# 7 The Family *Halobacteriaceae*

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Genus *Halorhabdus* Wainø, Tindall, and Ingvorsen 2000, 188$^{VP}$; emend. Antunes, Taborda, Huber, Moissl, Nobre, and Da Costa 2008, 218 ............. 99
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Genus *Halorubrum* McGenity and Grant 1996, 362$^{VP}$; Effective Publication: McGenity and Grant 1995, 241; emend. Oren, Arahal, and Ventosa 2009, 639 .................................. 99
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Genus *Halosimplex* Vreeland, Rosenzweig, Straight, Krammes, Dougherty, and Kamekura 2002, 450 (Validation list 92, 2003, 936$^{VP}$) ..................... 100
Genus *Halostagnicola* Castillo, Gutiérrez, Kamekura, Xue, Ma, Cowan, Jones, Grant, and Ventosa 2006, 1521$^{VP}$ ................................ 100

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Genus *Haloterrigena* Ventosa, Gutiérrez, Kamekura, and Dyall-Smith 1999b, 135$^{\mathrm{VP}}$; emend. Oren, Arahal, and Ventosa 2009, 640 ....... 100
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Genus *Natrialba* Kamekura and Dyall-Smith 1996, 625$^{\mathrm{VP}}$; Effective Publication: Kamekura and Dyall-Smith 1995, 347 (Validation list 57); emend. Oren, Arahal, and Ventosa 2009, 640 .................................. 101
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Genus *Natronolimnobius* Itoh, Yamaguchi, Zhou, and Takashina 2005, 1744$^{\mathrm{VP}}$ (Validation list no. 105); Effective Publication: Itoh, Yamaguchi, Zhou, and Takashina 2005, 114 ..................... 102
Genus *Natronomonas* Kamekura, Dyall-Smith, Upasani, Ventosa, and Kates 1997, 856$^{\mathrm{VP}}$, emend. Burns, Janssen, Itoh, Minegishi, Usami, Kamekura, and Dyall-Smith 2010, 1175 ........... 103
Genus *Natronorubrum* Xu, Zhou, and Tian 1999, 265$^{\mathrm{VP}}$; emend. Cui, Tothy, Feng, Zhou, and Liu 2006, 1517; emend. Oren, Arahal, and Ventosa 2009, 641 .................................. 103
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## Abstract

The family *Halobacteriaceae*, first proposed by Gibbons in 1974, is affiliated with the archaeal phylum Euryarchaeota. Currently (August 2012) it encompasses 40 genera: *Halobacterium* [type genus], *Haladaptatus, Halalkalicoccus, Halarchaeum, Halarchaeobius, Haloarcula, Halobaculum, Halobellus, Halobiforma, Halococcus, Haloferax, Halogeometricum, Halogranum, Halolamina, Halomarina, Halomicrobium, Halonotius, Halopelagius, Halopenitus, Halopiger, Haloplanus, Haloquadratum, Halorhabdus, Halorientalis, Halorubrum, Halosarcina, Halosimplex, Halostagnicola, Haloterrigena, Halovenus, Halovivax, Natrialba, Natrinema, Natronoarchaeum, Natronobacterium, Natronococcus, Natronolimnobius, Natronomonas, Natronorubrum*, and *Salarchaeum*, with a total of 137 species. All members of the family have a high requirement for salt, and most grow optimally at salt concentrations above 150–200 g/l. Most species are pigmented red-pink by carotenoid pigments and have an aerobic chemoheterotrophic metabolism. Some have the ability to grow anaerobically by fermentation, anaerobic respiration, or using bacteriorhodopsin to absorb light as an energy source.

## Taxonomy, Historical and Current

### Family *Halobacteriaceae* Gibbons 1974, 269$^{\mathrm{AL}}$

*Ha.lo.bac.te.ri.a.ce'ae.* N.L. neut. n. *Halobacterium*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Halobacteriaceae*, the *Halobacterium* family.

Type genus: *Halobacterium*.

The mol% G + C of the DNA varies between 46.9 and 71.2.

The family *Halobacteriaceae* (order *Halobacteriales*; Grant et al. 2001a) was circumscribed on the basis of the high salt requirement of its members, their physiological and chemotaxonomic features, and their phylogenetic affiliation with the Euryarchaeota phylum of the Archaea (Grant et al. 2001b). At the time of writing (August 2012), the family contained 40 genera with a total of 137 species whose names have standing in the nomenclature (➲ *Tables 7.1*, ➲ *7.2*, ➲ *7.3*, ➲ *7.4*, ➲ *7.5*, ➲ *7.6*, ➲ *7.7*, ➲ *7.8*, ➲ *7.9*, ➲ *7.10*, ➲ *7.11*, ➲ *7.12*, ➲ *7.13*, ➲ *7.14*, ➲ *7.15*, ➲ *7.16*, ➲ *7.17*, ➲ *7.18*, ➲ *7.19*, ➲ *7.20*, ➲ *7.21*, and ➲ *7.22*): *Halobacterium* [type genus; three-letter abbreviation *Hbt.*] (3 species), *Haladaptatus* (*Hap.*) (3 species), *Halalkalicoccus* (*Hac.*) (2 species), *Halarchaeum* (*Hla.*) (1 species), *Halarchaeobius* (*Hab.*) (1 species), *Haloarcula* (*Har.*) (9 species), *Halobaculum* (*Hbl.*) (1 species), *Halobellus*

**Table 7.1**

**Comparison of selected characteristics of the members of the genera *Halobacterium*, *Haladaptatus*, and *Halalkalicoccus***

| Genus | *Halobacterium*[a] | | | *Haladaptatus* | | | *Halalkalicoccus* | |
|---|---|---|---|---|---|---|---|---|
| Species | *Hbt. salinarum*[a] | *Hbt. jilantaiense*[b] | *Hbt. noricense*[c] | *Hap. paucihalophilus*[d] | *Hap. cibarius*[e] | *Hap. litoreus*[f] | *Hac. tibetensis*[g] | *Hac. jeotgali*[h] |
| Older names | *Halobacterium salinarium*; includes *Halobacterium halobium* and *Halobacterium cutirubrum* | | | | | | | |
| Type strain | ATCC 33171<br>CIP 104033<br>DSM 3754<br>JCM 8978<br>NBRC 102687<br>NCIMB 764<br>NRC 34002<br>VKM B-1769 | CGMCC 1.5337<br>JCM 13558 | ATCC BAA-852<br>DSM 15987<br>JCM 15102<br>NCIMB 13967 | ATCC BAA-1313<br>DSM 18195<br>JCM 13897<br>KCTC 4006 | DSM 19505<br>JCM 15962 | CGMCC 1.7737<br>JCM 15771 | AS 1.3240<br>JCM 11890 | CECT 7217<br>DSM 18796<br>JCM 14584<br>KCTC 4019 |
| Cell shape | Rods | Slender rods | Rods | Cocci-coccobacilli | Cocci-coccobacilli | Cocci | Cocci | Cocci |
| Cell size (μm) | 0.5–1.0 × 1.0–6.0 | 0.5–1.0 × × 1.0–3.0 | 1.2–2.0 | 1.2 | 1.0 | 1.0–1.5 | 1.0–1.5 | 1.0–1.5 |
| Motility | + | NR | + | – | + | – | – | – |
| Colony color | Pink | Red | Light red | Pink | Pink | Pink | Orange | Red |
| NaCl range for growth and optimum (%) | 18–30 (Opt. 20–25) | 16–30 (Opt. 18–20) | >12.5 (Opt. 15.0-17.5) | 5–30 (Opt. 18) | 10–0 (Opt. 15) | 10–30 (Opt. 30) | 8–30 (Opt. 20) | 10–30 (Opt. 5) |
| Lysis in distilled water | + | + | + | – | – | – | – | – |
| Magnesium requirement and optimum (M) | 0.05–0.1 | 0.05–0.3 (Opt. 0.1–0.2) | Opt. 0.7–0.8 | > 0.005 | >0.005 (Opt. 0.02) | >0.05 | – | NR |
| pH range for growth and optimum | 5.5–8.0 | 5.5–8.5 (Opt. 7.0–7.5) | 5.2–7.0 | 5.0–7.5 (Opt. 6.0–6.5) | 6.0–8.0 (Opt. 7.0) | 6.0–8.5 (Opt. 7.0) | 8.0–10.5 (Opt. 9.5–10.0) | 6.5–9.5 (Opt. 7.0) |
| Temperature range for growth and optimum (°C) | 20–55 (Opt. 50) | 22–55 (Opt. 40) | 28–50 (Opt. 37–45) | 25–45 (Opt. 25–30) | 15–50 (Opt. 37) | 25–55 (Opt. 37–40) | 23–47 (Opt. 40) | 21–50 (Opt. 37–45) |

**Table 7.1 (continued)**

| Genus | *Halobacterium*[a] | | | *Haladaptatus* | | | *Halalkalicoccus* | |
|---|---|---|---|---|---|---|---|---|
| **Species** | *Hbt. salinarum*[a] | *Hbt. jilantaiense*[b] | *Hbt. noricense*[c] | *Hap. paucihalophilus*[d] | *Hap. cibarius*[e] | *Hap. litoreus*[f] | *Hac. tibetensis*[g] | *Hac. jeotgali*[h] |
| Organic substrates used | Glyc | Glyc | Glyc (w) Star (w) | Acet Citr Fruc Fuma Gala Gluc Glyc Mala Manni Pyru Sucr Treh Xylo | Acet Form Fruct Lacto Gluc Sucr | Acet Fuma Gala Gluc Glyc Lact Malt Mann Manni Pyru Star Sucr | Acet Fruc Gluc Lacto Malt Manni Sorb Succ | Acet Citr Gluc Lacto Sucr |
| Acid produced from | – | – | – | Fruc Gala Gluc Glyc Manni Star Sucr Xylo | Gluc Sucr | Gala Gluc Glyc Malt Star Sucr | – | NR |
| Organic substrates not used | Gala Gluc Malt Sucr Xylo | Fruc Gala Gluc Lacto Malt Mann Manni Ribo Sorbi Sucr Xylo | Gala Gluc Malt Sucr Xylo | Dulc Lacto Sorbi Succ | Citr Manni | Fruc Lacto Mala Sorb Succ Ribo Xylo | Arab Gala Mann Raff Rham Ribo Sucr Xylo | Fruc |
| Indole from typtophan | + | + | NR | + | + | + | – | NR |
| Starch hydrolysis | – | – | – | + | – | + | – | NR |
| Gelatin liquefaction | + | + | – | NR | + | + | – | NR |
| Nitrate reduction | – | + | – | – | – | + | + | – |
| Polar lipids | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-TGD-1, S-TeGD, TGD-1 | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-TGD-1, S-TeGD, TGD-1 | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-TeGD, TGD-1 | PG, PGP-Me, PGS, two unidentified glycolipids | PG, PGP-Me, two unidentified glycolipids | PG, PGP-Me, PGS, three glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me | PG, PGP-Me |
| Respiratory quinones | MK-8, MK-8($H_2$), traces of MK-7($H_2$), MK-7, MK-6 | NR | MK-8, MK-8($H_2$), traces of MK-7($H_2$), MK-9 | NR | NR | NR | MK-8, small amounts of MK-8($H_2$) | NR |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Sensitivity to antibiotics | Sensitive: Ani Nov | Sensitive: Ani Nov | Sensitive: Ani Nov | Sensitive: Ani Aph Bac Nov | Sensitive: Ani Aph Chl Rif | Sensitive: Bac Nov Rif | Sensitive: Chl (slight) Nov Rif | Sensitive: Ani Aph Nov |
| | Resistant: Amp Chl Gen Kan Str Tet Van | Resistant: Amp Bac Chl Ery Gen Kan Pen Rif Str Tet | Resistant: Amp Bac Chl Gen Kan Str Tet Van | Resistant: Amp Chl Ery Neo Pen | Resistant: Amp Ery Kan Pol Str | Resistant: Amp Chl Cip Ery Kan Neo Pen Tet | Resistant: Amp Bac Neo Pen Pol Str Tet | Resistant: Amp Bac Chl Ery Pen |
| G + C content of DNA (mol%) | 66–70.9 (major component);<br>57–60 (minor component) | 64.2 | 54.3–54.5 | 60.5 | 56.5 | 54.0 | 61.5 | 63.2 |
| Sample source and site | Salt lakes, salted food products | Salt lake, Inner Mongolia | Permian rock salt, Austria | Low-salt sulfidic spring, Oklahoma | Korean salt-fermented shellfish | Saltern, China | Salt lake, Tibet | Shrimp jeotgal (Korean food) |

Data taken from:

[a] Grant (2001a)

[b] Yang et al. (2006)

[c] Gruber et al. (2004)

[d] Savage et al. (2007)

[e] Roh et al. (2010a)

[f] Cui et al. (2010a)

[g] Xue et al. (2005)

[h] Roh et al. (2007a)

Additional data on growth substrates and other properties can be found in the original species descriptions

General notes:

Most data were derived from the original species descriptions as cited; other sources may provide different data

Abbreviations of sugars, organic acids and other growth substrates: *Acet* Acetate, *Arab* Arabinose, *Benz* Benzoate, *Buta* Butanol; *Buty* Butyrate; *Cell* Cellobiose, *Citr* Citrate, *Dulc* Dulcitol, *Etha* Ethanol, *Form* Formate, *Fruc* Fructose, *Fuco* Fucose, *Fuma* Fumarate, *Gala* Galactose, *Gluc* Glucose, *Glyc* Glycerol, *Lact* Lactate, *Lacto* Lactose, *Mala* Malate; *Malt* Maltose, *Mann* Mannose, *Manni* Mannitol, *Meli* Melibiose, *Oxal* Oxalate, *Prop* Propionate, *Pyru* Pyruvate, *Raff* Raffinose, *Ribo* Ribose; *Rham* Rhamnose, *Sorb* Sorbose, *Sorbi* Sorbitol, *Star* Starch, *Succ* Succinate, *Sucr* Sucrose, *Treh* Trehalose, *Xylo* Xylose

Abbreviation of lipids: *PG* phosphatidyl glycerol, *PGP-Me* methyl ester of phosphatidyl glycerophosphate, *PGS* phosphatidyl glycerosulfate, *DGD* diglycosly diether lipid, *S-DGD* sulfated diglycosyl diether lipid, $S_2$-*DGD* bis-sulfated diglycosyl diether lipid, *TGD* triglycosyl diether lipid, *S-TGD* sulfated triglycosyl diether lipid, *S-TeGD* sulfated tetraglycosyl diether lipid.

