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Taxonomic Note

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# Emended descriptions of genera of the family *Halobacteriaceae*

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The family *Halobacteriaceae* currently contains 96 species whose names have been validly published, classified in 27 genera (as of September 2008). In recent years, many novel species have been added to the established genera but, in many cases, one or more properties of the novel species do not agree with the published descriptions of the genera. Authors have often failed to provide emended genus descriptions when necessary. Following discussions of the International Committee on Systematics of Prokaryotes Subcommittee on the Taxonomy of *Halobacteriaceae*, we here propose emended descriptions of the genera *Halobacterium*, *Haloarcula*, *Halococcus*, *Haloferax*, *Halorubrum*, *Haloterrigena*, *Natrialba*, *Halobiforma* and *Natronorubrum*.

The family *Halobacteriaceae* was established by Gibbons (1974) to accommodate the genera *Halobacterium* and *Halococcus*. At the time of writing (September 2008), the family contained 96 species whose names have been validly published, classified in 27 genera. Descriptions of the properties of these genera can be found in the original articles in which the establishment of the genera was proposed. The second edition of *Bergey's Manual of Systematic Bacteriology* (Grant *et al.*, 2001 and subsequent chapters) also provides much useful information.

Many novel species have been added to previously established genera in the past two decades, but authors have generally failed to determine whether the properties of the novel species agree with the published descriptions of the genera. Only in a few cases have emended genus descriptions been proposed, such as those for the genera *Halobacterium* (Kamekura & Dyall-Smith, 1995), *Natronorubrum* (Cui *et al.*, 2006a) and *Halorhabdus* (Antunes *et al.*, 2008).

In recent years, there has been a tendency to base the establishment of new genera of the *Halobacteriaceae* on 16S rRNA gene sequence-based phylogenetic trees rather than on true polyphasic taxonomy such as recommended for the family (Oren *et al.*, 1997). As a result, there are often few, if any, phenotypic properties that enable the discrimination of the genera within the family. The same is undoubtedly the case for other groups of prokaryotes. Statements found in some protologues of new genus descriptions like 'the genus constitutes a group that shares more than *x*% 16S rRNA gene sequence similarity' (McGenity & Grant, 2001; Hezayen *et al.*, 2002) are not very helpful when delineating genera based on a polyphasic approach.

Polar lipid composition has been used in the past to discriminate between different genera of the *Halobacteriaceae*, and certain lipid components were used as chemotaxonomic signatures for certain genera (Torreblanca *et al.*, 1986). Discovery of novel taxa and reclassification of existing taxa based on a system biased toward 16S rRNA gene sequences has now led to a situation in which polar lipid composition can no longer be considered as a suitable characteristic for certain genera. For example, most species of *Haloterrigena* possess the bi-sulfated diglycosyl diether lipid $S_2$-DGD-1 (1-*O*-[α-D-mannose-(2′,6′-$SO_3$H)-α-D-(1′→2′)-glucose]-2,3-di-*O*-phytanyl- or phytanyl sesterterpenyl-*sn*-glycerol) (*Haloterrigena longa*, *Htg. limicola*, *Htg. thermotolerans*, *Htg. salina*); however, $S_2$-DGD-1 cannot be considered a signature lipid of the genus, as *Haloterrigena hispanica* was reported to contain S-DGD (sulfated diglycosyl diether derivative of phosphatidylglycerol) instead (Romano *et al.*, 2007). The nature of the

Abbreviations: Me-PGP, methyl ester of phosphatidylglycerophosphate; PG, phosphatidylglycerol; PGS, phosphatidylglycerosulfate; S-DGD, sulfated diglycosyl diether derivative of PG; $S_2$-DGD, bis-sulfated diglycosyl diether derivative of PG; $S_2$-DGD-1, 1-*O*-[α-D-mannose-(2′,6′-$SO_3$H)-α-D-(1′→2′)-glucose]-2,3-di-*O*-phytanyl- or phytanyl sesterterpenyl-*sn*-glycerol.

