane. A *Bacillus brevis* strain secreting an extracellular cellulase was found in another soil (Singh and Kumar, 1998), and Wenzel et al. (2002) found a cellulolytic *Brevibacillus brevis* in the gut of the termite *Zootermopsis angusticollis*. Isolates identified as *Brevibacillus brevis* have been reported from the airborne dust of schools and children's daycare centers (Andersson et al., 1999), food packaging products of paper and board (Pirttijarvi et al., 2000), the submerged rhizosphere of the seagrass *Vallisneria americana* (wild celery) in an estuarine environment (Kurtz et al., 2003), and in the humus of Norway spruce (*Picea abies*) (Elo et al., 2000).

The sources of the type strains of the species *Brevibacillus agri*, *Brevibacillus borstelensis*, *Brevibacillus choshinensis*, *Brevibacillus formosus*, *Brevibacillus ginsengisoli*, and *Brevibacillus reuszeri* were soils. Foodstuffs are readily contaminated by soil organisms; *Brevibacillus centrosporus* has been isolated from spinach and *Brevibacillus parabrevis* from cheese. *Brevibacillus centrosporus* has also been found in estuarine seagrass rhizosphere (Kurtz et al., 2003). Strains of *Brevibacillus invocatus* and *Brevibacillus agri* were repeatedly isolated from a pharmaceutical fermenter plant and its antibiotic raw product over a period of several months (Logan et al., 2002). *Brevibacillus agri* has also been isolated from sterilized milk, a gelatin processing plant, clinical specimens, and a public water supply where it was implicated in an outbreak of waterborne illness

FIGURE 4. Composite photomicrograph of type strain of *Brevibacillus laterosporus* viewed by phase-contrast microscopy, The ellipsoidal spores are cradled in parasporal bodies, are borne paracentrally and subterminally, and are displaced laterally so that the sporangia are swollen into spindle shapes. Bar = 2 µm. Photomicrograph prepared by N.A. Logan.



(Logan et al., 2002). *Brevibacillus centrosporus* was isolated from a bronchio-alveolar lavage, *Brevibacillus parabrevis* was found in a breast abscess, and both species have been isolated from human blood (Logan et al., 2002). The original strain of the thermophilic species *Brevibacillus thermoruber* was isolated from mushroom compost (Craveri et al., 1966; Guicciardi et al., 1968), *Brevibacillus borstelensis* or a close relative of this species was found to be a prominent member of the flora of hot synthetic compost (Dees and Ghiorse, 2001), and a hydrogen sulfide decomposing strain of *Brevibacillus formosus* has been isolated from pig feces compost (Nakada and Ohta,

TABLE 3. Utilization of carbon compounds by *Brevibacillus* species[a]

Utilization of:[b]	*B. brevis*	*B. agri*	*B. borstelensis*	*B. centrosporus*	*B. choshinensis*	*B. formosus*	*B. ginsengisoli*	*B. invocatus*	*B. laterosporus*	*B. levickii*[c]	*B. limnophilus*	*B. parabrevis*	*B. reuszeri*	*B. thermoruber*[d]
Acetate							+							w
Adonitol	–	–	–	–	–	–	–	–	–	+		–	–	
D-Alanine	+	+	+	–	–	+		–	–	+		+	+	
L-Alanine	+	+	+	–	–	+	+	+	+	+		+	+	
4-Aminobutyrate	d	–	+	–	–	–		–	–	d		–	+	
L-Arabinose	–	–	–	–	–	–	–	–	–	–		–	–	+
L-Arabitol	–	–	–	–	–	–	–	–	–	+		–	–	
Cellobiose	d	–	–	–	–	+	+	–	+	–		+	d	
Citrate	d	–	–	–	d	–	–	–	–	+	–	+	–	–
Ethanolamine	d	+	+	–	–	+		–	d	–		+	d	
D-Fructose	+	+	+	–	d	+	–	–	+	+		–	+	+
Galactose	–	–	–	–	–	–	–	–	–	d		–	–	+
Gentiobiose	–	–	–	–	–	–	–	–	+	d		+	d	
Gluconate	d	+	+	–	d	+	–	–	–	+		+	+	
Glucosamine	–	–	–	–	–	–		–	–	–		d	–	
L-Glucose	+	+	–	+	d	+	+	–	+	+		+	+	+
DL-Glycerate	–	–	+	–	–	–		–	+	+		–	+	
Glycerol	+	+	d	–	–	+	+	–	+	+		+	–	+
3-Hydroxybutyrate	+	+	+	d	–	+	+	–	+	–		+	+	
Inositol	–	d	–	–	–	–	–	–	–	–		–	–	+
2-Ketogluconate	–	–	–	–	–	–	–	–	–	+		–	–	
5-Ketogluconate	–	–	–	–	–	–		–	–	+		–	–	
Lactose	–	–	–	–	–	–	–	–	–	+		–	–	
L-Malate	–	+	+	–	–	–		d	d	+		–	–	–
Maltitol	–	–	–	–	–	–		–	–	–		+	–	
Maltose	+	+	–	–	–	+	–	–	+	+		+	–	+
Maltotriose	+	+	–	–	–	+		–	+	+		+	–	
Mannitol	+	+	–	+	d	+	–	+	+	+		+	+	+
Melezitose	+	–	–	–	–	+	–	–	–	–		d	–	
1-*O*-Methyl-β-D-galactopyranoside	–	–	–	–	–	–		–	–	+		–	–	
1-*O*-Methyl-α-D-glucopyranoside	–	d	–	–	–	–	–	–	–	–		+	–	
1-*O*-Methyl-β-D-glucopyranoside	–	–	–	–	–	–		–	+	+		–	–	
Mucate	–	–	–	–	–	–		–	–	d		–	–	
2-Oxoglutarate	d	+	d	+	–	+		+	d	d		+	+	
Palatinose	+	+	–	–	–	+		–	–	–		+	–	
Phenylacetate	d	+	–	+	d	d	–	+	–	–		+	+	
Proline	+	+	+	–	–	+	+	–	+	+		+	+	
Putrescine	–	+	–	d	–	–		–	–	+		+	+	
Pyruvate														–
Quinate	–	–	–	–	–	–		+	–	+		–	–	
Rhamnose	–	–	–	+	–	–	–	–	–	–		–	–	
D-Ribose	+	–	+	d	+	+	–	–	+	d		–	+	+
Saccharate	–	–	–	–	–	–		–	–	d		–	–	
L-Serine	+	+	+	–	–	+	+	–	+	+		+	+	
Sorbitol	–	–	–	–	–	–	–	–	–	+		–	–	
Succinate	–	+	+	+	–	d		–	+	+		–	+	w
Sucrose	+	+	–	–	–	+	–	–	–	+		+	–	
meso-Tartrate	–	–	–	–	–	–		–	–	+		–	–	
Trehalose	+	+	–	–	–	+	–	–	+	d		+	–	+
Tryptophan	–	–	–	–	–	–		–	–	d		–	–	
L-Tyrosine	–	d	d	d	–	+		–	d	–		d	–	
D-Xylose	–	–	–	–	–	–	–	–	–	–		–	–	+

[a]Symbols: +, >85% positive; d, results differ between strains (16–84% positive); -, 0–15% positive; +/v, positive or variable reaction within a strain; +/v/-, positive, variable or negative reaction within a strain; v, reaction varies within a strain; w, weak reaction; +/w, positive or weak positive reaction; d/w, results differ between strains, but positive reactions are weak; no entry indicates that no data are available.