Abbreviations of quinones: *DMK* dimethylated menaquinone, *MMK* monomethylated menaquinone, *MK* menaquinone

Abbreviations of antibiotics: *Amp* Ampicillin, *Ani* Anisomycin, *Aph* Aphidicolin, *Bac* Bacitracin, *Chl* Chloramphenicol, *Cip* Ciprofloxacin, *Ery* Erythromycin, *Gen* Gentamicin, *Kan* Kanamycin, *Neo* Neomycin, *Nor* Norfloxacin, *Nov* Novobiocin, *Pen* Penicillin, *Pol* Polymyxin, *Rif* Rifampicin, *Str* Streptomycin, *Tet* Tetracycline, *Van* Vancomycin

*NR* not reported; v, variable, depending on growth conditions; w, weakly positive

**Table 7.2**

**Comparison of selected characteristics of the members of the genera *Halarchaeum*, *Haloarchaeobius*, *Halobaculum*, and *Halobellus***

| Genus | *Halarchaeum* | *Haloarchaeobius* | *Halobaculum* | *Halobellus* | | |
|---|---|---|---|---|---|---|
| Species | *Hla. acidiphilum*[a] | *Hab. iranensis*[b] | *Hbl. gomorrense*[c] | *Hbs. clavatus*[d] | *Hbs. limi*[e] | *Hbs. salinus*[e] |
| Type strain | CECT 7534<br>DSM 22442<br>JCM 16109 | IBRC-M 10013<br>KCTC 4048 | ATCC 700876<br>DS2807<br>DSM 9297<br>JCM 9908 | CGMCC 1.10118<br>JCM 16424 | CGMCC 1.10331<br>JCM 16811 | CGMCC 1.10710<br>DSM 18730<br>JCM 14359 |
| Cell shape | Pleomorphic, discs and triangular shapes | Rods | Rods | Rods | Pleomorphic | Pleomorphic |
| Cell size (μm) | ~2 | 1.5–2.0 × 3–7 | 0.5–1.0 × 5–10 | ~0.5 × 1.0–1.6 | NR | NR |
| Motility | − | + | + (w) | + | + | + |
| Colony color | Non-pigmented | Orange-red | Red | Red | Red | Red |
| NaCl range for growth and optimum (%) | 18–30 (Opt. 21–24) | 12–30 (Opt. 20) | > 6 (Opt. 9–12) | 10–30 (Opt. 15) | 8–30 (Opt. 15–23) | 15–30 (Opt. 20) |
| Lysis in distilled water | + | + | + | NR | + | + |
| Magnesium requirement and optimum (M) | >0.001 | −(Opt. 0.2) | Opt. 0.6–1.0 | Opt. 0.05 | −(Opt. 0–0.1) | >0.01 (Opt. 0.05) |
| pH range for growth and optimum | 4.0–6.0 (Opt. 4.4–4.5) | 6.0–8.0 (Opt. 7.5) | 5.5–8.0 (Opt. 6.0–7.0) | 5.5–9.0 (Opt. 7.0–7.5) | 5.5–9.5 (Opt. 7.0) | 5.5–9.5 (Opt. 7.0–7.5) |
| Temperature range for growth and optimum (°C) | 15–45 (Opt. 37) | 25–50 (Opt. 40) | Up to 45 (Opt. 40) | 20–50 (Opt. 37) | 25–55 (Opt. 45) | 25–45 (Opt. 37) |
| Organic substrates used | Arab Cello Fruc Gala Gluc Glyc Raff Sucr Xylo | Fruc Gala Gluc Lacto Malt | Gala Gluc Glyc Lact Malt Sucr Star Treh Xylo | Fuma Gala Gluc Glyc Lact Lacto Mala Malt Mann Pyru Succ Sucr | Gala Gluc Glyc Lact Lacto Malt Mann Manni Pyru Sorbi Sucr | Citr Gluc Glyc Lact Mala Pyru Sorbi Sucr |
| Acid produced from | NR | Gluc Malt | Gala Gluc Glyc Malt Star Sucr Treh Xylo | Gala Gluc Lacto Malt Mann Sucr | Gala Gluc Lacto Mann Sucr | Gala Gluc Lacto Mann Sucr |
| Organic substrates not used | Citr Lacto Malt Manni Ribo Sorbi Treh | Arab Manni Ribo Sucr | Acet Arab Citr Lacto Manni Prop Ribo Sorbi Succ | Fruc Manni Ribo Sorb Sorbi Xylo | Acet Citr Fruc Fuma Mala Ribo Sorb Succ Xylo | Acet Gala Fruc Fuma Lacto Malt Mann Ribo Sorb Succ Xylo |
| Indole from typtophan | − | − | − | − | − | − |
| Starch hydrolysis | − | − | + | − | − | − |
| Gelatin liquefaction | − | + | − | − | − | − |
| Nitrate reduction | − | − | + | + | + | − |

**Table 7.2 (continued)**

| Genus | *Halarchaeum* | *Haloarchaeobius* | *Halobaculum* | *Halobellus* | | |
|---|---|---|---|---|---|---|
| Species | *Hla. acidiphilum*[a] | *Hab. iranensis*[b] | *Hbl. gomorrense*[c] | *Hbs. clavatus*[d] | *Hbs. limi*[e] | *Hbs. salinus*[e] |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, and 4 unidentified glycolipids | PG, PGP-Me, PGS, 3 unidentified glycolipids, 1 minor phospholipid | PG, PGP-Me, S-DGD-1 | PG, PGP-Me, PGS, S-DGD-1, minor amounts of other glycolipids | PG, PGP-Me, PGS, S-DGD-1, DGD-1 three minor unidentified glycolipids | PG, PGP-Me, PGS, S-DGD-1, DGD-1, one minor unidentified glycolipid |
| Respiratory quinones | NR | MK-8(II-$H_2$) | NR | NR | NR | NR |
| Sensitivity to antibiotics | Sensitive: Ani Bac Nov Rif Tet | Sensitive: Bac Nov Rif | Sensitive: Ani Bac Nov | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Bac Nov Rif | Sensitive: Ani Bac Kan Nor Nov Rif |
| | Resistant: Amp Chl Ery Kan Neo Pen | Resistant: Amp Chl Ery Kan Neo Pen Str Tet | Resistant: Amp Chl Kan Neo Pen Str | Resistant: Amp Chl Ery Kan Neo Nor Pen Tet | Resistant: Amp Chl Cip Ery Kan Neo Nor Pen Str Tet | Resistant: Amp Chl Cip Ery Neo Pen Str Tet |
| G+C content of DNA (mol %) | 61.4 | 67.7 | 70 | 61.5–62.4 | 69.2 | 67.0 |
| Sample source and site | Australian solar salt imported to Japan | Salt lake, Iran | The Dead Sea | Solar saltern, China | Solar saltern, China | Solar saltern, Australia |

Data taken from:
[a] Minegishi et al. (2010b)
[b] Makhdoumi-Kakhki et al. (2012b)
[c] Oren (2001), Oren et al. (1995)
[d] Cui et al. (2011d)
[e] Cui et al. (2012a)
Additional data on growth substrates and other properties can be found in the original species descriptions

(*Hbs.*) (3 species), *Halobiforma* (*Hbf.*) (3 species), *Halococcus* (Hcc.) (7 species), *Haloferax* (*Hfx.*) (11 species), *Halogeometricum* (*Hgm.*) (2 species), *Halogranum* (*Hgn.*) (4 species), *Halolamina* (*Hlm.*) (1 species), *Halomarina* (*Hmr.*) (1 species), *Halomicrobium* (*Hmc.*) (3 species), *Halonotius* (*Hns.*) (1 species), *Halopelagius* (*Hpl.*) (1 species), *Halopenitus* (*Hpt.*) (1 species), *Halopiger* (*Hpg.*) (2 species), *Haloplanus* (*Hpn.*) (3 species), *Haloquadratum* (*Hqr.*) (1 species), *Halorhabdus* (*Hrd.*) (2 species), *Halorientalis* (*Hos.*) (1 species), *Halorubrum* (*Hrr.*) (25 species), *Halosarcina* (*Hsn.*) (2 species), *Halosimplex* (*Hsx.*) (1 species), *Halostagnicola* (*Hst.*) (3 species), *Haloterrigena* (*Htg.*) (9 species), *Halovenus* (*Hvn.*) (1 species), *Halovivax* (*Hvx.*) (2 species), *Natrialba* (*Nab.*) (7 species), *Natrinema* (*Nnm.*) (7 species), *Natronoarchaeum* (*Nac.*) (1 species), *Natronobacterium* (*Nbt.*) (1 species), *Natronococcus* (*Ncc.*) (3 species), *Natronolimnobius* (*Nln.*) (2 species), *Natronomonas* (*Nmn.*) (2 species), *Natronorubrum* (*Nrr.*) (5 species), and *Salarchaeum* (*Sar.*) (1 species). The three-letter abbreviations for the genus names within the family have been endorsed by the International Committee on Systematics of Prokaryotes Subcommittee on the Taxonomy of *Halobacteriaceae* (http://www.the-icsp.org/taxa/halobacterlist.htm; accessed October 29, 2012). At the time of writing, descriptions were in press of *Hla. salinum* sp. nov. (Yamauchi et al. 2012) and *Hbl. magnesiiphilum* (Shimoshige et al. 2012). The names *Hrr. sfaxense* (Trigui et al. 2011) and *Salinarchaeum laminariae* gen. nov., sp. nov. (Cui et al. 2011c) were effectively published, but were not yet validated. These taxa were not included in ➜ *Tables 7.1*, ➜ *7.2*, ➜ *7.3*, ➜ *7.4*, ➜ *7.5*, ➜ *7.6*, ➜ *7.7*, ➜ *7.8*, ➜ *7.9*, ➜ *7.10*, ➜ *7.11*, ➜ *7.12*, ➜ *7.13*, ➜ *7.14*, ➜ *7.15*, ➜ *7.16*, ➜ *7.17*, ➜ *7.18*, ➜ *7.19*, ➜ *7.20*, ➜ *7.21*, and ➜ *7.22*.

DasSarma and DasSarma (2008) proposed to rename the family as "*Haloarchaeaceae*." This name is not validly published, and the proposed change is in violation of the General Considerations, Principles, and Rules of the International Code of Nomenclature of Prokaryotes (Oren 2008).

When in the late 1970s 16S rRNA sequence information was first used to obtain phylogenetic information on the prokaryotes, it was quickly realized that the *Halobacteriaceae* belong to the newly defined group of the Archaea (Magrum et al. 1978). A short history of the taxonomy of the family, documenting how our concepts on the systematics of the group have changed over the years with the advance of new methods for the characterization of prokaryotes, was given by Oren (2012). Until the late 1970s, the diversity of the group was considered to be low

**Table 7.3**
**Comparison of selected characteristics of the members of the genus *Haloarcula***

| Genus | *Haloarcula*[a,b] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Har. vallismortis*[c] | *Har. amylolytica*[d] | *Har. argentinensis*[e] | *Har. hispanica*[f] | *Har. japonica*[g] | *Har. marismortui*[h] | *Har. quadrata*[i] | *Har. salaria*[j] | *Har. tradensis*[j] |
| Older names | Basonym: *Halobacterium vallismortis* | | | | | Synonyms:<br>"*Halobacterium marismortui*"<br>"*Flavobacterium maris-mortui*" | | | |
| Type strain | ATCC 29715<br>DSM 3756<br>IFO (now NBRC) 14741<br>JCM 8877<br>VKM B-1791 | CGMCC 1.5335<br>JCM 13557 | ATCC 700875<br>CIP 105173<br>DSM 12282<br>JCM 9737 | ATCC 33960<br>DSM 4426<br>JCM 8911<br>NBRC 102182<br>VKM B-1755 | ATCC 49778<br>DSM 6131<br>JCM 7785<br>NBRC 101032<br>VKM B-2009 | ATCC 43049<br>CGMCC 1.1784<br>DSM 3752<br>JCM 8966<br>VKM B-1809 | ATCC 700850<br>DSM 11927<br>JCM 11048 | BCC 40029<br>JCM 15759<br>PCU 313 | BCC 40030<br>JCM 15760<br>PCU 314 |
| Cell shape | Pleomorphic rods | Rods | Triangular flat discs | Short rods | Triangular, with asymmetric division | Pleomorphic flat | Square to pleomorphic flat | Pleomorphic | Pleomorphic rods |
| Cell size (μm) | 0.6–1.0 × 3.0–5.0 | 0.6–0.8 × 2.0–2.5 | 1.0 × 3.0 | 0.3 × 0.5–1.0 | 0.2–0.3 × 1.0–2.0 | 1.0–2.0 × 2.0–3.0 | 2.0–3.0 | 0.6–0.8 × 1.0–2.0 | 0.8–1.2 × 1.0–2.5 |
| Motility | + | + | + | + | + | + (w) | + | – | – |
| Colony color | Pink | Red | Orange-red | Red-orange | Red | Red | Red-orange | Red | Red |
| NaCl range for growth and optimum (%) | >15 (Opt. 25) | 12–30 (Opt. 17–19) | 12–26 (Opt. 15–18) | 15–30 (Opt. 20–25) | 10–25 (Opt. 15–25) | 10–30 (Opt. 20–23) | 16–25 (Opt. 20–25) | >15 (Opt. 20–25) | >15 (Opt. 20–25) |
| Lysis in distilled water | + | + | NR | NR | NR | NR | + | + | + |
| Magnesium requirement and optimum (M) | NR | 0.005–0.7 (Opt. 0.1–0.3) | >0.03 (Opt. 0.1) | > 0.005 | 0.04–0.65 (Opt. 0.16) | NR | > 0.05 (Opt. 0.1–0.5) | 0.08–0.4 | 0.08–0.4 |
| pH range for growth and optimum | 5.5–8.5 (Opt. 7.4–7.5) | 6.5–9.0 (Opt. 7.0–7.5) | NR | 6.0– > 8.0 (Opt. 7.0) | 6.0–8.0 (Opt. 7.0–7.5) | NR | 5.9–8.0 (Opt. 6.5– 7.0) | 6.0–8.0 (Opt. 7.0) | 6.0–8.0 (Opt. 7.0) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Temperature range for growth and optimum (°C) | 20–45 (Opt. 40) | 20–52 (Opt. 41) | Opt. 40 | 25–50 (Opt. 35–40) | 24–45 (Opt. 42) | Opt. 40–50 | Opt. 50–53, up to 55 | 15–45 (Opt. 37) | 15–45 (Opt. 37) |
| Organic substrates used | Fruc Gala Gluc Glyc Malt Star Sucr Tre | Gala Gluc Mann Manni Sorbi Sucr | NR | Acet Citr Gluc Glyc Lact Mala Manni Pyru Sorbi Succ Sucr | Arab Cell Gala Glyc Malt Rham Sucr Treh Xylo | Acet Fruc Gluc Glyc Mala Succ Sucr | Gala Gluc Glyc Malt Manni Pyru Sorbi Succ Sucr | Cell Gluc Glyc Raff | Cell Gala Gluc Glyc Raff Sorbi |
| Acid produced from | Fruc Gluc Malt | Gala Gluc Mann Manni Sorbi Sucr | Fruc Gala Gluc Glyc Malt Mann Ribo Sucr | NR | Arab Cell Gala Glyc Malt Rham Sucr Treh Xylo | Fruc Gluc Glyc Malt Manni Ribo Sorbi Sucr Xylo | Gala Gluc Ribo Sucr Xylo | Raff | – |
| Organic substrates not used | Arab Cell Mann Xylo | Fruc Lacto Ribo Sorb Xylo | Lacto | NR | Lacto Mann | NR | Acet Arab Citr Fruc Lacto Mala Mann Ribo Xylo | Gala Sorbi Treh | Treh |
| Indole from typtophan | + | + | NR | v | + | – | – | – | – |
| Starch hydrolysis | + | + | NR | + | – | + (w) | + | + | + (w) |
| Gelatin liquefaction | – | + | NR | + | – | NR | – | – | – |
| Nitrate reduction | + | + | NR | + | + | + | + | – | – |
| Polar lipids | PG, PGP-Me, PGS, TGD-2, DGD-2 | PG, PGP-Me, PGS TGD-2, an unknown diglycosyl diether | PG, PGP-Me, PGS, TGD-2, DGD-2 | PG, PGP-Me, PGS, TGD-2 | PG, PGP-Me, PGS, TGD-2, 3 unknown minor lipids | PG, PGP-Me, PGS, TGD-2, | PG, PGP-Me, PGS, TGD-2, | PG, PGP-Me, PGS, TGD-2, DGD, 2 unknown phospholipids | PG, PGP-Me, PGS, TGD-2, DGD, 2 unknown phospholipids |
| Respiratory quinones | NR | NR | NR | NR | NR | NR | NR | MK-8, MK-8($H_2$) | MK-8, MK-8($H_2$) |