A comparison of the properties of the nine genera for which emended descriptions are presented is available as supplementary material with the online version of this paper.

glycolipids of *Haloterrigena turkmenica*, the type species of the genus, has apparently never been ascertained. The polar lipid composition of the members of the genus *Haloterrigena* deserves an in-depth study to assess to what extent the lipid composition may support the 16S rRNA gene-based phylogeny. However, some genera (*Halobacterium*, *Haloferax*, *Haloarcula*) are still consistent as far as polar lipid composition is concerned, and this chemotaxonomic feature can be considered as an important taxonomic marker for genus delineation.

Evaluation of the G+C content of the genomic DNA shows many cases of genera with an unusually broad range reported: *Halobacterium* with 54.3–71.2 mol%, *Halorubrum* with 60.2–71.2 mol%, *Halococcus* with 59.5–67 mol% and *Haloterrigena* with 59.2–67 mol%. To what extent the wide differences may be due to different methods used in the analyses or may reflect true genetic differences within each genus remains to be assessed. Many species within the family contain large plasmids, representing a minor component DNA with a G+C content different from that of the chromosome (Grant *et al.*, 2001).

The International Committee on Systematics of Prokaryotes Subcommittee on the Taxonomy of *Halobacteriaceae* at its open meeting in Istanbul on 7 August 2008 (Oren & Ventosa, 2008) has discussed the problematic nature of many protologues of genera within the family, and decided that emended and corrected descriptions are necessary for a number of genera. After an exhaustive search, we propose to update the genus descriptions of some taxa and we here present emended descriptions of the genera *Halobacterium*, *Haloarcula*, *Halococcus*, *Haloferax*, *Halorubrum*, *Haloterrigena*, *Natrialba*, *Natrinema* and *Halobiforma*. The properties of these genera are compared in Supplementary Table S1, available in IJSEM Online.

## Emended description of the genus *Halobacterium* Elazari-Volcani 1957, 207[AL], emend. Larsen and Grant 1989, 2219, emend. Kamekura and Dyall-Smith 1995, 344

*Halobacterium* [Ha.lo.bac.te′ri.um. Gr. n. *hals*, *halos* the sea, salt; N.L. n. *bacterium* bacterium from Gr. n. *bakterion* a small rod; N.L. neut. n. *Halobacterium* salt (-requiring) bacterium].

This emended description is based on Kamekura & Dyall-Smith (1995), Grant (2001a), Gruber *et al.* (2004), Yang *et al.* (2006) and Yachai *et al.* (2008).

Cells are rod-shaped under optimal growth conditions, 0.5–1.2 × 1.0–6.0 μm, and stain Gram-negative. Cells are motile by tufts of polar flagella or by peritrichous flagella. Colonies are red or pink due to the presence of bacterioruberin carotenoids; purple retinal pigments may be present as well. Some strains possess gas vesicles. Cells lyse in distilled water. Oxidase-positive or -negative; catalase-positive. Extremely halophilic, with growth occurring in media containing 2.5–5.2 M NaCl; most strains grow best at 3.5–4.5 M NaCl. The optimum magnesium concentration varies between 0.05 and 0.6 M. Temperatures between 15 and 55 °C and pH between 5.2 and 8.5 may support growth. Chemo-organotrophic; amino acids are required for growth. Most are proteolytic. Grow by aerobic respiration. Many strains grow anaerobically by fermentation of arginine; some grow photoheterotrophically using the light-driven proton pump bacteriorhodopsin or by anaerobic respiration in the presence of nitrate. Some species reduce nitrate to nitrite. Sugars are poorly used, and no acid is formed in the presence of sugars. The major polar lipids are $C_{20}C_{20}$ glycerol diether derivatives of PG (phosphatidylglycerol), Me-PGP (methyl ester of phosphatidylglycerophosphate), PGS (phosphatidylglycerosulfate) and the glycolipids S-TGD-1 (1-*O*-[β-D-galactose-(3′-$SO_3$H)-(1′→6′)-α-D-mannose-(1′→2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), S-TeGD (1-*O*-[β-D-galactose-(3′-$SO_3$H)-(1′→6′)-α-D-mannose-(3′←1′)-α-D-galactofuranose)-(1′→2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol) and TGD-1 (1-*O*-[β-D-galactose-(1′→6′)-α-D-mannose-(1′→2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol). The DNA G+C content is between 54.3 and 71.2 mol%. The DNA is usually composed of a major component and a minor component (up 10–30 % of the total DNA) lower in G+C content than the major component. Isolated from rock salt, salt lakes, salted fish and fish products and salted hides. The type species is *Halobacterium salinarum*.