[b]*Brevibacillus brevis*, *Brevibacillus agri*, *Brevibacillus borstelensis*, *Brevibacillus centrosporus*, *Brevibacillus choshinensis*, *Brevibacillus formosus*, *Brevibacillus invocatus*, *Brevibacillus laterosporus*, *Brevibacillus levickii*, *Brevibacillus parabrevis*, and *Brevibacillus reuszeri* were negative for utilization of: L-arabinose, D-arabitol, dulcitol, L-fucose, lactulose, lyxose, melibiose, 1-*O*-methyl-α-galactopyranoside, 3-*O*-methyl-D-glucopyranose, raffinose, sorbose, xylitol, D-xylose, histamine, trigonelline, tryptamine, 5-aminovalerate, betain, caprate, *m*-coumarate, gentisate, glutarate, 3-hydroxybenzoate, 4-hydroxybenzoate, itaconate, 3-phenylpropionate, protocatechuate, D-tartrate, L-tartrate, tricarballylate.

[c]Data for this species (other than growth temperature tests) were obtained by incubating at 40°C, and (excepting acid and alkali production from carbon sources – see [f] below) were obtained at pH 5.5.

[d]Data for this species were obtained by incubating at 45°C.

FIGURE 5. Glossy colonies of the type strain of *Brevibacillus brevis* grown on trypticase soy agar for 24–36 h. Bar = 2 mm. Photograph prepared by N.A. Logan.

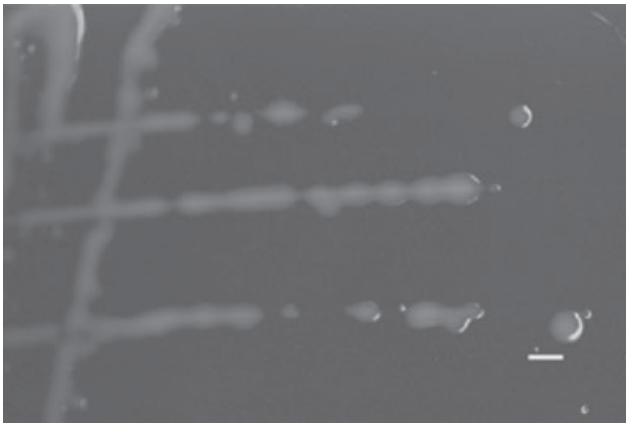
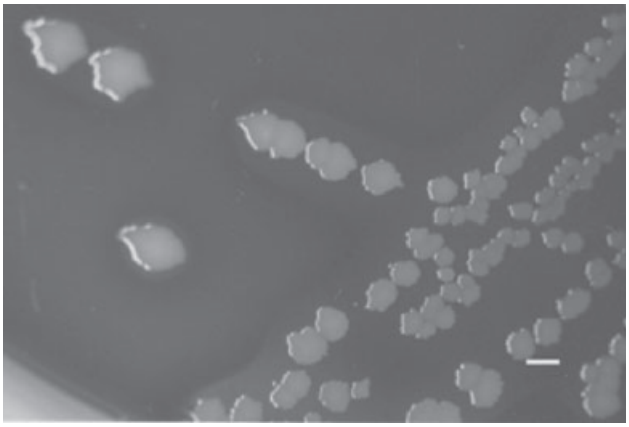


FIGURE 6. Type strain of *Brevibacillus laterosporus* grown on trypticase soy agar for 24–36 h, showing creamy-white and smooth colonies with irregular margins. Bar = 2 mm. Photograph prepared by N.A. Logan.



2001). The geothermal soil of the northwest slope of Mount Melbourne, a volcano in Antarctica, yielded strains of a moderately thermophilic and moderately acidophilic species, *Brevibacillus levickii*, that were isolated in small numbers along with *Bacillus fumarioli* (Allan et al., 2005; Logan et al., 2000).

The specific epithet of *Brevibacillus laterosporus* is derived from the organism's unique sporangial morphology. It produces parasporal bodies (PBs) that displace the spore laterally in the sporangium (Figure 4); these bodies have been described as resembling canoes or the keels of ships. Montaldi and Roth (1990) examined sporangia by thin-section transmission electron microscopy and found three kinds of PB: i) a large one, associated with the spore, and of similar volume to it, with a lamellar structure of sequentially smaller layers, ii) a smaller globular or angular one of 100–200 nm in diameter that appeared at the same time as the lamellar PB but which was not attached to the spore in any way, and iii) a striated, rod-shaped PB with diameter of at least 200 nm. *Brevibacillus laterosporus* was originally isolated from water (Laubach, 1916), but McCray (1917) isolated other strains with sporangial morphologies similar to the Laubach et al. strain from the diseased larvae of bees. White (1920), who had named his bee larvae isolates as *Bacillus orpheus* in 1912 but had not described them, recognized the similarity between the two species. *Bacillus orpheus* is thus a synonym of *Brevibacillus laterosporus*. Endosporeformers named *Bacillus pulvifaciens* by Katznelson (1950) were isolated from diseased honeybee larvae (including cases of powdery scale). Gordon et al. (1973) thought that they might form a connection between *Bacillus larvae* and *Bacillus laterosporus* and included them as unassigned strains in their listing of the latter species, however, Nakamura (1984a) revived *Bacillus pulvifaciens* as a distinct species. *Bacillus pulvifaciens* was later transferred to *Paenibacillus*. Heyndrickx et al. (1996a) showed that *Paenibacillus pulvifaciens* was a later subjective synonym of *Paenibacillus larvae* and proposed that the two species should become subspecies of *Paenibacillus larvae* because they represent distinct pathovars. In a recent taxonomic proposal, this subspecies distinction was again abandoned (Genersch et al., 2006). Although the strains of *Brevibacillus laterosporus* originally named *Bacillus orpheus* were isolated from diseased bees, it was not clear that they were clinically significant and this species is now considered to be a secondary invader. Falcon (1971) noted that *Bacillus laterosporus* had been isolated along with other bacteria in association with a natural epizootic of high mortality affecting Cabbage Moth (*Mamestra brassicae*) caterpillars on cabbage. Some *Bacillus laterosporus* strains have been convincingly shown to be pathogenic for mosquito and blackfly (*Simulium*) larvae (Favret and Yousten, 1985). Their pathogenicities are very low, and apparently are toxin-mediated but not associated with their spores. Subsequently, other strains (one of them isolated from dead insects) were found to produce crystalline inclusions during sporulation (Smirnova et al., 1996) which were toxic for larvae of the mosquito species *Aedes aegypti* and *Anopheles stephensi*, and toxic to a lesser extent for *Culex pipiens* (Orlova et al., 1998). *Bacillus laterosporus* and *Brevibacillus laterosporus* have also been isolated from a case of endophthalmitis following penetrating injury (Yabbara et al., 1977), sweet curdling milk spoilage (Heyndrickx and Scheldeman, 2002), bread dough (Bailey and von Holy, 1993), spontaneously fermenting soybeans (Sarkar et al., 2002), food packaging paper and board products (Pirttijarvi et al., 2000), tannery processing (Birbir and Ilgaz, 1996), sea

water (Barsby et al., 2002), and from an estuarine seagrass rhizosphere (Kurtz et al., 2003). Garabito et al. (1998) identified some of their isolates from salterns and saline soils as *Brevibacillus laterosporus* but found that these strains showed different substrate utilization patterns from that of the type strain of this species.