**Table 7.3 (continued)**

| Genus | *Haloarcula*[a,b] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Har. vallismortis*[c] | *Har. amylolytica*[d] | *Har. argentinensis*[e] | *Har. hispanica*[f] | *Har. japonica*[g] | *Har. marismortui*[h] | *Har. quadrata*[i] | *Har. salaria*[j] | *Har. tradensis*[j] |
| Sensitivity to antibiotics | Sensitive: Bac Nov | Sensitive: Bac Nov | Sensitive: Ani Nov | Sensitive: Nov | Sensitive: Ani Bac Nov | Sensitive: Bac Nov | Sensitive: Ani Bac Nov | Sensitive: Bac | Sensitive: Bac Nov |
| | Resistant: Chl Ery Kan Pen Str Tet Van | Resistant: Amp Chl Cip Ery Kan Neo Pen Rif Str Tet Van | Resistant: Chl Kan Pen | Resistant: Amp Bac Chl Ery Gen Kan Neo Pen Str Tet | | | Resistant: Amp Chl. Ery Neo Pen Rif | Resistant: Amp Chl Gen Nov Rif Str | Resistant: Amp Chl Gen Rif Str Tet |
| G + C content of DNA (mol%) | 61.8[k] | 62.4 | 62 | 62.7 | 63.3 | 61.1[k] | 60.1 | 61.6 | 62.2 |
| Sample source and site | Dearth Valley, CA, USA | Salt Lake, China | Salt flat, Argentina | Saltern, Spain | Saltern, Japan | The Dead Sea | Brine pool, Sinai, Egypt | Fish sacuce, Thailand | Fish sacuce, Thailand |

Data taken from:

[a] Ventosa (2001a)

[b] Torreblanca et al. (1986)

[c] Gonzalez et al. (1978)

[d] Yang et al. (2007)

[e] Ihara et al. (1997)

[f] Juez et al. (1986)

[g] Horikoshi et al. (1993)

[h] Oren et al. (1990)

[i] Oren et al. (1999)

[j] Namwong et al. (2011)

[k] Calculated from the genome sequence (see ❯ *Table 7.21*)

Additional data on growth substrates and other properties can be found in the original species descriptions

**Table 7.4**

**Comparison of selected characteristics of the members of the genera *Halobiforma*, *Halogeometricum*, and *Halogranum***

| Genus | *Halobiforma* | | | *Halogeometricum*[d] | | *Halogranum* | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Hbf. haloterrestris*[a] | *Hbf. lacisalsi*[b] | *Hbf. nitratireducens*[a,c] | *Hgm. borinquense*[e] | *Hgm. rufum*[f] | *Hgn. rubrum*[g] | *Hgn. amylolyticum*[h] | *Hgn. gelatinilyticum*[h] | *Hgn. salarium* |
| Older names | | | Basonym: *Natronobacterium nitratireducens* | | | | | | |
| Type strain | DSM 13078<br>JCM 11627 | CGMCC 1.3738<br>JCM 12983 | AS 1.1980<br>JCM 10879 | ATCC 700274<br>DSM 11551<br>JCM 10706 | CGMCC 1.7736<br>JCM 15770 | CGMCC 1.17738<br>JCM 15772 | CGMCC 1.10121<br>JCM 16428 | CGMCC 1.10119<br>JCM 16426 | DSM 23171<br>KCTC 4066 |
| Cell shape | Rods, pleomorphic cells, cocci | Rods, pleomorphic cells, cocci | Rods | Pleomorphic | Pleomorphic | Pleomorphic | Pleomorphic | Pleomorphic | Pleomorphic |
| Cell size (μm) | 0.5–1.5 × 2–8 (rods), 1.25–2.0 diameter (cocci) | 0.5–0.8 × 3.0–5.0 (rods), 0.5–1.5 diameter (cocci) | 0.4–0.8 × 3–7 | 1–2 × 1–3 | NR | 1–2 | 1–2 | 1–2 | 0.5–2.0 |
| Motility | + | + | + | + | + | + | − | + | + |
| Colony color | Red | Reddish | Red | Pink | Red | Red | Red | Red | Red |
| NaCl range for growth and optimum (%) | 13–30 (Opt. 20) | >10 (Opt. 15−25) | 15–30 (Opt. 20) | >8 (Opt. 20–25) | 12–30 (Opt. 23) | 15–25 (Opt. 23) | 8–30 (Opt. 20–23) | 10–30 (Opt. 20–23) | 8–30 (Opt. 15–20) |
| Lysis in distilled water | + (rods only) | + (rods only) | + | NR | NR | + | + | + | + |
| Magnesium requirement and optimum (M) | − | 0–0.5 | NR | Opt. 0.04–0.08 | 0.05–0.7 (Opt. 0.3) | Opt. 0.3 | − (Opt. 0.05) | Opt. 0.1 | − (Opt. 0.05–0.15) |
| pH range for growth and optimum | 6.0–9.2 (Opt. 7.5) | 6.5–9.0 (Opt. 7.5) | 8.0–10.5 (Opt. 8.5) | 6.0–8.0 (Opt. 7.0) | 6.0–8.5 (Opt. 7.0) | 6.0–8.0 (Opt. 7.5) | 5.5–9.0 (Opt. 6.5) | 5.5–9.0 (Opt. 7.0) | 5.0–8.0 (Opt. 7.0) |
| Temperature range for growth and optimum (°C) | Opt. 42<br>Max 58 | 24–57 (opt 42–45) | 26–44 (Opt. 36–41) | 22–50 (Opt. 40) | 25–55 (Opt. 42) | 20–50 (Opt. 37) | 20–50 (Opt. 37) | 20–50 (Opt. 37) | 15–50 (Opt. 37) |

**Table 7.4 (continued)**

| Genus | *Halobiforma* | | | *Halogeometricum*[d] | | *Halogranum* | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Hbf. haloterrestris*[a] | *Hbf. lacisalsi*[b] | *Hbf. nitratireducens*[a,c] | *Hgm. borinquense*[e] | *Hgm. rufum*[f] | *Hgn. rubrum*[g] | *Hgn. amylolyticum*[h] | *Hgn. gelatinilyticum*[h] | *Hgn. salarium* |
| Organic substrates used | Arab Acet Buty Gluc Glyc Malt Pyru Sucr | Acet Fruc Gluc Glyc Lact Pyru | Acet (w) Fruc Gluc (w) Pyru Manni (w) | Cell Fruc Gluc Glyc Malt Mann Raff Treh Xylo | Acet Gala Gluc Glyc Lact Lacto Mann Malt Pyru Sorbi Sucr | Acet Fuma Gala Gluc Glyc Lact Lacto Mala Malt Mann Pyru Sorbi Star Sucr Succ | Acet Fuma Gala Gluc Glyc Lact Lacto Mala Malt Mann Manni Pyru Sorbi Sucr Succ | Acet Gala Gluc Glyc Lact Lacto Mann Pyru Sorbi Sucr | Acet Arab Fruc Fuco Gala Gluc Glyc Lact Malt Mann Manni Meli Pyru Ribo Sorb Sorbi Star Sucr Xylo |
| Acid produced from | Arab Gluc Malt Sucr Xylo | Gluc Glyc | – | Arab Fruc Lacto Ribo Sucr Xylo | Carbohydrates | Gala Gluc Glyc Malt Sucr | Arab Gala Gluc Lacto Mann Sucr Xylo | Gala Gluc Lacto Mann Sucr | Arab Fruc Gluc Glyc Malt Mann Sucr Xylo |
| Organic substrates not used | Citr Fruc Gala Lacto Manni Sorbi Xylo | Arab Citr Fuma Gala Lacto Mala Malt Manni Prop Rham Ribo Sorbi Succ Sucr Xyl | Arab Fuma Gala Glyc Lacto Mala Malt Mann Prop Raff Rham Ribo Sorbi Succ Sucr Xylo | NR | Citr Fruc Fuma Mala Manni Ribo Sorb Succ Xylo | Citr Fruc Manni Ribo Sorb Xylo | Fruc Fuma Mala Manni Rham Ribo Sorb Succ Xylo | Citr Fuma Fruc Mala Malt Manni Ribo Rham Sorb Succ Xylo | Citr Fuma Lacto Mala Rham Succ |
| Indole from typtophan | NR | – | – | + | + | – | + | + | – |
| Starch hydrolysis | – | – | + | – | – | w | + or w | + (w) | – |
| Gelatin liquefaction | + | + | + | + | – | + | – | + | + |
| Nitrate reduction | + | – | + | + | – | + | + | – | – |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, S-TGD,TGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG, PGP-Me, glycolipid | PG, PGP-Me, a minor phospholipid PL1 | PG, PGP-Me, 1 glycolipid resembling TGD-2 | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1, 1 unidentified phospholipid | PG, PGP-Me, trace of PGS S-DGD-1, DGD-1, 2 unidentified glycolipids | PG, PGP-Me, trace of PGS S-DGD-1, DGD-1, 3 unidentified glycolipids | PG, PGP-Me, S-DGD-1, DGD-1, 1 unidentified phospholipid |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Respiratory quinones | MK-8<br>MK-8[VIII-$H_2$] | NR | NR | NR | NR | NR | NR | NR | NR |
| Sensitivity to Antibiotics | Sensitive: Ani Bac Nov Rif | Sensitive: Tet | Sensitive: Ani Aph Bac Ery Nov Rif | Sensitive: Bac Nov | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif |
| | Resistant: Chl Ery Pen Str Tet | Resistant: Amp Kan Str | Resistant: Amp Chl Neo Pen | Resistant: Amp Chl Ery Kan Pen Tet Van | Resistant: Amp Chl Cip Ery Gen Kan Neo Nor Pen Str Tet | Resistant: Amp Chl Cip Ery Gen Kan Neo Nor Pen Str Tet | Resistant: Amp Chl Cip Ery Gen Kan Neo Nor Pen Str Tet | Resistant: Amp Chl Cip Ery Gen Kan Neo Nor Pen Str Tet | Resistant: Amp Chl Cip Ery Gen Kan Neo Nor Pen Str Tet |
| G + C content of DNA (mol %) | 66.9 | 65.4[j] | 63.8 | 59.9[j] | 64.9 | 55.7 | 62.0 | 64.0 | 63.7–64.4 |
| Sample source and site | Hypersaline soil, Egypt | Salt lake, China | Salt lake, Inner Mongolia | Solar Saltern, Puerto Rico | Solar saltern, China | Soil from solar saltern, China | Solar saltern, China | Solar saltern, China | Salt on seashore, Korea |

Data taken from:

[a] Hezayen et al. (2002)

[b] Xu et al. (2005a)

[c] Xin et al. (2001)

[d] Oren et al. (2001)

[e] Montalvo-Rodríguez et al. (1998)

[f] Cui et al. (2010f)

[g] Cui et al. (2010b)

[h] Cui et al. (2011e)

[i] Kim et al. (2011)

[j] Calculated from the genome sequence (see *Table 7.21*)

Additional data on growth substrates and other properties can be found in the original species descriptions

**Table 7.5**

**Comparison of selected characteristics of the members of the genus *Halococcus***

| Genus | *Halococcus*[a] | | | | | | |
|---|---|---|---|---|---|---|---|
| Species | *Hcc. morrhuae*[b] | *Hcc. dombrowskii*[c] | *Hcc. hamelinensis*[d] | *Hcc. qingdaonensis*[e] | *Hcc. saccharolyticus*[f] | *Hcc. salifodinae*[g] | *Hcc. thailandensis*[h] |
| Type strain | ATCC 17082<br>DSM 1307<br>IFO (now NBRC) 14719<br>JCM 8876<br>VKM B-1772 | ATCC BAA-364<br>DSM 14522<br>JCM 12289<br>NCIMB 13803 | ACM 5227<br>JCM 12892 | CGMCC 1.4243<br>JCM 13587 | ATCC 49257<br>CCM 4147<br>DSM 5350<br>JCM 8878<br>VKM B-1770 | ATCC 51437<br>DSM 8989<br>JCM 9578<br>VKM B-2108 | BCC 20213<br>JCM 13552<br>PCU 278 |
| Cell shape | Cocci | Cocci | Cocci | Cocci | Cocci | Cocci | Cocci |
| Cell size (μm) | 0.8–1.5 | 0.8–1.2 | 0.8–1.2 | 0.6–1.5 | 0.8–1.5 | 0.8–1.2 | 0.8–1.2 |
| Motility | – | – | – | – | – | – | – |
| Colony color | NR | Light-red | Orange-pink | Red | Red-orange | Pink (colorless at pH 9.5) | Red |
| NaCl range for growth and optimum (%) | 20–30 | 20–30 (Opt. 20–25) | 12.5–30 (Opt. 15) | >10 (Opt. 18) | 20–30 | 20–30 | >15 (Opt. 20–30) |
| Lysis in dist. water | – | – | NR | – | – | – | – |
| Magnesium requirement and optimum (M) | 0.005 | + (Opt. 0.02–0.06) | + (Opt. 0.0005–0.05) | Opt. 0.04 | >0.4 | < 0.0001 | – |
| pH range for growth and optimum | 5.5–8.0 (Opt. 7.2) | 5.2–8.0 | 4.0–9.0 | 4.0–9.0 (Opt. 6.0) | 6.0–8.0 (Opt. 7.2) | >6.0– < 10.5 (Opt. 6.8–9.5) | 6–10 (Opt. 6–8) |
| Temperature range for growth and optimum (°C) | Opt. 37 | Opt. 37 | Opt. 37 | Opt. 35–40 | 28–42 (Opt. 37–40) | 28–50 (Opt. 40) | 15–45 (Opt. 37) |
| Organic substrates used | Buty Treh | Arab Fruc Gala Xylo | Etha Gluc Glyc Malt Manni Sucr Treh, Xylo | Gluc | Etha Fruc Gala Gluc Glyc Lact Lacto Malt Mann Manni Prop Sorbi Treh | Arab Fruc Gala Gluc Glyc Lacto Raff Rham Treh Xylo | Arab Fruc Gluc Xylo |
| Acid produced from | – | – | Gluc (w) Glyc (w) Malt Sucr Treh Xylo | NR | Gluc | Gluc | Arab Cell Gluc Lacto Manni Sucr Treh |
| Organic substrates not used | Arab Etha Fuma Lact Lacto Mann Raff Rham Sorbi | Gala Gluc Lacto Raff | Fuma Lacto Mann Sorbi Raff | Lacto | Meli Raff Ribo Rham Sucr Treh Xylo | NR | Gala |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Indole from typtophan | + | NR | – | NR | + | NR | – |
| Starch hydrolysis | v (type strain: –) | – | + | + | – | – | – |
| Gelatin liquefaction | v (type strain: +) | + | – | – | v | + | – |
| Nitrate reduction | + | + | + | – | + | + | + |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG, PGP-Me, S-DGD-1 | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG, PGP-Me, S-DGD-1 | PG, PGP-Me, S-DGD-1 | PG, PGP-Me, S-DGD-1 | PG, PGP-Me, S-DGD-1, unidentified phospholipids and glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG, PGP-Me, S-DGD-1, unidentified glycolipids present | PG, PGP-Me, S-DGD-1, unidentified glycolipids |
| Respiratory quinones | "Normal menaquinones" | MK-8($H_2$), MK-7($H_2$), MK-8 | NR | NR | NR | MK-8($H_2$), MK-8 | MK-8($H_2$) |
| Sensitivity to antibiotics | Sensitive: Bac Nov | Sensitive: Ani (w) Chl (w) Bac Nov Rif Tet (w) | Sensitive: Bac Nov Rif | Sensitive: Bac Chl (w) Neo (w) Rif | Sensitive: Ani Bac | Sensitive: Ani Aph Bac Nov | Sensitive: Bac Nov Rif |
| | Resistant: Pen Str Tet | Resistant: Amp Chl Kan Pen Str Tet | Resistant: Kan Neo Pen Str Tet | Resistant: Ery Kan Pen Str Tet | Resistant: Chl Neo Nov Pen Str Tet | Resistant: Chl (w) Pen Str Tet (w) | Resistant: Amp Chl Kan Str Tet |
| G + C content of DNA (mol%) | 61–66 | 61.3 ± 1 | 60.1[i] | 61.2 | 59.5 | 62 ± 1 | 60.2–61.8 |
| Sample source and site | Saline lakes, salterns, salted products | Permian rock salt, Austria | Shark Bay, W. Australia | Crude sea salt, China | Saltern, Spain | Permian rock salt, Austria | Fish sauce fermentation, Thailand |