## Emended description of the genus *Haloarcula* Torreblanca *et al.* 1986, 573[VP]

*Haloarcula* [Ha.lo.ar′cu.la. Gr. n. *hals*, *halos* the sea, salt; L. fem. n. *arcula* small box; N.L. fem. n. *Haloarcula* salt (-requiring) small box].

Effective publication: Torreblanca, Rodriguez-Valera, Juez, Ventosa, Kamekura & Kates 1986, 98.

This emended description is based on the genus description by Torreblanca *et al.* (1986) and emendations based on Juez *et al.* (1986), Takashina *et al.* (1990), Ihara *et al.* (1997), Oren *et al.* (1999) and Yang *et al.* (2007).

Cells are short pleomorphic rods, with shapes ranging from almost regular rods to triangular and irregular shapes under optimal growth conditions, 0.2–1 × 2–5 μm, and stain Gram-negative. Most species are motile. Colonies are red or pink due to the presence of bacterioruberin carotenoids; retinal pigments may be present as well. Pigmentation does not vary with the salt concentration of the medium. Cells lyse in distilled water. Oxidase- and catalase-positive. Extremely halophilic, with growth occurring in media containing 2–5.2 M NaCl; most strains grow best at 2.5–3.5 M NaCl. The optimum magnesium concentration varies between 0.005 and 0.1 M. Temperatures between 20 and 55 °C and pH between 6.5 and 9 may support growth. Chemo-organotrophic; amino acids are not required for growth. Grow by aerobic respiration; some grow by anaerobic respiration in the presence of nitrate. All species reduce nitrate to nitrite and

produce acid from sugars. A wide range of substrates can be used as carbon and energy sources. Most are lipolytic (Tween 40) and produce $H_2S$ from cysteine. The major polar lipids are $C_{20}C_{20}$ glycerol diether derivatives of PG, Me-PGP, PGS and TGD-2 (1-*O*-[*β*-D-glucose-(1′→6′)-α-D-mannose-(1′→2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol). All species have at least two different copies of the 16S rRNA gene. The DNA G+C content is between 60.1 and 65 mol%. The DNA may contain a major and a minor component. Isolated from solar salterns and salt lakes. The type species is *Haloarcula vallismortis*.

## Emended description of the genus *Halococcus* Schoop 1935, 817[AL]

*Halococcus* [Ha.lo.coc′cus Gr. n. *hals*, *halos* the sea, salt; N.L. n. *coccus* coccus from Gr. n. *kokkos* a berry; N.L. masc. n. *Halococcus* salt (-requiring) coccus].

This emended description is based on the genus description by Grant (2001b) and emendations based on Stan-Lotter *et al.* (2002), Namwong *et al.* (2007) and Wang *et al.* (2007).