Brevibacillus strains, especially of *Brevibacillus brevis*, *Brevibacillus choshinensis*, and *Brevibacillus laterosporus*, have attracted considerable interest owing to their production or transformation of valuable compounds, or their potentials as biocontrol agents. The characteristically very high productivity of heterologous polypeptides and proteins by "*Bacillus brevis*" and *Brevibacillus brevis* strains have been harnessed for the production of human growth hormone (Kajino et al., 1997), human interleukin-2 (Takimura et al., 1997), cholera toxin B subunit for use as a mucosal adjuvant (Goto et al., 2000), a thermostable alkaline protease for use as a laundry detergent additive (Banerjee et al., 1999), acetolactate decarboxylase to prevent diacetyl formation during the accelerated maturation of beer (Outtrup and Jørgensen, 2002), and artificially designed gelatins (Kajino et al., 2000). *Brevibacillus choshinensis* has been used for the production of recombinant chicken interferon-γ as a growth-promoting agent for poultry (Yashiro et al., 2001) and for the production of recombinant human epidermal growth factor multimers and their transformation into the monomeric, native form (Miyauchi et al., 1999).

An unidentified *Brevibacillus* strain isolated from petroleum-contaminated soil was found to be capable of degrading petroleum hydrocarbons (Grishchenkov et al., 2000). A strain identified as *Bacillus brevis* was isolated from soil contaminated with hexachlorocyclohexane where it degraded this polluting pesticide (Gupta et al., 2000). Another strain of this species was found to degrade the insecticide teflubenzuron (Finkelstein et al., 2001). A strain of *Brevibacillus laterosporus* was able to break down polyvinyl alcohol to acetate (Lim and Park, 2001). An isolate closely related to *Brevibacillus thermoruber* has been found to depolymerize xanthan (Nankai et al., 1999).

Brevibacillus brevis produces the broad-spectrum, topically useful peptide antibiotic gramicidin S, which attacks the lipid bilayer of the inner membranes of susceptible organisms (Prenner et al., 1999). *Brevibacillus laterosporus* was the original source of the immunosuppressive drug spergualin (Takeuchi et al., 1981), synthetic analogs of which may be used as antitumor drugs and to prevent or treat tissue rejection (Allison, 2000). Other antibiotics produced by *Brevibacillus laterosporus* include laterosporamine (Shoji et al., 1976), the anti-*Candida* basiliskamides, and tupuseleiamides (Barsby et al., 2002). *Brevibacillus* strains with antifungal properties are potentially valuable biocontrol agents. These include a *Bacillus brevis* strain active against fusarial wilt of pigeon pea (Bapat and Shah, 2000), *Brevibacillus brevis* antagonistic to *Botrytis cinerea* (Edwards and Seddon, 2001), and a *Brevibacillus laterosporus* effective against four foliar necrotrophic pathogens of wheat (Alippi et al., 2000).

Enrichment and isolation

For most species, enrichment and selective isolation methods have not been reported. An isolation method for detecting colonies of the fungicidal, gramicidin-producing *Bacillus brevis* Nagano strain was developed by Edwards and Seddon (2000) for the recovery of this organism from plants and soil in field trial experiments. It utilized the ability of this strain to decompose tyrosine, producing light-brown colonies surrounded by haloes on tyrosine agar. The Nagano strain and any other isolates producing gramicidin could then be identified by paper chromatography of ethanolic extracts with detection by ninhydrin. Tyrosine agar contains nutrient broth (Oxoid), 6.6 g; tyrosine, 5 g; agar, 15 g; water, 1000 ml. After autoclaving, it is continuously stirred with a magnetic stirrer (to reduce the size of the tyrosine crystals) until it has reached 50°C, whereupon it is poured immediately, resulting in an opaque, off-white, solid medium. Tyrosine utilization is found among other *Brevibacillus* species and in many organisms outside this genus, so this method is by no means specific for *Brevibacillus brevis*. *Brevibacillus laterosporus* may be isolated from larval remains in outbreaks of European foulbrood in honeybees where they are considered to be secondary invaders (Alippi, 1991). Wakisaka and Koizumi (1982) noted that some aerobic endosporeformers that appeared to form minor components of soil floras, including *Bacillus brevis* and *Bacillus laterosporus*, showed slow and/or uneven germination compared with the more frequently encountered *Bacillus* species such as *Bacillus cereus*, *Bacillus megaterium*, *Bacillus sphaericus*, and *Bacillus subtilis*. Members of these minor populations were isolated with difficulty by the standard dilution-plate technique, but could be enriched by removing the rapidly germinating, fast-growing members of the predominant flora even though the latter might outnumber the minor flora by 100- to 1000-fold. The dried soil sample (0.5 g) was suspended in 5 ml of sterile saline and stirred with three to five 4 mm diameter glass beads for 1 min, then placed in a vacuum desiccator for 30 min to eliminate air. The mixture was then heated at 65°C for 10 min to destroy vegetative bacteria and prompt spore germination; 1 ml of this suspension was combined with

1 ml of germination medium and incubated for 2–3 h at 30°C with gentle shaking (90 r.p.m.) followed by heating it at 65°C for 10 min to kill the newly emerged and vulnerable vegetative cells of the predominant members of the flora. After cooling, the suspension was serially diluted, and 0.5 ml quantities (of 1-, 10- and 100-fold dilutions, usually) were plated on Gly IM medium (see below), followed by incubation at 30°C for 2–12 days to recover the members of the minor population. Germination medium contained: glucose, 10 g; Casamino acids, 5 g; beef extract, 3 g; yeast extract, 1 g; DL-alanine, 1 g; water, 1000 ml; pH 6.8. Autoclave at 110°C for 15 min. Gly IM agar contained: NaCl, 3 g; beef extract, 2.5 g; polypeptone, 2.5 g; yeast extract, 2.5 g; soluble starch, 2 g; glycerol, 2 g; agar, 12.5 g; water, 1000 ml; pH 6.8.

Brevibacillus ginsengisoli was originally isolated from ginseng field soil. The sample was suspended in 50 mM phosphate buffer (pH 7.0), and the suspension was spread on one-fifth-strength modified R2A agar plates (tryptone, 0.25 g; peptone, 0.25 g; yeast extract, 0.25 g; malt extract, 0.125 g; beef extract, 0.125 g; Casamino acids, 0.25 g; soytone, 0.25 g; glucose, 0.5 g; soluble starch, 0.3 g; xylan, 0.2 g; $C_3H_3NaO_3$, 0.3 g; K_2HPO_4, 0.3 g; $MgSO_4$, 0.05 g; $CaCl_2$, 0.05 g; agar, 15 g; water) after being serially diluted with 50 mM phosphate buffer (pH 7.0). The plates were incubated for 1 month at room temperature in an anaerobic chamber. The headspace was substituted with a gas mixture comprising $N_2/CO_2/H_2$ (80:15:5, by vol). Single colonies on the plates were purified by transferring them onto new plates that were incubated using the modified R2A agar or half-strength modified R2A agar under anaerobic conditions. The organism was routinely cultured on R2A agar at 30°C.