Data taken from:
[a] Grant (2001b)
[b] Kocur and Hodgkiss (1973)
[c] Stan-Lotter et al. (2002)
[d] Goh et al. (2006)
[e] Wang et al. (2007)
[f] Montero et al. (1989)
[g] Denner et al. (1994)
[h] Namwong et al. (2007)
[i] Calculated from the genome sequence (see *Table 7.21*)
Additional data on growth substrates and other properties can be found in the original species descriptions

**▪ Table 7.6**

**Comparison of selected characteristics of the members of the genus *Haloferax* (part A)**

| Genus | *Haloferax*[a,b] | | | | | |
|---|---|---|---|---|---|---|
| **Species** | ***Hfx. volcanii*[c]** | ***Hfx. alexandrinus*[d]** | ***Hfx. denitrificans*[e,f]** | ***Hfx. elongans*[g]** | ***Hfx. gibbonsii*[h]** | ***Hfx. larsenii*[i]** |
| Older names | Basonym: *Halobacterium volcanii* | | Basonym: *Halobacterium denitrificans* | | | |
| Type strain | ATCC 29605<br>DSM 3757<br>IFO (now NBRC) 14742<br>JCM 8879<br>NCCB 85050<br>NCIMB 2012<br>VKM B-1768 | CIP 107620<br>JCM 10717<br>KCTC 12962<br>NBRC 16590 | ATCC 35960<br>DSM 4425<br>JCM 8864<br>VKM B-1754 | ATCC BAA-1513<br>JCM 14791<br>UNSW 104100 | ATCC 33959<br>DSM 4427<br>JCM 8863<br>NBRC 102184<br>VKM B-1756 | CGMCC 1.5347<br>JCM 13917 |
| Cell shape | Disc-shaped, pleomorphic | Pleomorphic | Pleomorphic and disc-shaped | Pleomorphic rods, elongating during exponential growth | Pleomorphic discs, triangular forms, bulging rods | Pleomorphic |
| Cell size (μm) | 1–2 × 2–3 | 1.1–1.5 × 3.4–4.0 | 0.8–1.0 × 2.0–3.0 | up to 12 | 0.4 × 2.0–2.5 | 0.8 × 1.5 |
| Motility | + | – | – | + | + | + |
| Colony color | Pink | Red | Orange-red | Red | Orange-red | Orange-red |
| NaCl range for growth and optimum (%) | 9–26 (Opt. 10–15) | 10–30 (Opt. 25) | 9– > 26 (Opt. 12–18) | 10–30 (Opt. 15–20) | Opt. 20–25 (40 °C) 15–20 (30 °C) | 6–28 (Opt. 13–20) |
| Lysis in distilled water | + | + | + | + | NR | + |
| Magnesium requirement and optimum (M) | Opt. 0.2 | + (Opt. 0.3) | NR | >0.2 M (Opt. 0.4) | 0.01–0.02 | >0.005 (Opt. 0.2–0.5) |
| pH range for growth and optimum | NR | 5.5–7.5 (Opt. 7.2) | 6.0–8.0 (Opt. 6.7) | 7.0–9.0 (Opt. 7.4) | 5.0–8.0 (Opt. 6.5–7.0) | 6.0–8.5 (Opt. 6.5–7.0) |
| Temperature range for growth and optimum (°C) | Opt. 30–40 | ND (grown at 37) | 30–55 (Opt. 50) | 30–55 (Opt. 53) | 25–55 (Opt. 35–40) | 25–55 (Opt. 42–45) |
| Organic substrates used | NR | Gluc Glyc Succ | Acet Citr Fuma Fruc Gala Gluc Glyc Lact Mala Malt Pyru Succ Sucr | Gluc Glyc Malt Sucr Treh | NR | Fuma Gluc Glyc Lact Mala Mann Malt Pyru Star Succ Sucr |
| Acid produced from | NR | Arab Fruc Gluc Glyc Malt Rham Ribo Sucr Xylo | Fruc Gala Gluc Malt Sucr | Gluc Glyc Malt Sucr Treh | Arab Fruc Gala Gluc Malt Mann, Sucr Xylo | Fruc (w) Gluc (w) Glyc Malt Sucr (w) |
| Organic substrates not used | NR | Citr Gala Lacto Mann | Lacto Mann Ribo | Etha Fuma Lacto Mann Manni Raff Sorbi Xylo | NR | Acet Arab Citr Gala Lacto Manni Prop Rham Ribo Sorbi Xylo |
| Indole from typtophan | + | + | – | + | + | + |
| Starch hydrolysis | – | – | – | + | – | + |

**Table 7.6 (continued)**

| Genus | *Haloferax*$^{a,b}$ | | | | | |
|---|---|---|---|---|---|---|
| Species | *Hfx. volcanii*$^{c}$ | *Hfx. alexandrinus*$^{d}$ | *Hfx. denitrificans*$^{e,f}$ | *Hfx. elongans*$^{g}$ | *Hfx. gibbonsii*$^{h}$ | *Hfx. larsenii*$^{i}$ |
| Gelatin liquefaction | − | + | + | + | − | + |
| Nitrate reduction | + | + | + | − | v | + |
| Polar lipids | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1 |
| Respiratory quinones | NR | NR | MK-8, MK-8(VIII-H$_2$) | NR | NR | NR |
| Sensitivity to antibiotics | NR | Sensitive: Bac (high conc) Nov | Sensitive: Aph Bac Chl (high conc.) Ery Nov | Sensitive: Nov | Sensitive: Nov | Sensitive: Ani Aph Bac Nov Rif |
| | | Resistant: Bac (up to 20 μg/ml) Chl Ery Neo Rif Tet | Resistant: Pen Str | Resistant: Amp Bac Chl Ery Gen Neo Pen Rif Str Tet | Resistant: Amp Bac Chl Ery Gen Kan Neo Pen Str Tet | Resistant: Amp Chl Ery Kan Neo Pen Pen Str Tet |
| G + C content of DNA (mol%) | 63.4 | 59.5 ± 0.3 | 66.3$^{n}$ | 61.4 | 61.8 | 62.2 ± 0.8 |
| Sample source and site | The Dead Sea | Saltern, Egypt | Saltern, California, USA | Hamelin Pool, W. Australia | Saltern, Spain | Saltern, China |

(Colwell et al. 1979), but the use of more varied growth media and culture conditions, together with improved methods for the taxonomic characterization of strains, has led to our current insight that a great physiological and chemotaxonomic diversity exists within the family.

## Phylogenetic Structure of the Family and Its Genera

Phylogenetically the family *Halobacteriaceae* is affiliated with the *Euryarchaeota*. ➋ *Figure 7.1a* shows a grouped neighbor-joining tree based on 16S rRNA sequence comparisons, showing the genera of the family; an unfolded tree showing the type strains of species of the family is shown in ➋ *Fig. 7.1b*.

Most genera are well separated within the tree. A major exception is formed by the genera *Haloterrigena, Natrialba, Natrinema, and Natronorubrum* (see also Tindall 2003 and Wright 2006). The genus *Halomicrobium* may require a taxonomic reassessment. Alkaliphilic genera are found throughout the tree; there is no single haloalkaliphilic lineage such as was proposed in an early 16S RNA sequencing study (McGenity and Grant 1993).

A major problem encountered when constructing 16S rRNA-based phylogenetic trees of the family *Halobacteriaceae* is the fact that many species contain multiple 16S rRNA genes, and their sequences can differ by as much as 5 % or more. Mylvaganam and Dennis (1992) first documented the phenomenon for the *rrnA* and *rrnB* genes of *Har. marismortui*, which showed substitutions in 74 positions. Both genes can be expressed in each individual cell (Amann et al. 2000). *rrnB* appears to be preferentially expressed at higher growth temperatures (López-López et al. 2007). *Har. marismortui* has three divergent rRNA genes. Other *Haloarcula* species also show 16S rRNA polymorphism, and so do the members of the genus *Halomicrobium* (Cui et al. 2009). *Halosimplex carlsbadense* possesses three different 16S rRNA genes (Vreeland et al. 2002).

Genes encoding 23S rRNA have seldom been used for the reconstruction of the phylogenetic relationships within the *Halobacteriaceae.* In a study of six species for which both 16S and 23S rRNA gene sequences were known at the time, Briones and Amils (2000) obtained trees with different topologies for the two phylogenetic markers.

Other genetic markers have been proposed in recent years for phylogenetic tree reconstruction for the members of the family by multilocus sequence analysis (Dennis and Shimmin 1997; Enache et al. 2007a; Minegishi et al. 2010a, 2012a; Papke et al. 2007). Use of the markers *atpB*, EF-2, *radA*, *rpoB′*, and *secY* enabled differentiation of individual strains within species, as well as the delineation of species and genera, including the identification of potential novel species and even family-like relationships (Papke et al. 2011).

## Genome Analysis

At the time of writing (August 2012), information was available on the genome sequences of 27 isolates of *Halobacteriaceae*, 21 of which are type strains of species (➋ *Table 7.21*). Detailed information can be found in the specialized databases HaloLex (http://www.halolex.mpg.de;) (Pfeiffer et al. 2008b) and HaloWeb (http://halo4.umbi.umd.edu) (DasSarma et al. 2010),

**Table 7.7**
**Comparison of selected characteristics of the members of the genus *Haloferax* (part B)**

| Genus | *Haloferax* | | | | |
|---|---|---|---|---|---|
| **Species** | *Hfx. lucentense*[j] | *Hfx. mediterranei*[k] | *Hfx. mucosum*[g] | *Hfx. prahovense*[l] | *Hfx. sulfurifontis*[m] |
| Older names | Corrig. from *Haloferax lucentensis* | Basonym: *Halobacterium mediterranei* | | | |
| Type strain | CCM 7023<br>CECT 5871<br>CIP 107410<br>DSM 14919<br>JCM 9276<br>NCIMB 13854 | ATCC 33500<br>CCM 3361<br>DSM 1411<br>IFO (now NBRC) 14739<br>JCM 8866<br>VKM B-1748 | ATCC BAA-1512<br>JCM 14792<br>UNSW 104200<br>UNSW | DSM 18310<br>JCM 13924 | CCM 7217<br>CIP 108334<br>DSM 16227<br>JCM 12327 |
| Cell shape | Pleomorphic rods | Pleomorphic rods | Pleomorphic | Rods | Pleomorphic irregular shaped cells and rods |
| Cell size (μm) | 0.6 × 2.5 | 0.5–2.0 | NR | NR | 1.0–1.5 |
| Motility | + | + (w) | – | NR | – |
| Colony color | Pink | Pink | Pink-red | Beige-orange | Pink |
| NaCl range for growth and optimum (%) | 10–30 (Opt. 25) | Up to 30 (Opt. 17) | 10–30 (Opt. 15–20) | 15–30 (Opt. 20) | 6– > 30 |
| Lysis in distilled water | + | + | + | + | + |
| Magnesium requirement and optimum (M) | NR | 0.02–0.04 | >0.2 | Opt. 0.4 | >0.001 |
| pH range for growth and optimum | 5.0–9.0 (Opt. 7.5) | Opt. 6.5 | 6.0–10.0 (Opt. 7.4) | 6.0–8.5 (Opt. 7.0–7.5) | 4.5–9.0 (Opt. 6.4–6.8) |
| Temperature range for growth and optimum (°C) | 10–45 (Opt. 37) | Up to 45 (Opt. 35) | 30–55 (Opt. 53) | 23–51 (Opt. 38–48) | 18–50 (Opt. 32–37) |
| Organic substrates used | Acet Arab Buty Cell Fruc Fuma Gluc Glyc Rham Sucr Treh Xylo | Acet Citr Gluc Glyc Lact Lacto Mala Manni Pyru Sorbi Star Sucr Succ | Gluc Glyc Malt Sucr Treh | Acet Arab Citr Fuma Fruc Gala Gluc Glyc Lact Lacto Mala Malt Prop Pyru Raff Rham Star Succ Sucr Xylo | Acet Arab Benz Citr Fruc Fuma, Gala Gluc Glyc Mala Malt Succ Sucr Xylo |
| Acid produced from | Arab Fruc Gluc Glyc Malt Xylo | Arab (w) Fruc Gluc Malt Sucr Xylo | Gluc Glyc Malt Sucr Treh | Fruc, Lacto | Arab Fruc Gala Gluc Glyc Malt Sucr Xylo |
| Organic substrates not used | Citr Etha Gala Lacto Mala Malt Mann Manni Prop Raff Ribo Sorbi | NR | Etha Fuma Gala Lacto Mann Manni Raff Sorbi Xylo | Mann Manni Ribo Sorbi | Lacto Manni Ribo Sorbi Star |
| Indole from typtophan | + | + | + | + | + |
| Starch hydrolysis | – | + | – | + | – |
| Gelatin liquefaction | – | + | + | – | + |
| Nitrate reduction | – | + | – | – | + |
| Polar lipids | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1, DGD-1 | PG, PGP-Me, S-DGD-1 | PG, PGP-Me, S-DGD-1 |

**Table 7.7 (continued)**

| Genus | *Haloferax* | | | | |
|---|---|---|---|---|---|
| **Species** | ***Hfx. lucentense*[j]** | ***Hfx. mediterranei*[k]** | ***Hfx. mucosum*[g]** | ***Hfx. prahovense*[l]** | ***Hfx. sulfurifontis*[m]** |
| Respiratory quinones | NR | NR | NR | NR | NR |
| Sensitivity to antibiotics | NR | Sensitive: Ani Bac (high conc) Nov | Sensitive: Nov | Sensitive: Aph Ani Nov Rif | Sensitive: Aph Ani Bac (high conc) Nov |
| | | Resistant: Amp Bac (up to 40 μg/ml) Chl Ery Gen Kan Neo Pen Str Tet | Resistant: Amp Bac Chl Cip Ery Gen Neo Pen Rif Str Tet | Resistant: Amp Bac Chl Ery Neo Pen | Resistant: Amp Bac (up to 100 μg/ml) Chl Ery Gen Kan Pen Rif |
| G + C content of DNA (mol%) | 64.5 | 60.3[n] | 61.8[n] | 63.7 | 66.3[n] |
| Sample source and site | Saltern, Spain | Saltern, Spain | Hamelin Pool, W. Australia | Salt lake, Romania | Saline sulfur spring, Oklahoma |

Data taken from:

[a] Ventosa (2001b)

[b] Torreblanca et al. (1986)

[c] Mullakhanbhai and Larsen (1975)

[d] Asker and Ohta (2002a)

[e] Tomlinson et al. (1986)

[f] Tindall et al. (1989)

[g] Allen et al. (2008)

[h] Juez et al. (1986)

[i] Xu et al. (2007a)

[j] Gutierrez et al. (2002)

[k] Rodriguez-Valera et al. (1983)

[l] Enache et al. (2007b)

[m] Elshahed et al. (2004)

[n] Calculated from the genome sequence (see ➲ *Table 7.21*)

Additional data on growth substrates and other properties can be found in the original species descriptions

as well as in the UCSC Archaeal Genome Browser http://archaea.ucsc.edu (all accessed November 1, 2012). Based on genomic information, comparative studies are possible, e.g., of carbohydrate and amino acid degradation pathways (Anderson et al. 2011).