Cells are cocci, occurring in pairs, tetrads, sarcina packets or irregular clusters, 0.6–1.5 μm in diameter. Most cells stain Gram-negative. Non-motile. Colonies are small and red or pink due to the presence of bacterioruberin carotenoids; pigmentation may be reduced at high pH. Cells do not lyse in distilled water or in the presence of *N*-laurylsarcosine. Oxidase-positive or -negative; catalase-positive. Extremely halophilic, with growth occurring in media containing 1.7–5.2 M NaCl; most strains grow best at 3–4.5 M NaCl. The optimum magnesium concentration varies between 0.001 and 0.04 M. Temperatures between 15 and 50 °C and pH between 4.0 and 9.5 may support growth. Chemo-organotrophic; many species require amino acids for growth. Strictly aerobic. Some species reduce nitrate to nitrite and some grow on sugars with or without production of acids. The major polar lipids are $C_{20}C_{20}$ and sometimes $C_{20}C_{25}$ glycerol diether derivatives of PG, Me-PGP and S-DGD. The DNA G+C content is between 59.5 and 67 mol%. The DNA may contain a major and a minor component. Isolated from salt lakes, crude sea salt, seawater, rock salt and fermented fish sauce. The type species is *Halococcus morrhuae*.

## Emended description of the genus *Haloferax* Torreblanca *et al.* 1986, 573[VP]

*Haloferax* [Ha.lo.fe′rax. Gr. n. *hals*, *halos* salt; L. neut. adj. *ferax* fertile; N.L. neut. n. *Haloferax* salt (-requiring) and fertile].

Effective publication: Torreblanca, Rodriguez-Valera, Juez, Ventosa, Kamekura & Kates 1986, 98.

This emended description is based on the genus description by Torreblanca *et al.* (1986) and emendations based on Juez *et al.* (1986), Asker & Ohta (2002), Gutierrez *et al.* (2002), Elshahed *et al.* (2004), Xu *et al.* (2007a) and Allen *et al.* (2008).

Cells are extremely pleomorphic, most commonly flattened discs or cups under optimal growth conditions, sometimes elongated, 0.5–3 × 0.4–12 μm, and stain Gram-negative. Some species are motile; motility is often difficult to observe. Colonies have a mucoid appearance. Colonies are red–purple to pink due to the presence of bacterioruberin carotenoids; pigmentation often depends on the salt concentration of the medium. Some strains possess gas vesicles. Cells lyse in distilled water. Most isolates are oxidase-positive, but oxidase-negative and oxidase-variable species have been reported; catalase-positive. Extremely halophilic, with growth occurring in media containing 1.0–5.1 M NaCl; most strains grow best at 2.5 M NaCl. The optimum magnesium concentration varies between 0.001 and 1.2 M. Temperatures between 20 and 55 °C and pH between 5 and 9 may support growth. Chemo-organotrophic; amino acids are not required for growth. Grow by aerobic respiration; some grow by anaerobic respiration in the presence of nitrate. Most species reduce nitrate to nitrite. Acid is produced from sugars. A wide range of substrates can be used as carbon and energy sources. Polyhydroxyalkanoates are accumulated under certain conditions. The polar lipids are characterized by the presence of $C_{20}C_{20}$ glycerol diether derivatives of PG, Me-PGP, S-DGD-1 (1-*O*-[α-D-mannose-(6′-$SO_3H$)-(1′→2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol) and DGD-1 (1-*O*-[α-D-mannose-(1′→2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol) and the absence of PGS. The DNA G+C content is between 59.1 and 65.5 mol%. The DNA may contain a major and a minor component. Isolated from solar salterns and salt lakes. The type species is *Haloferax volcanii*.

## Emended description of the genus *Halorubrum* McGenity and Grant 1996, 362[VP]

*Halorubrum* [Ha.lo.ru′brum. Gr. n. *hals*, *halos* salt; L. neut. adj. *rubrum* red; N.L. neut. n. *Halorubrum* salt (-requiring) and red].

Effective publication: McGenity & Grant 1995, 241.

This emended description is based on the description given by McGenity & Grant (2001) and emendations based on Lizama *et al.* (2002), Fan *et al.* (2004), Feng *et al.* (2004, 2005), Ventosa *et al.* (2004), Castillo *et al.* (2006, 2007), Cui *et al.* (2006b), Kharroub *et al.* (2006), Xu *et al.* (2007b) and Hu *et al.* (2008).