Brevibacillus levickii was isolated from geothermal soil samples collected from the northwest slope of Mount Melbourne, northern Victoria Land, Antarctica. 1 g quantities of soil were added to 9 ml *Bacillus fumarioli* broth (BFB) in duplicate at pH 5.5, and one of each pair was heat treated at 80°C for 10 min to kill vegetative cells. All broths were incubated at 50°C in waterbaths and inspected daily. Cultures which became turbid were subcultured by streaking onto plates of *Bacillus fumarioli* agar (BFA). Colonies appearing on streak plates were screened for vegetative and sporangial morphologies by phase-contrast microscopy, and sporeforming rods were streak purified and then transferred to slopes of the same medium for storage at 4°C after incubation and confirmation of sporulation by microscopy. The recipe for BFB is given under *Enrichment and isolation* in *Aneurinibacillus*, above.

Procedures for testing special characters

From the point of view of routine diagnostic laboratories, the aerobic endosporeformers comprise two groups, the reactive ones that will give positive results in various routine biochemical tests (and which are therefore more amenable to identification by traditional methods and modern developments of such approaches) and the nonreactive ones which give few if any positive results in such tests. Members of the genus *Brevibacillus* fall into the latter category. No special characters have been described for their differentiation, so their identification is difficult. They are largely unreactive in the carbohydrate utilization tests of the API 50CHB gallery (bioMérieux, Marcy l'Etoile, France) and insufficiently variable in the API 20E and supplementary tests so that species in this genus are largely inseparable by these means. *Bacillus laterosporus* is an exception and does give useful results in this system. The API Biotype 100 gallery (bioMérieux), which was developed as a research product for differentiating enterobacteria, proved to be of great value in differentiating species of *Brevibacillus* and *Aneurinibacillus* (Allan et al., 2005; Heyndrickx et al., 1997; Logan et al., 2002); it contained 99 tests for the assimilation of carbohydrates, organic acids, and amino acids, and one control tube. It was inoculated with a suspension in one of two semisolid media which differed in the number of growth factors they contained. After incubation, the tubes were examined for turbidity. Rigorous standardization of the suspension densities was essential. This system was adapted by using a suspension medium containing phenol red and examining the tubes for evidence of acid or alkali production (Albaser and Logan, unpublished results). The medium contained: KH_2PO_4, 1.5 g; $MgSO_4 \cdot 7H_2O$, 0.1 g; $CaCl_2 \cdot 2H_2O$, 0.125 g; $MnSO_4 \cdot 4H_2O$, 2.5 mg; phenol red 1 g; distilled water, 1000 ml; vitamin solution, 1 ml; pH 7.5. The vitamin solution contained: biotin 5 mg; thiamine, 5 mg; riboflavin, 5 mg; pyridoxal phosphate, 5 mg; pantothenate, 5 mg; nicotinic acid, 5 mg; *p*-aminobenzoic acid, 1 mg; folic acid, 0.5 mg; vitamin B_{12}, 0.5 mg; thioctic acid, 0.5 mg; deionized water, 50 ml. Several other commercially available biotyping kits have been investigated but do not give useful data for differentiating *Brevibacillus* species. Some of the special characters described in the section *Procedures for testing special characters* of *Bacillus* (see above) are applicable to *Brevibacillus*. It is strongly recommended that the original and emended descriptions of the more recently described species are consulted wherever possible and that cultures of those organisms are obtained for comparison when trying to distinguish between *Brevibacillus* species. It should be

appreciated that 16S rDNA sequencing is not always reliable as a standalone tool for identification (see Logan et al., 2002, for example) and that a polyphasic taxonomic approach is advisable for the identification of some of the more rarely encountered species and the confident recognition of new taxa. Nomenclatural types exist for a good reason and are usually easily available. There is no substitute for direct laboratory comparisons with authentic reference strains. It must also be remembered that cultures labeled *Brevibacillus brevis* in various laboratory collections around the world may not be authentic strains of this species if they were deposited prior to the extensive splitting of this species in the mid-1990s; the use of authentic type strains is therefore essential.

Taxonomic comments

Bacillus brevis was described by Migula in 1900, and the species attracted much interest in the early 1940s due to the production of the antibiotic gramicidin. Molluscicidal activity (Singer et al., 1988) and protein overproduction (Udaka et al., 1989) were subsequently reported for some strains. Because of such interest in potential applications, numerous isolations were made, but many isolates were found to differ from the reference strains, some in particular being thermophilic, and so the delineation of the species became uncertain. Following DNA–DNA reassociation studies and chemotaxonomic analyses, the taxonomy of *Bacillus brevis* was modified by assigning some *Bacillus brevis* strains to the new or revived species *Bacillus agri* and *Bacillus centrosporus* (Nakamura, 1993), *Bacillus migulanus*, *Bacillus choshinensis*, *Bacillus parabrevis*, and *Bacillus galactophilus* (Takagi et al., 1993) and *Bacillus reuszeri*, *Bacillus formosus*, and *Bacillus borstelensis* (Shida et al., 1995), but *Bacillus galactophilus* was later recognized to be a synonym of *Bacillus agri* (Shida et al., 1994a).

Studies on the 16S rDNA sequences of the type strain of *Bacillus brevis* suggested that *Bacillus aneurinolyticus* represents a distinct evolutionary line close to that of *Bacillus brevis* (Ash et al., 1991) or that it diverged early from the *Bacillus brevis* line (Farrow et al., 1992, 1994). On the basis of a 16S rDNA gene sequence analysis of the type strains only, Shida et al. (1996a) proposed the new genera *Brevibacillus* and *Aneurinibacillus*. The former accommodated *Brevibacillus brevis* and the seven species mentioned above that were derived from it, along with *Brevibacillus laterosporus* and the thermophile *Brevibacillus thermoruber*. *Aneurinibacillus* contained "*Bacillus aneurinolyticus*" and two other species. An earlier SDS-PAGE study supported this divergence of the *Bacillus brevis* and *Bacillus aneurinolyticus* groups (Shida et al., 1996b), but the individual species of the *Bacillus brevis* group were not always well separated by this method, a problem also noticed by Logan et al. (2002). The latter authors also found that 16S rDNA sequence analysis showed low discrimination potential for the species *Brevibacillus brevis*, *Brevibacillus choshinensis*, *Brevibacillus formosus*, *Brevibacillus parabrevis*, and *Brevibacillus reuszeri*, and that most species of the genus were difficult to separate by routine phenotypic tests. A further species, *Brevibacillus invocatus*, was proposed by Logan et al. (2002), who emphasized the difficulties of distinguishing between species of this genus. In the light of these problems of identification, Goto et al. (2004) examined the hypervariable (HV) region corresponding to the 5′ end of 16S rDNA (nucleotide positions 70–344 in *Bacillus subtilis* numbering) in 52 strains of aerobic endosporeformers, 31 of which were received as *Brevibacillus*, and 3 as unidentified *Brevibacillus* species. The HV region marker had already proved to be taxonomically useful in *Alicyclobacillus*, *Bacillus*, and *Paenibacillus*, and tentative identifications by this approach were then confirmed by DNA–DNA hybridizations. They found that 14 *Brevibacillus brevis* and three *Brevibacillus* species strains clustered in *Aneurinibacillus* and proposed one of these strains as the new species *Aneurinibacillus danicus*. Of the remaining 17 strains received as *Brevibacillus brevis*, five identified as *Bacillus methanolicus*, two strains clustered close to this species but showed less than 70% DNA homology with the type strain, and one identified as *Bacillus oleronius*. Only two strains clustered with *Brevibacillus brevis*, and they showed less than 60% DNA homology with the type strain of this species. Of the remainder, three strains identified as *Brevibacillus agri*, two as *Brevibacillus parabrevis*, and 1 strain which did not cluster with an existing species of the genus was proposed as the new species *Brevibacillus limnophilus*.