The chromosomes are between 2.0 and 4.5 Mbp in length and contain between 2,630 and 4,682 protein-coding genes. The number of rRNA operons encoded by these genomes varies between 1 and 3. Many species of *Halobacteriaceae* contain, in addition to the main chromosome, additional DNA in "minichromosomes," "megaplasmids," or plasmids. An extreme case is *Har. marismortui* with nine circular replicons: two "chromosomes" (3.1 and 0.28 MBp) and 7 plasmids. In many species 25–30 % of the genetic material is found outside the main chromosome. The presence of more than one kind of DNA in representatives of the family was first reported in a CsCl density gradient centrifugation of *Hbt. salinarum* DNA, which yielded two fractions with 67–68 % and 58–59 % mol% G+C (Joshi et al. 1963). The distinction between minichromosomes, megaplasmids, and plasmids, to be based on copy number, replication control, and evolutionary history, is not always clear (DasSarma et al. 2008; Ng et al. 1998). Out of 65 strains of haloarchaea tested, 75 % had at least one megaplasmid (Gutiérrez et al. 1986).

The paper describing the *Hrd. utahensis* genome (Bakke et al. 2009) is of special interest as it shows how three different genome annotation services (IMG, Joint Genome Institute Integrated Microbial Genome system; RAST, Rapid Annotation using Subsystems Technology server of the National Microbial Pathogen Data Resource NMPDR; and JCVI, J. Craig Venter Institute Annotation Service) differ considerably in gene calls and different other features. Based on the same raw sequence data, the number of predicted genes ranged from 2,898 to 3,254, and the average gene length ranged between 845 and 942 bp.

At the time of writing, the type strain of the type species of the family (*Hbt. salinarum*) had not yet been sequenced. For two related strains, the complete genome sequences are available: *Halobacterium* strain NRC-1, a strain that can be classified within the species (Gruber et al. 2004), and strain R1 (Pfeiffer et al. 2008a). The *Halobacterium* strain NRC-1 genome was the first complete *Halobacteriaceae* genome sequenced (Ng et al. 2000), and the data have been extensively used for computational analysis and functional genomics and transcriptomics studies (Kennedy et al. 2001; Soppa et al. 2008). The chromosome of strain R1 is completely colinear and virtually identical to that of NRC-1,

**Table 7.8**

**Comparison of selected characteristics of the members of the genera *Halolamina*, *Halomarina*, *Halomicrobium*, *Halonotius*, and *Halopelagius***

| Genus | *Halolamina* | *Halomarina* | *Halomicrobium*[c] | | | *Halonotius* | *Halopelagius* |
|---|---|---|---|---|---|---|---|
| Species | *Hlm. pelagica*[a] | *Hmr. oriensis*[b] | *Hmc. mukohataei*[d] | *Hmc. katesii*[e] | *Hmc. zhouii*[f] | *Hns. pteroides*[g] | *Hpl. inordinatus*[h] |
| Older names | | | Basonym: *Haloarcula mukohataei* | | | | |
| Type strain | CGMCC 1.10329<br>JCM 16809 | JCM 16495<br>KCTC 4074 | ATCC 700874<br>CIP 105174<br>DSM 12286<br>JCM 9738<br>NCIMB 13541 | CECT 7257<br>DSM 19301 | CGMCC 1.10457<br>JCM 17095 | CECT 7525<br>DSM 18729<br>JCM 14355 | CGMCC 1.7739<br>JCM 15773 |
| Cell shape | Pleomorphic | Irregular cocci or discs | Rods and pleomorphic cells | Rods | Pleomorphic | Flat rods with rounded ends | Pleomorphic |
| Cell size (μm) | NR | 0.6 × 2.0 | 0.5 × 1–8 | 1.8–2.2 × 2.2–2.8 | NR | 0.7–1.5 × 2–6 | NR |
| Motility | – | – | + | – | + | + | + |
| Colony color | Red | Pink | Red-orange | Orange | Red | Red | Red |
| NaCl range for growth and optimum (%) | 8–30 (Opt. 20–23 | 10–30 (Opt. 15) | 15–26 (Opt. 18–20) | 20–30 (Opt. 25) | 8–30 (Opt. 15) | 16–36 (Opt. 20–24) | 15–28 (Opt. 20–23) |
| Lysis in distilled water | + | – | NR | NR | NR | + | + |
| Magnesium requirement and optimum (M) | 0–0.7 (Opt. 0.01–0.05) | 0.01–1.0 (Opt. 0.2–0.5) | >0.003 | – | 0–1 (Opt. 0.05) | + (Opt. 0.2–0.6) | 0.03–0.7 (Opt. 0.5) |
| pH range for growth and optimum | 5.5–9.5 (Opt. 7.0–7.5) | 7.0–9.0 (Opt. 7.0–8.0) | 6.2–8.0 | 6.5–10.0 (Opt. 7.0–7.5) | 5.5–9.5 (Opt. 7.0) | 5.5–8.5 (Opt. 7.0–7.5) | 5.5–8.0 (Opt. 6.5–7.0) |
| Temperature range for growth and optimum (°C) | 25–50 (Opt. 37) | 20–42 (Opt. 37) | Opt. 40–45 | 35–50 (Opt. 37– 40) | 20–55 (Opt. 42) | 25–45 (Opt. 37–40) | 20–50 (Opt. 37) |
| Organic substrates used | Acet Gala Gluc Lact Mann Pyru Star | Fruc Gala Gluc Glyc Lacto Malt Mann Pyru Ribo Star Sucr Xylo | Gala Gluc Glyc Malt Mann Ribo Sucr | Acet Cell Fruc Gala Gluc Glyc Malt Manni Pyru Sorbi Star Treh | Acet Gala Gluc Glyc Lact Lacto Mann Pyru Sucr | Gluc Glyc Pyru | Acet Fruc Fuma Gala Gluc Glyc Lact Lacto Mala Malt Mann Pyru Sorbi Succ Sucr |
| Acid produced from | Gala Gluc Mann | Fruc Gala Gluc Glyc Lacto Malt Mann Pyru Ribo Star Xylo | Gala Gluc Glyc Malt Mann Ribo Sucr | Arab Fruc | Gala Gluc Lacto Mann Sucr | – | Fruc Gala Gluc Glyc Lacto Malt Mann Sorbi Sucr |
| Organic substrates not used | Citr Fruc Fuma Glyc Lacto Mala Malt Manni Ribo Sorb Sorbi Succ Sucr Xylo | Acet Citr Fuma Lact Mala Manni Sorbi Succ | Acet Ribo Succ | Arab Benz Citr Lacto Mala Mann Prop Raff Rham Sorb Succ Sucr Xylo | Citr Fruc Fuma Mala Malt Manni Sorb, Ribo Sorbi Star Succ Xylo | Acet Buty Cell Citr Fruc Fuma Gala Lact Lacto Mala Mann Mann Ribo Succ Sucr Xylo | Citr Manni Ribo Sorb Star Xylo |

**Table 7.8 (continued)**

| Genus | *Halolamina* | *Halomarina* | *Halomicrobium*[c] | | | *Halonotius* | *Halopelagius* |
|---|---|---|---|---|---|---|---|
| Species | *Hlm. pelagica*[a] | *Hmr. oriensis*[b] | *Hmc. mukohataei*[d] | *Hmc. katesii*[e] | *Hmc. zhouii*[f] | *Hns. pteroides*[g] | *Hpl. inordinatus*[h] |
| Indole from typtophan | – | – | – | – | – | – | + |
| Starch hydrolysis | + (w) | – | + | + | – | – | – |
| Gelatin liquefaction | – | + | – | v | – | NR | – |
| Nitrate reduction | + (v) | + | + | + | + | – | – |
| Polar lipids | PG, PGP-Me, PGS, S-DGD-1, DGD-1, TGD-1, 4 unknown glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG, PGP-Me, a glycolipid identical to TGD-2, 1 unknown glycolipid | PG, PGP-Me, PGS, S-DGD | PG, PGP-Me, a glycolipid resembling S-DGD-1, DGD-1 | PG, PGP-Me, PGS, a glycolipid resembling S-DGD-1, DGD-1 | PG, PGP-Me, a glycolipid resembling S-DGD-1 | PG, PGP-Me, two glycolipids resembling S-DGD-1 and DGD-1 |
| Respiratory quinones | NR | NR | NR | NR | NR | NR | NR |
| Sensitivity to antibiotics | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Rif | Sensitive: Ani Nov | Sensitive: Bac Nov | Sensitive: Bac Nov Rif | Sensitive: Ani Nov Rif | Sensitive: Ani Aph Bac Nov Rif |
| | Resistant: Amp Chl Cip Ery Gen Kan Neo Pen Str Tet Van | Resistant: Amp Chl Ery Neo Nov Pen Str Tet | Resistant: Chl Kan Pen | Resistant: Amp Chl Ery Gen Kan Neo Pen Str Tet | Resistant: Amp Chl Ery Gen Kan Neo Pen Str Tet | Resistant: Amp Bac Chl Ery Kan Neo Str Tet | Resistant: Amp Cip Chl Ery Gen Kan Neo Pen Str Tet Van |
| G+C content of DNA (mol%) | 64.8 | 67.7 | 65.5[i] | 52.4–52.9 | 69.1 | 58.4–58.7 | 59.9–61.0 |
| Sample source and site | Solar saltern, China | Seawater aquarium, Tokyo, Japan | Salt flat, Argentina | Salt lake, Chile; Sabkha, Algeria | Solar saltern, China | Saltern crystallizer Ponds, Australia | Solar saltern, China |

Data taken from:

[a] Cui et al. (2011b)

[b] Inoue et al. (2011)

[c] Oren et al. (2002)

[d] Ihara et al. (1997)

[e] Kharroub et al. (2008)

[f] Yang and Cui (2012)

[g] Burns et al. (2010b)

[h] Cui et al. (2010g)

[i] Calculated from the genome sequence (see *Table 7.21*)

Additional data on growth substrates and other properties can be found in the original species descriptions

but in addition, it possesses not 2 but 4 megaplasmids. A portion of 210 kb of sequence occurs only in strain R1. Pfeiffer et al. (2008a) concluded that the two strains were descendents of one isolate and that the differences observed were the result of rapid evolution in the laboratory. Further information about the origin and the relations between the two strains was provided by Ng et al. (2008) and Pfeiffer et al. (2008b).

The genome of *Hqr. walsbyi*, an unusually shaped square archaeon, which also has the lowest G+C content of all (47.9 mol%), is of special interest because of its low coding density (76 %) as compared to 86–91 % in other haloarchaea, a phenomenon caused by a very large average intergenic spacing (average 289 bp) and a high number (>1,000) intergenic regions. It also encodes the largest protein identified in the group: the 9,159 amino acid long halomucin.

**Table 7.9**
**Comparison of selected characteristics of the members of the genera *Halopenitus*, *Halopiger*, *Haloplanus*, and *Haloquadratum***

| Genus | *Halopenitus* | *Halopiger* | | *Haloplanus* | | | *Haloquadratum* |
|---|---|---|---|---|---|---|---|
| Species | *Hpt. persicus*[a] | *Hpg. xanaduensis*[b] | *Hpg. aswanensis*[c] | *Hpn. natans*[d] | *Hpn. aerogenes*[e] | *Hpn. vescus*[f] | *Hqr. walsbyi*[g] |
| Type strain | IBRC 10041<br>KCTC 4046 | CECT 7173<br>CGMCC 1.6379 | DSM 13151<br>JCM 11628 | DSM 17983<br>JCM 14081 | CGMCC 1.10124<br>JCM 16430 | CGMCC 1.8712<br>JCM 16055 | DSM 16854<br>JCM 12705 |
| Cell shape | Pleomorphic rods, triangles, disc-shaped | Pleomorphic rods | Pleomorphic rods | Flat pleomorphic | Flat pleomorphic | Flat pleomorphic | Flat squares |
| Cell size (μm) | 0.6–1.5 × 4.9-–8.7 | 0.5–1.0 × 3.0–13.0 | 0.6–0.9 × 1.25–6.5 | 2.5–8.0 | 1.0–2.0 | 1.0–2.0 | 0.2 × 2 × 2 |
| Motility | – | NR | + | – | + | + | – |
| Colony color | Pale pink | Red | Pink | Light pink | Pink | Pink | Pink |
| NaCl range for growth and optimum (%) | 10–25 (Opt. 17) | 15–30 (Opt. 25) | >10 (Opt. 22.5–25) | 15–25 (Opt. 18) | 15–25 (Opt. 18) | 8–30 (Opt. 12) | 14–36 (Opt. 18) |
| Lysis in distilled water | + | + | + | + | + | + | + |
| Magnesium requirement and optimum (M) | >0.05 | – | – | NR | 0–1 (Opt. 0.01) | 0.03–0.5 (Opt. 0.03) | – |
| pH range for growth and optimum | 6.5–8.5 (Opt. 7.5) | 6.0–11.0 (Opt. 7.5–8.0) | 6.0–9.2 (Opt. 7.5) | 6.5–8.0 (Opt. 7.0) | 6.0–9.0 (Opt. 7.5) | 5.5–7.5 (Opt. 6.0 –6.5) | 6.0–8.5 |
| Temperature range for growth and optimum (°C) | 25–50 (Opt. 40) | 28–45 (Opt. 37) | <55 (Opt. 40) | 37–52 (Opt. 40) | 25–50 (Opt. 37–40) | 30–50 (Opt. 40) | 25–45 |
| Organic substrates used | Fruc Gala Gluc Malt | Acet Gala Gluc Xylo | Some carbohydrates Acet Pyru | Acet Gluc Ribo | Acet Gala Gluc Lact Mann Pyru Sucr | Acet Gluc Lact Lacto Malt Mann Manni Pyru Sorbi | Pyru |
| Acid produced from | Gluc Malt | Arab Gluc Xylo | Arab Fruc Gluc Malt Star Sucr Xylo | NR | NR | NR | – |
| Organic substrates not used | Arab Manni Ribo Sucr | Fruc Fuma Glyc Lacto, Mala Malt Mann Manni Prop Raff Ribo, Sorbi Succ Treh | NR | Gala Glyc Malt Succ Sucr | Fruc Glyc Lacto Malt Manni Sorb Ribo Sorbi Star Succ Xylo | Citr Fruc Fuma Gala Glyc Mala Ribo Sorb Star Succ Sucr Xylo | Acet Arab Benz Cell Citr Fruc Fuma Gala Gluc Glyc Lact Lacto Mala Malt Mann Manni Prop Ribo, Succ Sucr Xylo |
| Indole from typtophan | – | – | + | v (type +) | + | + | – |
| Starch hydrolysis | – | – | + | – | – | – | – |
| Gelatin liquefaction | – | + | – | – | – | – | – |