Cells are rod-shaped or pleomorphic under optimal growth conditions, 0.3–1.2 × 0.6–12 μm, and stain Gram-negative or Gram-variable. Some species are motile. Colonies are red–orange due to the presence of bacterioruberin carotenoids, but some species may be almost colourless; retinal pigments may be present as well. Some strains possess gas vesicles. Cells lyse in distilled water. Oxidase- and catalase-positive. Extremely halophilic, with growth

occurring in media containing 1.0–5.2 M NaCl; the optimum magnesium concentration varies between 0.005 and 0.6 M. Temperatures between 4 and 58 °C may support growth. Neutrophilic or alkaliphilic with pH optima at 9–10 and growth up to pH 10.5. Chemo-organotrophic, aerobic. Many species reduce nitrate to nitrite. Some species grow on single carbon sources. Most species use sugars, some with the production of acids. The major polar lipids are $C_{20}C_{20}$ and sometimes $C_{20}C_{25}$ glycerol diether derivatives of PG, Me-PGP, PGS and a sulfated glucosyl mannosyl diether such as S-DGD-3 (1-*O*-[α-D-mannose-(2′-$SO_3H$)-α-D-(1′→4′)-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol). Alkaliphilic species lack PGS and glycolipids. The DNA G+C content is between 60.2 and 71.2 mol%. The DNA may contain a major and a minor component. Isolated from marine salterns, salt lakes, coastal sabkhas, hypersaline soda lakes and saline soils. The type species is *Halorubrum saccharovorum*.

## Emended description of the genus *Haloterrigena* Ventosa *et al.* 1999, 135[VP]

*Haloterrigena* [Ha.lo.ter.ri′ge.na. Gr. n. *hals*, *halos* the sea, salt; L. fem. adj. *terrigena* born from the earth; N.L. fem. adj. *Haloterrigena* salt (-requiring) and born from the earth].

This emended description is based on the genus description by Ventosa *et al.* (1999) and emendations based on Xu *et al.* (2005b), Cui *et al.* (2006c), Romano *et al.* (2007) and Gutiérrez *et al.* (2008).

Cells are coccoid or oval or rod-shaped under optimal growth conditions, 0.4–1.2 × 1.6–13 μm, and stain Gram-negative. Some species become coccoid in stationary cultures. Non-motile. Colonies are coloured light pink due to the presence of bacterioruberin carotenoids. Cells lyse in distilled water. Oxidase- and catalase-positive. Extremely halophilic, with growth occurring in media containing 1.7–5.1 M NaCl. The optimum magnesium concentration varies between 0 and 0.7 M. Temperatures between 30 and 60 °C and pH between 6.5 and 9 may support growth. Chemo-organotrophic, aerobic. Some species reduce nitrate to nitrite. Some species grow on single carbon sources. Most species use sugars, some with the production of acids. The major polar lipids are $C_{20}C_{20}$ and $C_{20}C_{25}$ glycerol diether derivatives of PG, Me-PGP and a glycolipid [$S_2$-DGD (bis-sulfated diglycosyl diether derivative of PG) or S-DGD]. PGS is absent. The DNA G+C content is between 59.2 and 67 mol%. Isolated from salt lakes, saltern crystallizer ponds and saline soil. The type species is *Haloterrigena turkmenica*.

## Emended description of the genus *Natrialba* Kamekura and Dyall-Smith 1995, 625[VP], emend. Hezayen *et al.* 2001

*Natrialba* [Na.tri.al′ba. Gr. n. *natron* derived from Arabic *natrun* soda (sodium carbonate); L. adj. *alba* white; L. fem. n. *Natrialba* sodium white; referring to the high sodium ion requirement and the pigmentless colonies of the type species].

Effective publication: Kamekura & Dyall-Smith 1995, 347.

This emended description is based on the genus description by Kamekura & Dyall-Smith (1995) and emendations based on Hezayen *et al.* (2001) and Xu *et al.* (2001).