Thus strains which might previously have been assigned to *Bacillus brevis* now represent some 12 mesophilic species in *Brevibacillus*. Their distinctions are based mainly upon DNA relatedness studies, molecular probing, and chemotaxonomic analyses of the relatively few available isolates using databases which are largely restricted to reference laboratories and unsuitable for organisms encountered only occasionally in routine laboratories. Distinction of most *Brevibacillus* species is not possible using the currently available *Bacillus* identification schemes, and separation remains difficult even with much wider selections of phenotypic tests (Heyndrickx et al., 1997; Logan, 2002). Also, another unreactive species, *Bacillus badius*, and species of *Aneurinibacillus* may easily be misidentified as a member of this genus. It is unfortunate that the extensive splitting proposed by the various recent taxonomic studies has not revealed

characteristic phenotypic profiles that would be of value in the routine laboratory. It has been questioned whether the current taxonomy of *Brevibacillus* best serves the needs of the diagnostic bacteriologist and whether certain species might better be merged to give a more practically useful classification of this genus (Logan et al., 2002). However, new genotypic approaches based on sequences of so-called housekeeping genes may provide more straightforward (genomic) differentiation and identification.

Maintenance procedures

Brevibacillus strains may be preserved on slopes of a suitable growth medium that encourages sporulation, such as nutrient agar or trypticase soy agar containing 5 mg/l of $MnSO_4 \cdot 7H_2O$. Slopes should be checked microscopically for spores before sealing (to prevent drying out) and storage in a refrigerator; on such sealed slopes the spores should remain viable for many years. For longer term preservation, lyophilization and liquid nitrogen may be used, as long as cryoprotectants are added.

List of the species of the genus *Brevibacillus*

Brevibacillus brevis (Migula 1900) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus brevis* Migula 1900, 583.)

bre'vis. L. adj. *brevis* short.

Strictly aerobic, Gram positive or Gram variable, motile, rod-shaped cells, 0.7–0.9 µm × 3.0–5.0 µm, occurring singly and in pairs. The ellipsoidal spores are borne subterminally and swell the sporangia (Figure 2). Grows on routine media such as nutrient agar and trypticase soy agar, producing glossy, butyrous, cream-colored colonies, 1–3 mm in diameter after 24–36 h (Figure 5). Growth at 30°C may initially be slow, with more rapid growth following 24 h incubation. Catalase- and oxidase-positive. Nitrate reduction positive for most strains. Casein, DNA, gelatin, and Tween 60 are hydrolyzed; starch and urea are not hydrolyzed. Hydrolysis of Tween 80 is variable. Hydrogen sulfide and indole are not produced. Most strains do not grow at 20° or below, or above 50°C. No growth occurs at pH 5.5 and most strains do not grow at pH 9.0. D-Fructose, D-glucose, glycerol, maltose, mannitol, ribose, trehalose, and a few other carbohydrates are assimilated, and acid is produced weakly, if at all, from them. Amino acids and some organic acids are used as carbon and energy sources.

Isolated mainly from soil; also found in airborne dust, milk, rhizospheres, and paper products.

DNA G+C content (*mol%*): 48.7 (HPLC).

Type strain: ATCC 8246, BCRC 14682, CCM 2050, CCUG 7413, CIP 52.86, DSM 30, HAMBI 1883, NBRC 15304, JCM 2503, LMG 7123, NCCB 48009, NCIMB 9372, NCTC 2611, NRRL B-14602, NRRL NRS-604, VKM B-503, W.W. Ford 27B.

GenBank accession number (*16S rRNA gene*): AB101593, AB271756, D78457, X60612.

Brevibacillus agri (Laubach 1916) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus agri* (ex Laubach, Rice and Ford 1916) Nakamura 1993, 23; *Bacillus galactophilus* Takagi, Shida, Kadowaki, Komagata and Udaka 1993, 229.)

ag'ri. L. gen. n. *agri* of a field.

Strictly aerobic, Gram positive, motile, rod-shaped cells, 0.5–1.0 µm × 2.0–5.0 µm. The ellipsoidal spores swell the sporangia. Grows on routine media such as nutrient agar and trypticase soy agar, producing nonpigmented, translucent, thin, smooth, circular, entire colonies of about 2 mm in diameter. Catalase-positive, oxidase-negative. Nitrate reduction negative. Casein and gelatin are hydrolyzed; starch and urea are not hydrolyzed. Minimum growth temperature varies between 5 and 20°C, optimum temperature for growth is 28°C, and maximum growth temperature is 40°C. Growth occurs at pH 5.6 and no growth occurs at pH 9.0. Grows in presence of 2% but not 3% NaCl. D-Fructose, D-glucose, glycerol, maltose, D-mannitol, D-trehalose, and a few other carbohydrates are assimilated, and acid is produced weakly, if at all, from them. Amino acids and some organic acids are used as carbon and energy sources.

Isolated from soil, water, clinical specimens, sterilized milk, and pharmaceutical manufacturing plants.

DNA G+C content (*mol%*): 53.5 (HPLC).

Type strain: ATCC 51663, CCUG 31345, CIP 104002, DSM 6348, NBRC 15538, JCM 9067, LMG 15103, NRRL NRS-1219.

GenBank accession number (*16S rRNA gene*): AB112716, D78454.

Brevibacillus borstelensis (Stührk 1935) Shida, Takagi, Kadowaki and Komagata 1996a, 945^{VP} (*Bacillus borstelensis* Shida, Takagi, Kadowaki, Udaka, Nakamura and Komagata 1995, 98.)

bor.stel.en'sis. N.L. adj. *borstelensis* referring to Borstel, Germany, where it was isolated.

Strictly aerobic, Gram positive, motile, rod-shaped cells, 0.5–0.9 µm × 2.0–5.0 µm. The ellipsoidal spores swell the sporangia. Grows on routine media such as nutrient agar and

trypticase soy agar, producing flat, smooth, circular, entire colonies. One of the 16 strains contributing to the original description produced brown-red pigmentation on nutrient agar. Catalase-positive, oxidase-negative. Nitrate is reduced. Casein and gelatin are hydrolyzed; starch and urea are not hydrolyzed. Growth occurs at 20°C, the maximum is 50°C, and the optimum temperature for growth is 30°C. Growth occurs at pH 5.5 and 5.6. Growth does not occur in the presence of 2% NaCl. D-Fructose, ribose, and a few other carbohydrates are assimilated, and acid is produced weakly, if at all, from them. D-Mannitol and D-trehalose are not assimilated. Amino acids and some organic acids, but not citrate, are used as carbon and energy sources.

Isolated from soil.

DNA G+C content (*mol%*):51.3 (HPLC).

Type strain: ATCC 51668, CIP 104545, DSM 6347, NBRC 15714, JCM 9022, LMG 16009, NRRL NRS-818.