**Table 7.9 (continued)**

| Genus | *Halopenitus* | *Halopiger* | | *Haloplanus* | | | *Haloquadratum* |
|---|---|---|---|---|---|---|---|
| Species | *Hpt. persicus*[a] | *Hpg. xanaduensis*[b] | *Hpg. aswanensis*[c] | *Hpn. natans*[d] | *Hpn. aerogenes*[e] | *Hpn. vescus*[f] | *Hqr. walsbyi*[g] |
| Nitrate reduction | − | − | + | + | + | + | − |
| Polar lipids | PG, PGP-Me, 1 unidentified glycolipid, 3 minor phospholipids | PG, PGP-Me, $S_2$-DGD-1 | PG, PGP-Me, $S_2$-DGD-1 | PG, PGP-Me, PGS, 1 glycolipid resembling S-DGD-1 | PG, PGP-Me, PGS, 1 glycolipid resembling S-DGD-1 | PG, PGP-Me, PGS, 1 glycolipid resembling S-DGD-1 | PG, PGP-Me, PGS, S-DGD-1[h] |
| Respiratory quinones | MK-8(II-$H_2$) | NR | MK-8<br>MK-8(VIII-$H_2$) | NR | NR | NR | NR |
| Sensitivity to antibiotics | Sensitive: Ani Bac Nov | Sensitive: Bac Nov | Sensitive: Ani Bac Nov Rif | Sensitive: Ani Bac Nov | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Chl Ery Nov Rif Tet |
| | Resistant: Amp Chl Ery Kan Neo Pen Rif Str Tet | Resistant: Amp Chl Ery Kan Neo Pen Rif Str Tet Van | Resistant: Chl Ery Pen Str Tet Van | Resistant: Amp Chl Neo Pen Rif | Resistant: Amp Chl Ery Kan Neo Pen Rif Str Tet Van | Resistant: Amp Chl Ery Kan Neo Pen Rif Str Van | Resistant: Amp Bac Kan Neo Str |
| G + C content of DNA (mol%) | 66.0 | 65.2[i] | 67.1 | 66.1–66.4 | 64.1 | 62.1 | 46.9–47.9[i] |
| Sample source and site | Salt lake, Iran | Salt lake, Inner Mongolia | Hypersaline soil, Egypt | Experimental mesocosm, the Dead Sea | Solar saltern, China | Solar saltern, China | Solar salterns, Spain, Australia |

Data taken from:
[a] Amoozegar et al. (2012)
[b] Gutiérrez et al. (2007)
[c] Hezayen et al. (2010)
[d] Elevi Bardavid et al. (2007)
[e] Cui et al. (2011a)
[f] Cui et al. (2010c)
[g] Burns et al. (2007)
[h] Lobasso et al. (2008)
[i] Calculated from the genome sequence (see ➜ *Table 7.21*)
Additional data on growth substrates and other properties can be found in the original species descriptions

In some cases, phage-like elements were encountered within the sequenced genomes. Thus, the *Nab. magadii* genome contains a phage-like element—halovirus ΦCh1.

## Phages

Since the first viruses lysing *Halobacterium* strains were described (Torsvik and Dundas 1974; Wais et al. 1975), a large number of viruses tageting different members of the *Halobacteriaceae* have been isolated and characterized in greater or lesser depth (Dyall-Smith et al. 2003; Pina et al. 2011). They have been classified within the Myoviridae, Siphoviridae, Fuselloviridiae, and "Pleolipoviruses." ➜ *Table 7.22* summarizes their properties. These viruses show different morphologies including head-tail, lemon-shaped, and pleomorphic types, and they may contain circular or linear double-stranded or single-stranded DNA. *Halorubrum* sp. virus HRPV-3 has double-stranded DNA with single-stranded interruptions (Senčilo et al. 2012). *Nab. magadii* halovirus ΦCh1 contains both linear double-stranded 55 kbp DNA and several RNA species (80–700 nt) (Witte et al. 1997). The recently discovered pleomorphic "Pleolipoviruses" are of special interest as they contain lipids derived from the host, as well as glycolipid spikes (Bamford et al. 2005; Pietilä et al. 2012a). Restriction and modification, known from bacteriophages of the Bacteria, have been identified for haloviruses as well (Daniels and Wais 1984).

**Table 7.10**

**Comparison of selected characteristics of the members of the genera *Halorhabdus*, *Halorientalis*, *Halosarcina*, and *Halosimplex***

| Genus | *Halorhabdus* | | *Halorientalis* | *Halosarcina* | | *Halosimplex* |
|---|---|---|---|---|---|---|
| Species | *Hrd. utahensis*[a] | *Hrd. tiamatea*[b] | *Hos. regularis*[c] | *Hsn. pallida*[d] | *Hsn. limi*[e] | *Hsx. carlsbadense*[f] |
| Type strain | DSM 12940<br>JCM 11049 | DSM 18392<br>JCM 14471 | CGMCC 1.10123<br>JCM 16425 | JCM 14848<br>KCTC 4017 | CGMCC 1.8711<br>JCM 16054 | ATCC BAA–75<br>JCM 11222 |
| Cell shape | Pleomorphic | Pleomorphic | Pleomorphic rods | Cocci | Pleomorphic | Pleomorphic rod |
| Cell size (µm) | 0.5–1.0 × 2–10 | 0.5–1.0 × 1–8 | ~0.5 × 1.0–1.6 | 0.8–1.0 | NR | ~0.95 × 5 |
| Motility | + | – | + | – | + | + |
| Colony color | Red | Non-pigmented | Red | Pink | Red | Pink-red |
| NaCl range for growth and optimum (%) | 9–30 (Opt. 27) | 10–30 (Opt. 27) | 15–30 (Opt. 18–20) | 10–25 (Opt 18) | 12–30 (Opt. 23) | 20–30 (Opt. 25) |
| Lysis in distilled water | + | + | + | + | | + |
| Magnesium requirement and optimum (M) | 0.002–0.8 | – (Opt. 0–1) | Opt. 0.01–0.03 | >0.001 | 0.05–0.7 (Opt 0.3) | >0.2 (Opt. 0.4–0.8) |
| pH range for growth and optimum | 5.5–8.5 (Opt. 6.7–7.1) | 5.5–8.5 (Opt. 6.5–7.0) | 6.0–9.0 (Opt. 7.0–7.5) | 5.0–8.5 (Opt. 6.5) | 6.5–8.0 (Opt. 7.0) | 7.0–8.0 (Opt. 7.5) |
| Temperature range for growth and optimum (°C) | 17–55 (Opt. 50) | 15–55 (Opt. 45) | 20–50 (Opt. 37) | 25–45 (Opt. 30) | 20–50 (Opt. 37) | 22–50 (Opt. 37–40) |
| Organic substrates used | Fruc Gluc Xylo | Fruc (w) Gala (w) Gluc (w) Malt Xylo (w) | Acet Fuma Gala Gluc Lact Mala Mann Pyru Succ | Acet Fruc Fuma Gala Gluc Glyc Lact Mala Pyru Sorbi Succ Sucr | Acet Gala Gluc Glyc Lact Lacto Mann Pyru Sucr | Acet Glyc Pyru |
| Acid produced from | Gluc and other carbohydrates | Malt | NR | Fruc Gala Gluc Glyc Lacto Sorbi Star Sucr | Gala Gluc Glyc Lacto Mann Sucr | – |
| Organic substrates not used | Acet Arab Citr Gala Glyc Lact Lacto Malt Pyru Sorbi Sucr | Acet Arab Citr Glyc Lact Lacto Pyru Sorbi | Fruc Lacto Malt Ribo Sorb Xylo | Citr Manni Xylo | Citr Fruc Fuma Mala Malt Manni Ribo Sorb Sorbi Succ Xylo | Arab Buta Citr Fruc Gala Gluc Lact Lacto Mala Mann Raff Rham Xylo Succ Sucr Treh |
| Indole from typtophan | – | – | + | + | – | – |
| Starch hydrolysis | – | w | w | – | w | – |
| Gelatin liquefaction | – | + | – | – | – | – |
| Nitrate reduction | – | + | + | + | + | – |
| Polar lipids | PG, PGP-Me, TGD, S-TGD, 1 unknown component | PG, PGP-Me, TGD, S-TGD, 1 unknown component | PG, PGP-Me, S-DGD-1, 3 unidentified glycolipids | PG, PGP-Me, S-DGD-1, DGD | PG, PGP-Me, S-DGD-1, $S_2$-DGD | PG, PGP-Me, S-TeGD, $S_2$-DGD, S-DGD-1, 1 unidentified glycolipid |
| Respiratory quinones | MK-8<br>MK-8(VIII-$H_2$) | MK-8<br>MK-8(VIII-$H_2$) | NR | NR | NR | NR |

**❯ Table 7.10 (continued)**

| Genus | *Halorhabdus* | | *Halorientalis* | *Halosarcina* | | *Halosimplex* |
|---|---|---|---|---|---|---|
| **Species** | ***Hrd. utahensis*[a]** | ***Hrd. tiamatea*[b]** | ***Hos. regularis*[c]** | ***Hsn. pallida*[d]** | ***Hsn. limi*[e]** | ***Hsx. carlsbadense*[f]** |
| Sensitivity to antibiotics | Sensitive: Bac Nov | Sensitive: Ani Aph Bac Chl (50 μg/ml) Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Ani Aph Bac Nov Rif | Sensitive: Bac Nov Rif |
| | Resistant: Amp Chl Ery Gen Neo Pen Rif Str Tet | Resistant: Amp Chl (25 μg/ml) Ery Pen Tet | Resistant: Amp Chl Cip Ery Kan Neo Pen Str Tet | Resistant: Amp Chl Ery Neo Pen | Resistant: Amp Chl Cip Ery Kan Neo Nor Pen Tet | Resistant: Ani Amp Aph Chl Ery Kan Neo Pen Tet |
| G + C content of DNA (mol%) | 62.9[g] | 62.0[g] | 61.5.61.9 | 65.4 | 61.2 | 64.4 |
| Sample source and site | Great Salt Lake, Utah | Deep-sea brine, Red Sea | Solar saltern, China | Saline sulfur spring, Oklahoma | Solar saltern, China | Salt crystals, Salado formation, New Mexico |

Data taken from:
[a] Wainø et al. (2000)
[b] Antunes et al. (2008)
[c] Cui et al. (2010d)
[d] Savage et al. (2008)
[e] Cui et al. (2010d)
[f] Vreeland et al. (2002)
[g] Calculated from the genome sequence (see ❯ *Table 7.21*)
Additional data on growth substrates and other properties can be found in the original species descriptions

Comparisons of haloviral genomes have shown that HHPV-1, a pleomorphic double-stranded DNA *Har. hispanica* virus that is released from the host without cell lysis, has remarkable synteny and amino acid sequence similarity to the single-stranded DNA *Halorubrum* sp. HRPV-1 virus. A provirus identified in the *Hfx. volcanii* chromosome is also a member of this group (Roine et al. 2010). Analysis of the genomes of haloviruses HF1 and HF2 yielded evidence for a recent and large recombination event. HF1, a virus with a broad host range (*Hbt. salinarum, Hfx. volcanii, Hfx. lucentense*), is 94.4 % identical to the *Hrr. coriense* HF2 genome but about 1.8 kb shorter. Except for a single base change, the first 48 kb are identical. Then there is an abrupt change, suggesting a recent recombination event between either HF1 or HF2 and another HF-like halovirus that has swapped most of the right-end 28 kb (Tang et al. 2004).

The true diversity of haloviruses in hypersaline ecosystem is probably much larger than that suggested in ❯ *Table 7.22*. A transmission electron microscopy study of the hypersaline Lake Retba, Senegal, showed a tremendous variety of virus like particle morphologies including spindle-shaped, spherical, and linear particles, chains of small globules, hook-shaped particles, reed-shaped particles consisting of a cylindrical body and thin tail, "tadpole" shape, and branched filaments. All these are likely archaeal viruses, although association with bacteria or with eukaryotes cannot be excluded. All these novel types are waiting to be isolated and further characterized. Less than 1 % of the viruslike particles observed had a head-and-tail morphology (Sime-Ngando et al. 2010).

## Phenotypic Analyses

### The Properties of the Genera and Species of *Halobacteriaceae*

❯ *Tables 7.1*, ❯ *7.2*, ❯ *7.3*, ❯ *7.4*, ❯ *7.5*, ❯ *7.6*, ❯ *7.7*, ❯ *7.8*, ❯ *7.9*, ❯ *7.10*, ❯ *7.11*, ❯ *7.12*, ❯ *7.13*, ❯ *7.14*, ❯ *7.15*, ❯ *7.16*, ❯ *7.17*, ❯ *7.18*, ❯ *7.19*, ❯ *7.20*, ❯ *7.21*, and ❯ *7.22* summarize the properties of the species of *Halobacteriaceae* whose names have been validly published until August 2012. A number of additional genus and species names have been effectively published but were not yet validated. These include the genus *Halorubellus* with species *Hrb. salinus* and *Hrb. litoreus* (Cui et al. 2012b) and the genus *Halorussus* with the species *Hrs. rarus* (Cui et al. 2010e).