Cells are rods, cocci or coccobacilli, sometimes occurring in tetrads, 0.3–1.0 × 1.0–6.0 μm, and stain Gram-negative. Some species lack pigmentation, while others are pigmented red by bacterioruberin carotenoids. Cells lyse in distilled water. Oxidase- and catalase-positive. Extremely halophilic, with growth occurring in media containing 1.6–5.3 M NaCl. Temperatures between 20 and 60 °C may support growth. Neutrophilic or alkaliphilic with growth up to pH 10.5–11. Chemo-organotrophic, aerobic. No growth on single substrates. Most species reduce nitrate to nitrite. Neutrophilic species produce acids from sugars. The major polar lipids are $C_{20}C_{20}$ and $C_{20}C_{25}$ glycerol diether derivatives of PG and Me-PGP; neutrophilic species possess $S_2$-DGD in addition. The DNA G+C content is between 60.3 and 64.3 mol%. The DNA may contain a major and a minor component. Isolated from salterns, beach sands, salty soil and soda lakes. The type species is *Natrialba asiatica*.

## Emended description of the genus *Halobiforma* Hezayen *et al.* 2002, 2278[VP]

*Halobiforma* (Ha.lo.bi.for′ma. Gr. n. *hals*, *halos* salt; L. prefix *bi* two; L. n. *forma* form; N.L. n. *Halobiforma* the halophile with two different shapes).

This emended description is based on the genus description by Hezayen *et al.* (2002) and emendations based on Xu *et al.* (2005a).

Cells are rod-shaped, coccoid or pleomorphic, 0.4–1.5 × 1.25–8 μm, and stain Gram-negative. Cells are motile. Colonies are red or pink due to the presence of bacterioruberin carotenoids. Cells lyse in distilled water. Oxidase- and catalase-positive. Extremely halophilic, with growth occurring in media containing 1.7–5.2 M NaCl; most strains grow best at 2.6–4.3 M NaCl. The optimum magnesium concentration varies between 0 and 0.5 M. Temperatures between 26 and 44 °C may support growth. Neutrophilic or alkaliphilic with growth up to pH 10.5. Chemo-organotrophic, grow by aerobic respiration; some species grow by anaerobic respiration in the presence of nitrate. Some species reduce nitrate to nitrite. No growth on single substrates. Some produce acids from sugars. The major polar lipids are $C_{20}C_{20}$ and $C_{20}C_{25}$ glycerol diether derivatives of PG and Me-PGP. Glycolipids may be present in some species. When present, the glycolipids are a triglycosyl diether and its sulfated derivative. The DNA G+C content is between 64.9 and 66.9 mol%. Isolated from salt lakes and saline soils. The type species is *Halobiforma haloterrestris*.

### Emended description of the genus *Natronorubrum* Xu *et al.* 1999, 265$^{VP}$, emend. Cui *et al.* 2006a

*Natronorubrum* [Na.tro.no.rub′rum. Gr. n. *natron* derived from Arabic *natrun* soda (sodium carbonate); L. neut. adj. *rubrum* red; N.L. neut. n. *Natronorubrum* the red of soda].

This emended description is based on the genus description by Xu *et al.* (1999), and emendations based on Cui *et al.* (2006a).

Cells are pleomorphic, flat, triangular, square or disc-shaped under optimal growth conditions, 0.8–3.6 μm in size, and stain Gram-negative. Cells are motile or non-motile. Colonies are red–purple due to the presence of bacterioruberin carotenoids. Cells lyse in distilled water. Oxidase- and catalase-positive. Extremely halophilic, with growth occurring in media containing 2.1–5.2 M NaCl. Temperatures between 20 and 55 °C support growth. Neutrophilic or alkaliphilic with growth up to pH 11. Sugars are metabolized, in some cases with formation of acids. The major polar lipids are $C_{20}C_{20}$ and $C_{20}C_{25}$ glycerol diether derivatives of PG and Me-PGP. Some species may also contain TGD-1 and additional, unidentified glycolipids. The DNA G+C content is between 59.9 and 61.2 mol%. Isolated from salt and soda lakes. The type species is *Natronorubrum bangense*.

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