GenBank accession number (*16S rRNA gene*): AB112721, D78456.

Brevibacillus centrosporus (Laubach 1916) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus centrosporus ex* Laubach, Rice and Ford 1916) Nakamura 1993, 24.)

cen.tro.spor'us. L. n. *centrum* the center; N.L. n. *spora* spore; N.L. adj. *centrosporus* with a central spore.

Strictly aerobic, Gram positive, motile, rod-shaped cells, 0.5–1.0 µm × 2.0–6.0 µm. The ellipsoidal spores swell the sporangia. Despite the species name, the spores do not tend to lie centrally in the sporangia. Grows on routine media such as nutrient agar and trypticase soy agar, producing nonpigmented, translucent, thin, smooth, circular, entire colonies 2–3 mm in diameter. Catalase-positive, oxidase-negative. Nitrate is reduced to nitrite by some strains. Casein, gelatin, starch, and urea are not hydrolyzed. Minimum temperature for growth is 10°C, maximum is 40°C, and the optimum temperature for growth is 28°C. Growth does not occur at pH 5.6. Growth does not occur in the presence of 3% NaCl. D-Glucose, D-mannitol, ribose, and a few other carbohydrates are assimilated, and acid is produced weakly, if at all, from them. D-Fructose and trehalose are not assimilated. Some amino acids and organic acids are used as carbon and energy sources.

Isolated from child's feces, clinical specimens, spinach, and estuarine seagrass rhizosphere.

DNA G+C content (*mol%*): 49.8 (HPLC).

Type strain: ATCC 51661, CCUG 31347, CIP 104003, DSM 8445, NBRC 15540, JCM 9071, LMG 15106, NRRL NRS-664.

GenBank accession number (*16S rRNA gene*): AB112719, D78458.

Brevibacillus choshinensis (Takagi, Shida, Kadowaki, Komagata and Udaka 1993) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus choshinensis* Takagi, Shida, Kadowaki, Komagata and Udaka 1993, 229.)

cho.shi.nen'sis. N.L. adj. *choshinensis* referring to Choshi, Japan, where it was isolated.

Strictly aerobic, Gram positive, motile, rod-shaped cells, with cell diameters greater than 0.5 µm and cell lengths greater than 3.0 µm. The ellipsoidal spores swell the sporangia and lie subterminally to terminally. Grows on routine media such as nutrient agar and trypticase soy agar, producing pale yellow colonies. Catalase- and oxidase-positive. Nitrate reduction negative. Casein, gelatin, starch, and urea are not hydrolyzed. Growth occurs at 15°C, but not at 50°C. Growth does not occur at pH 5.5 and pH 9.0. Does not grow in presence of 2% NaCl. Strains are very unreactive and very few carbohydrates are assimilated by some strains while acid is produced weakly, if at all, from them. Glycerol is not assimilated. A very few amino acids, citrate, and some other organic acids may be used as carbon and energy sources.

Isolated from soil.

DNA G+C content (*mol%*): 48.2 (Takagi et al., 1993)–49.8 (Logan et al., 2002) (both HPLC).

Type strain: HPD52, ATCC 51359, CIP 103838, DSM 8552, NBRC 15518, JCM 8505, LMG 15968, NCIMB 13345, NRRL B-23247.

GenBank accession number (*16S rRNA gene*): AB112713, D78459.

Brevibacillus formosus (Heigener 1935) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus formosus* Shida, Takagi, Kadowaki, Udaka, Nakamura and Komagata 1995, 98.)

for.mo'sus. L. adj. *formosus* beautiful.

Strictly aerobic, Gram positive, motile, rod-shaped cells, 0.5–0.9 µm × 2.0–5.0 µm. The ellipsoidal spores swell the sporangia. Description is based on the study of three strains. Grows on routine media such as nutrient agar and trypticase soy agar, producing colonies that are unpigmented, flat, smooth, circular and entire. Catalase-positive, oxidase-negative. Nitrate is reduced to nitrite. Casein and gelatin are hydrolyzed; starch and urea are not hydrolyzed. Growth occurs at 10°C and at 45°C, but not at 50°C; the optimum temperature for growth is 30°C. Growth occurs at

pH 5.5 and 5.6. Growth does not occur in the presence of 2% NaCl. D-Glucose, D-fructose, glycerol, and other carbohydrates are assimilated, and acid is produced weakly, if at all, from them. A range of amino acids and organic acids may be used as carbon and energy sources.

Isolated from soil.

DNA G+C content (*mol%*): 47.2 (HPLC).

Type strain: F12, ATCC 51669, CIP 104544, DSM 9885, NBRC 15716, JCM 9169, LMG 16010, NRRL NRS-863.

GenBank accession number (*16S rRNA gene*): AB112712, D78460.

Brevibacillus ginsengisoli Baek, Im, Oh, Lee, Oh and Lee 2006, 2667[VP]

gin.sen.gi.so'li. N.L. n. *ginsengum* ginseng; L. n. *solum* soil; N.L. gen. n. *ginsengisoli* of the soil of a ginseng field, the source of the organism.

Cells are Gram positive, aerobic or facultatively anaerobic, motile, slightly curved rods, 0.3–0.5 µm in diameter and 3.5–5.0 µm in length after 2 days culture on R2A agar. Colonies grown on R2A agar for 2 days are smooth, circular, glossy, white, and convex. Central and subterminal oval spores are formed in swollen sporangia. Grows well at 20–42°C and pH 5.0–8.5, but does not grow at 4 or 45°C. Growth occurs in the absence of NaCl and in the presence of 2.0% (w/v) NaCl but not 4% (w/v) NaCl. Grows anaerobically in denitrifying conditions. Casein and gelatin are hydrolyzed. Xylan, chitin, starch, cellulose, and DNA are not degraded. Urease, β-glucosidase, protease, and malic acid assimilation are positive in tests using API 20E and API 20NE strips. Reactions for ONPG hydrolysis, arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, citrate utilization, hydrogen sulfide production, tryptophan deaminase, indole production, acetoin production, and adipic acid assimilation are negative. Utilizes a small number of carbohydrates, amino acids, and organic acids as carbon sources. In addition to those shown in the tables, the following carbon sources are utilized in the API 50 CH and ID 32GN tests: L-histidine, salicin, and valeric acid. Utilization tests are negative for the following sub-strates: amygdalin, arbutin, D-arabinose, D-arabitol, D-fucose, D-lyxose, dulcitol, erythritol, L-fucose, glycogen, inulin, D-mannose, D-melibiose, methyl-α-D-mannopyranoside, methyl-β-D-xylopyranoside, D-raffinose, L-sorbose, D-tagatose, D-turanose, xylitol, L-xylose, capric acid, 3-hydroxybenzoic acid, 4-hydroxybenzoic acid, itaconic acid, propionic acid, sodium malonate, and suberic acid. MK-7 is the predominant respiratory quinone. The major cellular fatty acids are $C_{15:0\ iso}$, $C_{14:0\ iso}$, and $C_{15:0\ ante}$.

Isolated from soil from a ginseng field in Pocheon Province, South Korea.

DNA G+C content (*mol%*): 52.1 (HPLC).

Type strain: Gsoil 3088, KCTC 13938, LMG 23403.

GenBank accession number (*16SrRNA*): AB245376.