The tables provide a general overview only of the properties of the organisms, and do not list all characters that have been documented in the original species descriptions and in later studies. For example, a positive reaction for nitrate reduction as listed in ❯ *Tables 7.1*, ❯ *7.2*, ❯ *7.3*, ❯ *7.4*, ❯ *7.5*, ❯ *7.6*, ❯ *7.7*, ❯ *7.8*, ❯ *7.9*, ❯ *7.10*, ❯ *7.11*, ❯ *7.12*, ❯ *7.13*, ❯ *7.14*, ❯ *7.15*, ❯ *7.16*, ❯ *7.17*, ❯ *7.18*, ❯ *7.19*, ❯ *7.20*, ❯ *7.21*, and ❯ *7.22* can signify reduction of nitrate to nitrite only or true denitrification with production of $N_2$ and/or $N_2O$ coupled to anaerobic growth. The entry "Organic substrates used" may list compounds that stimulate growth or compounds that can be used as sole carbon and energy source. The species descriptions are not always clear in this respect. Some species are indeed able to grow on single carbon sources without amino acid supplement,

**Table 7.11**

**Comparison of selected characteristics of the members of the genus *Halorubrum* (part A)**

| Genus | *Halorubrum*[a,b] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Hrr. saccharovorum*[c] | *Hrr. aidingense*[a] | *Hrr. alkaliphilum*[e] | *Hrr. aquaticum*[f] | *Hrr. arcis*[g] | *Hrr. californiense*[h] | *Hrr. chaoviator*[i] | *Hrr. cibi*[j] | *Hrr. coriense*[k,l] |
| Older names | Basonym: *Halobacterium saccharovorum*; *Halorubrobacterium saccharovorum* is a later homotypic synonym | | | | | | | | *Halorubrobacterium coriense* is a later homotypic synonym |
| Type strain | ATCC 29252<br>CIP 105329<br>DSM 1137<br>IFO (now NBRC) 14717<br>JCM 8865<br>NCIMB 2081<br>VKM B-1747 | CGMCC 1.2670<br>JCM 13560 | AS 1.3528<br>JCM 12358 | CECT 7174<br>CGMCC 1.6377<br>JCM 14031 | CGMCC 1.5343<br>JCM 13916 | CECT 7256<br>DSM 19288<br>JCM 14715 | ATCC BAA-1602<br>DSM 19316<br>NCIMB 14426 | DSM 19504<br>JCM 15757<br>KCTC 4026 | ACM 3911<br>CIP 105331<br>DSM 10284<br>JCM 9275 |
| Cell shape | Rods | Rods | Short rods | Rods | Rods | Rods | Rod-shaped to pleomorphic | Rods | Pleomorphic |
| Cell size (μm) | 0.6–1.2 × 2.5 | 0.9–1.0 × 3.6–6.4 | 0.8–1.0 × 1.8–2.0 | 1.0–1.2 × 2.0–6.0 | 0.5–1.0 × 2.0–4.0 | 0.5–1.0 × 1.5 | 0.5–0.8 × 2.0–5.0 | 0.4–0.5 × 0.8– 1.1 | 0.5–5 |
| Motility | + | + | + | − | + | + | + | + | + |
| Colony color | Red-orange | Red | Red | Red | Red | Pink | Red | Red | Red-orange |
| NaCl range for growth and optimum (%) | 9–30 (Opt. 20–26) | 10–25 (Opt. 15) | 10–30 (Opt. 23–25) | 15–30 (Opt. 20) | 13–30 (Opt. 20– 23 | 15–30 (Opt. 20–26) | 12–30 (Opt. 25) | 15–30 (Opt. 23–25) | >13 (Opt. 13–16) |
| Lysis in distilled water | + | NR | NR | + | + | NR | + | + | NR |
| Magnesium requirement and optimum (M) | > 0.005 | − | − | − | − (Opt. 0.02–0.2) | 0.17–1.7 (Opt. 0.2) | v (0–0.05) | + | > 0.005 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| pH range for growth and optimum | NR | 7.0–9.0 (Opt. 7.5) | 8.0–10.5 (Opt. 9.0–10.0) | 6.0–9.0 (Opt. 7.5) | 6.0–8.5 (Opt. 7.5) | 6.8–8.5 (Opt. 7.3) | 7.0–8.5 (Opt. 7.4) | 7.0–8.5 (Opt. 7.5) | NR |
| Temperature range for growth and optimum (°C) | 30–56 (Opt. 50) | 25–52 (Opt. 40–42) | 20–44 (Opt. 38) | 25–50 (Opt. 35–40) | 25–55 (Opt. 42) | 25–42 (Opt. 37) | 28–50 (Opt. 37) | 17–45 (Opt. 30–37) | 30–60 (Opt. 50) |
| Organic substrates used | Fruc Gala Gluc Lacto Malt Mann Ribo Sucr | Fruc Gala Gluc Malt Mann Manni Sucr | Fruc Gluc Glyc Lact Malt Mann | Arab Fruc Fuma Gluc Glyc Lacto Malt Manni Star Sucr Treh | Gluc Glyc Malt Star | Gala Gluc Lacto | Fruc Gala Gluc Lacto Malt | Lacto | Gluc Glyc Lacto Sucr |
| Acid produced from | Fruc Gala Gluc Lacto Sucr Xyl | Fruc Gala Gluc Malt Mann Manni Sucr | Fruc Gluc Malt Mann | – | Gluc Glyc Malt | – | Gala Gluc Lacto Malt | NR | NR |
| Organic substrates not used | NR | Lacto Ribo Sorb Sorbi Xylo | Gala Lacto Manni Raff Rham Ribo Sorbi Sucr | Acet Mala Mann Prop Raff Ribo Sorbi Succ Xylo | Acet Arab Citr Fruc Fuma Gala Lact Lacto Mala Mann Manni Prop Pyru Rham Ribo Sorbi Succ Sucr Xylo | Acet Fruc Mann | | Acet Citr Fruc, Gluc Sucr | NR |
| Indole from typtophan | – | + | – | – | NR | + | – | – | – |
| Starch hydrolysis | – | – | – | – | + | – | + | – | NR |
| Gelatin liquefaction | – | – | – | – | – | – | – | – | NR |
| Nitrate reduction | + | + | + | + | + | + | Variable | – | NR |
| Polar lipids | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG and PGP-Me | PG, PGP-Me, S-DGD, unidentified glycolipids | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | PG, PGP-Me, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD |
| Respiratory quinones | NR | NR | NR | NR | NR | NR | NR | NR | NR |

**Table 7.11 (continued)**

| Genus | *Halorubrum*[a,b] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Hrr. saccharovorum*[c] | *Hrr. aidingense*[a] | *Hrr. alkaliphilum*[e] | *Hrr. aquaticum*[f] | *Hrr. arcis*[g] | *Hrr. californiense*[h] | *Hrr. chaoviator*[i] | *Hrr. cibi*[j] | *Hrr. coriense*[k,l] |
| Sensitivity to antibiotics | Sensitive: Pol | Sensitive: Bac Nov Rif | Sensitive: NR | Sensitive: Bac Ery Nov Str | Sensitive: Ani Bac Nov Rif | Sensitive: Bac Kan | Sensitive: Bac Nov | Sensitive: Ani Amp Aph Bac Nov | Sensitive: Bac Nov |
| | Resistant: Bac Chl Ery Kan Pen Str | Resistant: Amp Chl Ery Kan Neo Pen Str Tet Van | Resistant: Bac Chl Neo Pen | Resistant: Amp Chl Neo Rif | Resistant: Amp Chl Ery Neo Pen | Resistant: Amp Chl Ery Rif Str | Resistant: Amp Ani Chl Ery Kan Neo Rif Tet | Resistant: Chl Ery Pen | Resistant: Amp Kan Tet |
| G + C content of DNA (mol %) | 71.2 | 64.2 | 62.1 | 62.1 | 65.7 | 69.4 | 66.5 | 61.7 | NR |
| Sample source and site | Saltern, California, USA | Salt lake, China | Soda lake, China | Saline lake, Inner Mongolia | Salt lake, Tibet | Saltern, California, USA | Evaporitic salt, Baja California, Mexico, Salt pools, Australia and Greece | Salt-fermented seafood, Korea | Saltern, Australia |

Data taken from:
[a] McGenity and Grant (2001)
[b] McGenity and Grant (1995)
[c] Tomlinson and Hochstein (1976)
[d] Cui et al. (2006a)
[e] Feng et al. (2005)
[f] Gutiérrez et al. (2011)
[g] Xu et al. (2007b)
[h] Pesenti et al. (2008)
[i] Mancinelli et al. (2008)
[j] Roh and Bae (2009)
[k] Nuttall and Dyall-Smith (1993b)
[l] Kamekura and Dyall-Smith (1995)
Additional data on growth substrates and other properties can be found in the original species descriptions

**Table 7.12**

**Comparison of selected characteristics of the members of the genus *Halorubrum* (part B)**

| Genus | *Halorubrum* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | *Hrr. distributum*[a,b,c,d] | *Hrr. ejinorense*[e] | *Hrr. ezzemoulense*[f] | *Hrr. kocurii*[g] | *Hrr. lacusprofundi*[h,i] | *Hrr. lipolyticum*[j] | *Hrr. litoreum*[k] | *Hrr. luteum*[l] |
| Older names | Basonym: *Halobacterium distributum*; *Halorubrobacterium distributum* is a later homotypic synonym | | | | Basonym: *Halobacterium lacusprofundi*; *Halorubrobacterium lacusprofundi* is a later homotypic synonym | | | |
| Type strain | ATCC 51197<br>CIP 105238<br>JCM 9100<br>JCM 10118<br>VKM B-1733 | CECT 7194<br>CGMCC 1.6782<br>JCM 14265 | CECT 7099<br>DSM 17463 | CECT 7322<br>CGMCC 1.7018<br>JCM 14978 | ACAM 34<br>ATCC 49239<br>CIP 105334<br>DSM 5036<br>JCM 8891<br>UQM 3107<br>VKM B-1753 | CGMCC 1.5332<br>JCM 13559 | CGMCC 1.5336<br>JCM 13561 | CECT 7303<br>CGMCC 1.6783 |
| Cell shape | Pleomorphic | Rods | Rods | Rods | Rods and pleomorphic | Rods | Rods | Pleomorphic |
| Cell size (μm) | 0.8–1.0 × 2.5–7.0 | 1.0–1.5 × 5.0–8.0 | 0.6 × 1.5–3.0 | 0.9–1.1 × 2.0–5.0 | Up to 12 | 0.9–1.2 × 1.8–5.5 | 0.3–0.5 × 2.0–5.0 | 0.5–0.9 × 0.6–1.5 |
| Motility | + | – | + | – | + | + | + | + |
| Colony color | Orange-red | Red | Red | Red | Red | Red | Red | Orange |
| NaCl range for growth and optimum (%) | 10–30 (Opt. 15–25) | 15–30 (Opt. 20) | 15–25 (Opt. 20) | >15 (Opt. 20) | 9–26 (Opt. 15–20) | 10–28 (Opt. 15) | 12–30 (Opt. 20) | 15–30 (Opt. 23–25) |
| Lysis in distilled water | NR | NR | + | + | + | NR | NR | + |
| Magnesium requirement and optimum (M) | NR | – | + | – | NR | + | 0.03–0.7 | – |
| pH range for growth and optimum | NR | 6–10 (Opt. 7.5) | 6.5–9.0 (Opt. 7.0–7.5) | 6.0–9.0 (Opt. 7.5) | NR | 7.0–9.0 (Opt. 7.5) | 6.5–9.0 (Opt. 7.0–7.5) | 7.5–10.5 (Opt. 9.5–10.0) |

**Table 7.12 (continued)**

| Genus | *Halorubrum* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | *Hrr. distributum*[a,b,c,d] | *Hrr. ejinorense*[e] | *Hrr. ezzemoulense*[f] | *Hrr. kocurii*[g] | *Hrr. lacusprofundi*[h,i] | *Hrr. lipolyticum*[j] | *Hrr. litoreum*[k] | *Hrr. luteum*[l] |
| Temperature range for growth and optimum (°C) | 26–50 (Opt. 37–45) | 25–50 (Opt. 37) | 22–50 (Opt. 37–40) | 25–55 (Opt. 37) | 4– < 45 (Opt. 31–37) | 25–58 (Opt. 45–48) | 20–55 (Opt. 37–42) | 17–41 (Opt. 33–37) |
| Organic substrates used | NR | Treh | Acet Arab Citr Gluc, Glyc Mala Malt Manni Oxal Sucr | Xylo | Acet Etha Form Gala Gluc Glyc Lact Lacto Mann Prop Ribo Succ | Fruc Gala Gluc Malt Mann Sucr | Acet Fuma Gala Gluc Glyc Lacto Mala Malt Pyru Sucr | Citr Fuma Gluc Glyc Lact Lacto Mala Malt Mann Manni Pyru Sorbi Succ |
| Acid produced from | Gala Gluc Glyc Surc | – | Gala Gluc Lacto Rham Xylo | NR | – | Fruc Gala Gluc Malt Mann Sucr | NR | – |
| Organic substrates not used | Gala Gluc Sucr | Acet Arab Fuma Fruc Glyc Lacto Manni Prop Raff Ribo Sorbi Succ Xylo | Cell Fruc Fuma Gala Lacto Mann Raff Rham Xylo | Acet Arab Fruc Fuma Gala Gluc Glyc Lacto Mala Malt Mann Manni Prop Raff Ribo Sorbi Succ Star Treh | | Acet Lacto Manni Ribo Sorbi Sorb Succ Xylo | Citr Fruc Lact Mann Manni Ribo Sorb Sorbi Star Succ Xylo | Acet Fruc Gala Ribo Sorb Sucr Xylo |
| Indole from typtophan | – | – | – | – | – | – | – | + |
| Starch hydrolysis | NR | – | – | – | – | + | – | – |
| Gelatin liquefaction | – | – | – | – | – | + | – | – |
| Nitrate reduction | NR | + | + | + | w | + | + | + |
| Polar lipids | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | PG, PGP-Me | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | PG, PGP-Me, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | PG, PGP-Me |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Respiratory quinones | NR | NR | NR | NR | NR | NR | NR | NR |
| Sensitivity to antibiotics | NR | Sensitive: Bac Nov | Sensitive: Bac Nov | Sensitive: Bac Nov Rif | Sensitive: Bac Nov | Sensitive: Bac Nov Rif | Sensitive: Nov Rif | Sensitive: Ery Nov |
| | | Resistant: Amp Chl Ery Gen Kan Neo Pen Pol Rif Str Van | Resistant: Amp Chl Neo Pen Rif Str | Resistant: Amp Chl Ery Gen Kan Neo Rif Str | Resistant: Amp Chl Gen Neo Rif Str Tet | Resistant: Amp Chl Cip Ery Kan Neo Rif Str Tet | Resistant: Amp Bac Chl Cip Ery Kan Neo Pen Str Tet Van | Resistant: Amp Bac Chl Kan Neo Pen Pol Rif Str Tet Van |
| G + C content of DNA (mol %) | 63.6 (major comp.); 54.6 (minor) | 64.0 | 61.9 | 69.4 | 65.3–65.8 (major comp.); 54.8–56.5 (minor) | 65.9 | 64.9 | 60.2 |
| Sample source and site | Salinie soil, USSR | Salt lake, China | Sabkha, Algeria | Salt lake, Inner Mongolia | Deep Lake, Antarctica | Salt lake, China | Saltern, China | Salt lake, Inner Mongolia |

Data taken from:

[a] Zvyagintseva and Tarasov (1987)

[b] Zvyagintseva et al. (1996)

[c] Ventosa et al. (2004)