Brevibacillus invocatus Logan, Forsyth, Lebbe, Goris, Heyndrickx, Balcaen, Verhelst, Falsen, Ljungh, Hansson and De Vos. 2002, 964[VP]

in.vo.ca'tus. L. adj. *invocatus* uninvited, referring to the isolation of strains of this organism as contaminants of an industrial fermentation.

Gram negative, motile, rod-shaped cells, 0.5–1.0 µm × 2.0–6.0 µm. Strictly aerobic. The ellipsoidal spores are borne subterminally and occasionally terminally, and swell the sporangia. Grows on routine media such as nutrient agar and trypticase soy agar. Growth at 30°C is initially slow, with more rapid growth following 24 h incubation; after 3–4 days the slightly umbonate colonies are 1–8 mm in diameter, with slightly irregular margins. Colonies are brownish-yellow, some with a single whitish concentric zone at the margin, and they are butyrous and have silky surfaces; the centers are opaque and the edges translucent. Catalase-positive. Nitrate reduction negative. Casein, gelatin, starch, and urea are not hydrolyzed; indole is not produced. Growth temperatures range from 15–35°C. Growth occurs between pH 6.0 and 8.5. Few carbohydrates are assimilated, only weakly, and acid is not produced from them; some amino acids and organic acids are used as carbon sources.

Isolated from a pharmaceutical fermentation plant and its antibiotic raw product.

DNA G+C content (*mol%*): 49.7 (HPLC).

Type strain: B2156, CIP 106911, JCM 12215, LMG 18962, NCIMB 13772.

GenBank accession number (*16SrRNA*): AB112718.

Brevibacillus laterosporus (Laubach 1916) Shida, Takagi, Kadowaki and Komagata 1996a, 945[VP] (*Bacillus laterosporus* Laubach 1916, 505.)

la.te.ro.spor'us. L. n. *latus, lateris* the side; N.L. n. *spora* spore; N.L. adj. *laterosporus* with lateral spores.

Gram positive, Gram negative, and Gram variable, motile, rod-shaped cells, 0.5–0.9 µm × 2.0–5.0 µm. Facultatively anaerobic. Strains of this species commonly exhibit distinctive sporangial morphologies. The ellipsoidal spores are cradled in parasporal bodies (PBs) that have been described

as C-shaped, or resembling canoes or the keels of ships. The spores, with their attached PBs, are borne centrally, paracentrally, and subterminally and are displaced laterally in the sporangia by the PBs, so that the sporangia are swollen into spindle shapes (Figure 4). Other species of aerobic endosporeforming bacteria may produce spores that lie laterally, but the PBs, which tend to remain firmly adherent to the spore after sporangial lysis, appear to be unique to this species. The proportion of sporangia containing PBs may vary with the strain and growth conditions. Grows on routine media such as nutrient agar and trypticase soy agar. Colonies are 1–3 mm in diameter, creamy-white, and smooth, and may have slightly irregular margins (Figure 6). Catalase-positive. Nitrate is reduced. Casein and gelatin are hydrolyzed, and starch and urea are not hydrolyzed; indole is not produced. Growth temperatures range from minima between 15 and 20°C to maxima between 35 and 50°C, with optima around 30°C. Growth does not occur at pH 5.7 but does occur at pH 6.8. D-Fructose, D-glucose, glycerol, maltose, D-mannitol, D-mannose, D-ribose, trehalose, and several other carbohydrates are assimilated, and acid is produced from them in larger quantities, so it is more readily detected than is the case with most other species of *Brevibacillus*. Some amino acids and organic acids are also used as carbon and energy sources. Some strains are pathogenic for mosquito and blackfly larvae. Parasporal toxin crystals, visible by electron microscopy, may be produced by some strains.

Isolated from soil, salterns, tap water, diseased honey bee larvae, other insects, foods, paper products, marine environments, and an eye infection.

DNA G+C content (*mol%*): 40.2 (T_m), 40.5 (Bd).

Type strain: ATCC 4517, ATCC 64, ATCC 8248, CCM 2116, BCRC 10607, CCUG 7421, CFBP 4222, CIP 52.83, DSM 25, HAMBI 1882, IAM 12465, NBRC 15654, JCM 2496, LMG 6931, LMG 16000, NCCB 75013, NCCB 48016, NCIMB 8213, NCIMB 9367, NCTC 6357, NRRL NRS-314, NRRL NRS-340, VKM B-499.

GenBank accession number (*16S rRNA gene*): AB112720, D16271, X60620.

Brevibacillus levickii Allan, Lebbe, Heyrman, De Vos, Buchanan and Logan 2005, 1048[VP]

le.vic.ki'i. N.L. gen. n. *levickii* of Levick, named after G. Murray Levick, surgeon and biological scientist of Captain R.F. Scott's Northern Party, the first scientific expedition to visit the vicinity of Mt. Melbourne in 1912.

Microaerophilic and weakly catalase-positive. Cells are Gram positive, becoming Gram negative after 48 h, motile, round-ended rods (0.7–0.8 µm × 2–5 µm) occurring singly, in pairs, and in chains. Endospores are ellipsoidal, occurring subterminally or terminally in swollen sporangia (Figure 3). After 48 h incubation at 40°C on 1/2 BFA (pH 5.5), colonies are circular, flat, up to 3.0 mm in diameter, and cream-colored with a matt appearance. Colony consistency becomes tough and difficult to break with a loop. Minimum growth temperature lies between 15 and 20°C, with the optimum temperature for growth being between 40 and 45°C, and the maximum growth temperature lying between 50 and 55°C. Growth occurs between pH 4.5 and 6.5 and the optimum pH for growth lies between pH 5.0 and 5.5. Horse blood agar is partially hemolyzed. Gelatin is hydrolyzed, starch hydrolysis is weak, and casein hydrolysis is weak and variable. In the API 20E strip reactions for arginine dihydrolase, citrate utilization and Voges–Proskauer reaction are positive. Nitrate reduction is variable. A range of carbohydrates, amino acids, and organic acids is assimilated in the API Biotype 100 gallery as sole carbon sources. The major cellular fatty acid is $C_{15:0\ ante}$, accounting for approximately 74 % of the total fatty acid content. The following fatty acids are present in smaller amounts (at least 1 %): $C_{14:0\ iso}$, $C_{15:0\ iso}$, $C_{16:0}$, $C_{16:0\ iso}$, summed feature 4 ($C_{17:1\ iso}$ and/or $C_{17:1\ ante}$), and $C_{17:0\ ante}$.

Isolated from geothermal soil collected from the northwest slope of Mt. Melbourne, northern Victoria Land, Antarctica.

DNA G+C content (*mol%*): 50.3 (HPLC).

Type strain: B-1657, CIP 108307, LMG 22481.

GenBank accession number (*16S rRNA gene*): AJ715378.

Brevibacillus limnophilus Goto, Fujita, Kato, Asahara and Yokota 2004, 426[VP]

lim.no'phi.lus. Gr. n. *limnos* lake; Gr. adj. *philos* loving or friendly to; N.L. masc. adj. *limnophilus* lake-loving.

Strictly aerobic, Gram variable, motile rods, 0.5–0.6 µm × 2.2–4.0 µm. Ellipsoidal spores are borne subterminally in swollen sporangia. Description is based upon a single isolate. Colonies on nutrient agar are circular, entire, smooth, convex, translucent, and whitish-beige, and they are 3–4 mm in diameter after 48 h. The temperature range for growth is 20–45°C, and the temperature for optimum growth is 30–35°C. Optimum pH for growth is 7.0–7.5, growth occurs at pH 6.5–8.0 and does not occur at pH 6.0 or 8.5. Growth is weak in the presence of 2% NaCl and is inhibited by 5% NaCl. Catalase-positive and oxidase-negative. Urease, citrate utilization, and nitrate reduction are negative. Esculin is hydrolyzed, DNA is weakly hydrolyzed, and arbutin, casein, gelatin, starch, and tyrosine are not hydrolyzed. Acid is

produced from L-arabinose, D-fructose, glycerol, rhamnose (weakly), and ribose. The major fatty acids are $C_{15:0\ iso}$, $C_{16:0}$, and $C_{17:0\ iso}$. The main quinone is menaquinone 7.

This organism was deposited in the ARS Culture collection as "*Bacillus limnophilus*" by Porter in 1940 and identified by Smith et al. (1952) as "*Bacillus brevis*".

Source of the type strain not reported; *Bacillus limnophilus* was described by Stührk (1935). Goto et al. (2004) did not refer to the original description, but they did indicate that the name they proposed was a revival for the strain that was deposited with this name in the ARS Culture Collection by Porter in 1940. Smith et al. (1952) considered it to be a synonym of *Bacillus brevis*.

DNA G+C content (*mol%*): 51.9 (HPLC).

Type strain: DSM 6472, NRRL NRS-887.

GenBank accession number (*16S rRNA gene*): AB112717.

Brevibacillus parabrevis (Takagi, Shida, Kadowaki, Komagata and Udaka 1993) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus parabrevis* Takagi, Shida, Kadowaki, Komagata and Udaka 1993, 229.)

pa.ra.bre'vis. Gr. prep. *para* alongside of, like; N.L. adj. *brevis* short; N.L. *parabrevis brevis*-like, referring to *Bacillus* (now *Brevibacillus*) *brevis*.

Strictly aerobic, Gram positive or Gram variable, motile, rod-shaped cells, 0.5–0.9 µm × 2.0–4.0 µm. The ellipsoidal spores are borne subterminally to terminally and swell the sporangia. Grows on routine media such as nutrient agar and trypticase soy agar, producing flat, smooth, yellowish-gray colonies. Catalase- and oxidase-positive. Nitrate reduction positive. Casein, DNA, gelatin, Tween 60, and Tween 80 are hydrolyzed; starch, and urea are not hydrolyzed. Hydrogen sulfide and indole are not produced. Growth occurs at 20°C, some strains grow at 15°C and most at 50°C, but no growth occurs at 55°C. Most strains will not grow at pH 5.5 or pH 9.0. Most strains will grow in presence of 2% NaCl, but not with 5% NaCl. D-Glucose, glycerol, maltose, D-mannitol, trehalose, and other carbohydrates are assimilated, but acid is produced weakly, if at all, from them. D-Fructose is not assimilated. Some amino acids and organic acids are used as carbon and energy sources.

Source of type strain not reported; other strains found in clinical specimens and cheese.

DNA G+C content (*mol%*): 51.8 (Takagi et al., 1993)–52.2 (Logan et al., 2002) (both HPLC).

Type strain: ATCC 10027, CIP 103840, DSM 8376, NBRC 12334, JCM 8506, LMG 15971, NCIMB 13346, NRRL NRS-605, NRRL NRS-815.

GenBank accession number (*16S rRNA gene*): AB112714, D78463.

Brevibacillus reuszeri (Shida, Takagi, Kadowaki, Udaka, Nakamura and Komagata 1995) Shida, Takagi, Kadowaki and Komagata 1996a, 943^{VP} (*Bacillus reuszeri* Shida, Takagi, Kadowaki, Udaka, Nakamura and Komagata 1995, 98.)

reus.ze'ri. N.L. gen. n. *reuszeri* of Reuszer, referring to H.W. Reuszer, who isolated the organism.

Strictly aerobic, Gram positive, motile, rod-shaped cells, 0.5–0.9 µm × 2.0–5.0 µm. The ellipsoidal spores swell the sporangia. Grows on routine media such as nutrient agar and trypticase soy agar, producing unpigmented, flat, smooth, circular, entire colonies. Catalase-positive, oxidase-negative. Nitrate is not reduced to nitrite. Casein, gelatin, starch, and urea are not hydrolyzed. Growth occurs at 10°C and at 45°C, and the optimum temperature for growth is 30°C. Growth occurs at pH 5.5 and 5.6. Growth occurs in the presence of 2% NaCl but not with 3% NaCl. D-Fructose, D-glucose, D-mannitol, and a few other carbohydrates are assimilated, and acid is produced weakly, if at all, from them. Shida et al. (1995) found that this organism produced acid from glycerol and maltose, but Logan et al. (2002) found that neither was assimilated. Some amino acids and organic acids are used as carbon and energy sources.

Isolated from soil.

DNA G+C content (*mol%*): 46.5 (HPLC).

Type strain: H.W. Reuszer Army strain 39, ATCC 51665, CIP 104543, DSM 9887, NBRC 15719, JCM 9170, LMG 16012, NRRL NRS-1206.

GenBank accession number (*16S rRNA gene*): AB112715, D78464.

Brevibacillus thermoruber (Guicciardi, Biffi, Manachini, Craveri, Scolastico, Rindone and Craver 1968) Shida, Takagi, Kadowaki and Komagata 1996a, 945^{VP} (*Bacillus thermoruber* (*ex* Guicciardi, Biffi, Manachini, Craveri, Scolastico, Rindone and Craver 1968) Manachini, Fortina, Parini and Craveri 1985, 495.)

ther'mo.ru.ber. Gr. n. *therme* heat; L. adj. *ruber* red; N.L. masc. adj. *thermoruber* heat-loving and red-pigment producing.

Moderately thermophilic, strictly aerobic, Gram positive, motile, rod-shaped cells, 0.8–1.0 µm × 2.5–4.8 µm. The ellipsoidal spores are borne terminally and subterminally and swell the sporangia. Description is based upon study of a single isolate. Requires biotin or thiamin for growth. Grows on glucose yeast extract agar, producing colonies

that are spreading, smooth, shiny and red, with glossy, mucilaginous surfaces. The red pigment is endocellular and nondiffusible. Grows on routine media supplemented with yeast extract; biotin or thiamine required for growth. Growth in glucose-yeast extract broth is homogeneous. Catalase-negative or weakly positive. Nitrate is not reduced to nitrite. Casein, gelatin, and starch are hydrolyzed. Growth occurs between 34°C and 58°C, and the optimum temperature for growth is 45–48°C. No growth occurs in the presence of 5% NaCl. D-Fructose, D-glucose, D-mannitol, D-trehalose, and other carbohydrates are utilized as sole carbon sources according to Manachini et al. (1985), but Logan et al. (2002) were unable to reproduce these results.

Isolated from mushroom compost.

DNA G+C content (*mol%*): 57.0 ± 0.8 (HPLC).

Type strain: BT2, MIM 30.8.38, CIP 105255, CIP 105298, DSM 7064, HAMBI 2105, LMG 16910.

GenBank accession number (*16S rRNA gene*): AB112722, Z26921.

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