[d] Oren and Ventosa (1996)

[e] Castillo et al. (2007a)

[f] Kharroub et al. (2006)

[g] Gutiérrez et al. (2008a)

[h] Franzmann et al. (1988)

[i] McGenity and Grant (1995)

[j] Cui et al. (2006a)

[k] Cui et al. (2007a)

[l] Hu et al. (2008)

Additional data on growth substrates and other properties can be found in the original species descriptions

**◘ Table 7.13**

**Comparison of selected characteristics of the members of the genus *Halorubrum* (part C)**

| Genus | *Halorubrum* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | *Hrr. orientale*[a] | *Hrr. sodomense*[b,c] | *Hrr. tebenquichense*[d] | *Hrr. terrestre*[e,f] | *Hrr. tibetense*[g] | *Hrr. trapanicum*[c] | *Hrr. vacuolatum*[h,i] | *Hrr. xinjiangense*[j] |
| Older names | | Basonym: *Halobacterium sodomense*; *Halorubrobacterium sodomense* is a later homotypic synonym | | Formerly classified as a strain of *Hrr. distributum* | | Basonym: *Halobacterium trapanicum* | Basonym: *Natronobacterium vacuolatum* corrig. | |
| Type strain | CECT (7145)<br>CGMCC 1.6295<br>JCM 13889 | ATCC 33755<br>CIP 105330<br>DSM 3755<br>IFO (now NBRC) 14740<br>JCM 8880<br>NCIMB 2197<br>VKM B–1771 | CECT 5371<br>DSM 14210<br>JCM 12290 | JCM 10247<br>VKM B-1739 | AS 1.3239<br>JCM 11889 | NCCB 71076<br>NRC 34021<br>VKM B-2026 | CIP 104547<br>DSM 8800<br>JCM 9060<br>NCIMB 13189 | AS 1.3527<br>JCM 12388 |
| Cell shape | Pleomorphic | Rods | Irregular discs | Pleomorphic, flat and disc-shaped | Irregular rods | Pleomorphic rods | Short rods; spherical in the stationary phase | Short rods |
| Cell size (μm) | 1.0–2.0 × 1.5–2.0 | 0.5 × 2.5–5.0 | 0.8–1.2 × 1.0–1.5 | 1.0–1.5 × 1.5–2.5 | 0.5–1.0 × 1.5–2.5 | 0.7–1.0 × 1.5–3.0 | 0.5–0.7 × 1.5–3.0 | 0.8–1.2 × 1.8–2.6 |
| Motility | + | + | NR | + | – | – | – | + |
| Colony color | Red | Red-orange | Red-orange | Orange-red | Red | Pale orange to almost colorless | Pink | Red |
| NaCl range for growth and optimum (%) | 15–30 (Opt. 20) | 3–25 (Opt. 10–15) | 15–30 | 15–30 (Opt. 25) | 10–30 (Opt. 18–20) | 15–30 | 15–30 (Opt. 20) | 12–30 (Opt. 18–20) |
| Lysis in distilled water | NR | + | NR | NR | + | NR | + | NR |
| Magnesium requirement and optimum (M) | – | + (Opt. 0.6–1.2) | – | NR | – | NR | – | – |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| pH range for growth and optimum | 6.0–10.0 (Opt. 8.0) | NR | 7.0–10.0 | 5.0–9.0 (Opt. 7.5) | 8.0–10.5 (Opt. 9.0–9.5) | NR | 8.5–10.5 (Opt. 9.5) | 6.0–10.0 (Opt. 7.0–7.5) |
| Temperature range for growth and optimum (°C) | 25–50 (Opt. 35–40) | 20–50 (Opt. 40) | 35–50 | 28–50 (Opt. 37–45) | 22–45 (Opt. 37–40) | Opt. 37 | 20–50 (Opt. 35–40) | 10–54 (Opt. 40) |
| Organic substrates used | Fruc Fuma Gluc Glyc Malt Star | Fruc Gluc Glyc Malt Sucr | Acet Fruc Gala Glyc Mann Pyru Treh | NR | Acet Gluc Lacto Malt Mann Manni Sorb Succ Sucr Star | Fruc Gala Gluc Glyc Mann Malt Sucr Treh | Acet Citr Fuma Gala Gluc Succ Sucr | Fruc Gluc Malt Sucr |
| Acid produced from | – | Fruc Gluc Glyc Malt Sucr | – | Glyc | – | Fruc Gala Gluc Glyc Mann Malt Sucr Treh | – | Fruc Malt Gluc Sucr |
| Organic substrates not used | Acet Arab Lacto Mala Manni Prop Sorbi Succ Raff Ribo Xylo | Gala Lacto Mann Ribo | NR | Cell Etha Manni Raff Rham Sorbi Treh | Gala | Arab Lacto Manni Raff Rham Ribo Sorb Star Xyl | Fruc Manni Pyru | Gala Glyc Lacto Mann Manni Raff Rham Ribo Sorbi organic acids |
| Indole from typtophan | – | – | – | – | – | – | NR | – |
| Starch hydrolysis | – | + | – | – | – | – | – | – |
| Gelatin liquefaction | – | – | – | – | – | – | – | NR |
| Nitrate reduction | + | + (w) | + | – | + | + | + | – |
| Polar lipids | PG, PGP-Me, S-DGD | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | PG, PGP-Me, S-DGD-3, 2 minor unidentified lipids | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG and PGP, 5 minor phospholipids | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG and PGP | $C_{20}C_{20}$ derivatives of PG, PGP-Me, PGS, S-DGD |
| Respiratory quinones | NR | NR | NR | NR | NR | NR | MK-8 | NR |

**Table 7.13 (continued)**

| Genus | *Halorubrum* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | *Hrr. orientale*[a] | *Hrr. sodomense*[b,c] | *Hrr. tebenquichense*[d] | *Hrr. terrestre*[e,f] | *Hrr. tibetense*[g] | *Hrr. trapanicum*[c] | *Hrr. vacuolatum*[h,i] | *Hrr. xinjiangense*[j] |
| Sensitivity to antibiotics | Sensitive: Amp Bac Chl Ery Gen Neo Nov Rif Str | Sensitive: Bac Nov | Sensitive: Bac Nov | Sensitive: Ani Bac Nov | Sensitive: Nov Pol | | Sensitive: Ery (w) Nov | NR |
| | Resistant: Pen Rif | Resistant: Chl Ery Kan Neo Kan Pen Str Tet | Resistant: Chl Kan Pen Tet | Resistant: Amp Chl Kan Pen Pol Str Tet | Resistant: Bac Chl Ery Neo Pen Rif Str Tet | | Resistant: Amp Chl Str Tet | |
| G + C content of DNA (mol%) | 64.2 | 68 | 63.2 | 64.2–64.9 | 63.3 | 64.3 | 62.7 | 68.0 |
| Sample source and site | Salt lake, Inner Mongolia | The Dead Sea | Hypersaline lake, Atacama Desert | Saline soil | Soda lake, Tibet | Solar salt, Italy | Lake Magadi, Kenya | Salt lake, China |

Data taken from:

[a] Castillo et al. (2006a)

[b] Oren (1983)

[c] McGenity and Grant (1995)

[d] Lizama et al. (2002)

[e] Ventosa et al. (2004)

[f] Zvyagintseva et al. (1996)

[g] Fan et al. (2004)

[h] Mwatha and Grant (1993)

[i] Kamekura et al. (1997)

[j] Feng et al. (2004)

Additional data on growth substrates and other properties can be found in the original species descriptions

**■ Table 7.14**

**Comparison of selected characteristics of the members of the genus *Haloterrigena***

| Genus | *Haloterrigena*[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Htg. turkmenica*[b,c] | *Htg. daqingensis*[d] | *Htg. hispanica*[e] | *Htg. jeotgali*[f] | *Htg. limicola*[g] | *Htg. longa*[g] | *Htg. saccharevitans*[h] | *Htg. salina*[i] | *Htg. thermotolerans*[j] |
| Older names | Basonym: *Halococcus turkmenicus* | | | | | | | | |
| Type strain | ATCC 51198<br>CIP 106419<br>DSM 5511<br>JCM 9101<br>NCIMB 13204<br>VKM B–1734 | CGMCC 1.8909<br>NCRB 105739 | ATCC BAA-1310<br>DSM 18328 | CECT 7218<br>DSM 18794<br>JCM 14585<br>KCTC 4020 | CGMCC 1.5333<br>JCM 13563 | CGMCC 1.5334<br>JCM 13562 | AS 1.3730<br>JCM 12889 | CGMCC 1.6203<br>JCM 13891 | ATCC 700275<br>DSM 11552<br>JCM 11050<br>NBRC 102635 |
| Cell shape | Coccoid to oval | Coccoid | Coccoid | Rods | Rods | Rods | Rods; coccoid in stationary cultures | Coccoid | Rods |
| Cell size (μm) | 1.5–2.0 | 0.8–1.3 | 1.5–2.0 | 0.4 × 1.0 | 0.6–0.8 × 1.8–3.6 | 0.5–0.6 × 2.8–11 | 0.4–1.0 × 3–10 | 1.2 × 1.6 | 0.7–1.0 × 4–13 |
| Motility | – | – | NR | – | + | – | + | – | – |
| Colony color | Red | Orange | Light red | Light red | Red | Red | Light red | Light-red | Pale red |
| NaCl range for growth and optimum (%) | Opt. 15–25 | 10–30 (Opt. 12–15) | 13–23 (Opt. 20) | 10–30 (Opt. 15–20) | 10–30 (Opt.18) | 10–30 (Opt.18) | >10 (Opt.18–20) | 15–30 (Opt. 20) | >12 (Opt.18–20) |
| Lysis in distilled water | – | – | + | + | NR | NR | NR | NR | + |
| Magnesium requirement and optimum | NR | NR | 0–0.4 (Opt. 0.2) | – | 0.005–0.7 (Opt. 0.05) | 0–1 (Opt. 0.1) | Opt. 0–0.2. | – | 0.005 |
| pH range for growth and optimum | NR | 8.0–10.5 (Opt. 10.0) | 6.5–8.5 (Opt. 7.0) | 6.5–8.5 (Opt. 7.0–7.5) | 6.5–9.0 (Opt. 7.0) | 6.5–9.0 (Opt. 7.0–7.5) | 6.5–8.5 (Opt. 7.5) | 6.0–9.0 (Opt. 7.0–8.0) | 6.5–8.2 (Opt. 7.0–7.5) |
| Temperature range for growth and optimum (°C) | Opt. 45 | 20–50 (Opt. 35) | 37–60 (Opt. 50) | 17–50 (Opt. 37–45) | 30–61 (Opt. 45–50) | 30–56 (Opt. 41–45) | 24–58 (Opt. 42–45) | 25–50 (Opt. 37) | <60 (Opt. 50) |

**Table 7.14 (continued)**

| Genus | *Haloterrigena*[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | *Htg. turkmenica*[b,c] | *Htg. daqingensis*[d] | *Htg. hispanica*[e] | *Htg. jeotgali*[f] | *Htg. limicola*[g] | *Htg. longa*[g] | *Htg. saccharevitans*[h] | *Htg. salina*[i] | *Htg. thermotolerans*[j] |
| Organic substrates used | Fruc Gluc Malt Mann Sucr | Acet Glyc Pyru Succ | Acet Citr Glyc Prop | Acet Fruc Lacto | Acet Pyru | Acet Gluc Malt Pyru Sucr | Acet Fuma Glyc Lact Mala Prop Pyru Succ | Acet Arab Fruc Gala Gluc Glyc, Lacto Malt Mann Xylo | NR |
| Acid produced from | Fruc (w) Gluc Glyc Mann (w) Ribo Sucr | Glyc | NR | – | – | Gluc, Sucr | Glyc | – | – |
| Organic substrates not used | Lacto Ribo | Arab Cell Citr Fruc Fuma Gala Gluc Lact Lacto Malt Mann Manni Rham Ribo Sorbi Sucr Treh Xylo | Arab Cell Gala Fruc Gluc Mann Ribo Sucr Treh Xylo | Citr Gluc Sucr | Fruc Gala Gluc Lacto Malt Mann Manni Ribo Sorb Sorbi Sucr Xylo | Fruc, Gala Lacto Mann Manni Ribo Sorb, Sorbi Xylo | Arab Citr Fruc Gala Gluc Lacto Malt Mann Manni Rham Ribo Sorbi Sucr Xylo | Mala Manni Raff Sorbi Succ Treh | Arab Cell Fruc Gluc Gala Glyc Sucr Mann Manni Lacto Rham Ribo Treh Xylo |
| Indole from typtophan | – | – | + | + | – | + | – | – | – |
| Starch hydrolysis | – | – | – | – | – | – | – | – | – |
| Gelatin liquefaction | – | – | – | – | – | – | – | – | w |
| Nitrate reduction | + | – | + | – | + | – | + | + | + (w) |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD | PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, S-DGD | PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Respiratory quinones | NR | NR | NR | NR | NR | NR | NR | NR | NR |
| Sensitivity to antibiotics | NR | Sensitive: Cip Ery Nov Rif | Sensitive: Bac Nov | Sensitive: Ani Aph Nov | Sensitive: Nov Rif | Sensitive: Nov Rif | Sensitive: Tet | | Sensitive: Ani Bac Nov |
| | | Resistant: Amp Bac Chl Kan Neo Pen Str Tet Van | Resistant: Amp Chl Ery Kan Neo Pen Str Tet Van | Resistant: Amp Bac Chl Ery Pen | Resistant: Amp Bac Chl Ery Kan Neo Pen Str Tet Van | Resistant: Amp Bac Chl Ery Kan Neo Pen Str Tet Van | Resistant: Amp Kan Str Van | Resistant: Amp Chl Ery Neo Pen Str Tet | Resistant: Amp Chl Ery Kan Neo Pen Str Tet Van |
| G + C content of DNA (mol %) | 59.8 | 59.3 | 62.0 | 62.3 | 61.9 | 63.2 | 66.6 | 67.0 | 63.3 |
| Sample source and site | Saline soil, Turkmenia | Saline alkaline soil, China | Salt lake, Spain | Fermented food, Korea | Salt lake, China | Salt lake, China | Salt lake, China | Salt lake, Inner Mongolia | Saltern, Puerto Rico |

Data taken from:

[a] Ventosa and Kamekura (2001)

[b] Zvyagintseva and Tarasov (1987)

[c] Ventosa et al. (1999)

[d] Wang et al. (2010)

[e] Romano et al. (2007)

[f] Roh et al. (2009)

[g] Cui et al. (2006c)

[h] Xu et al. (2005c)

[i] Gutiérrez et al. (2008b)

[j] Montalvo-Rodríguez et al. (2000)

Additional data on growth substrates and other properties can be found in the original species descriptions

**Table 7.15**

**Comparison of selected characteristics of the members of the genera *Halostagnicola*, *Halovenus*, and *Halovivax***

| Genus | *Halostagnicola* | | | *Halovenus* | *Halovivax* | |
|---|---|---|---|---|---|---|
| Species | *Hst. larsenii*[a] | *Hst. alkaliphila*[b] | *Hst. kamekurae*[c] | *Hvn. aranensis*[d] | *Hvx. asiaticus*[e] | *Hvx. ruber*[f] |
| Type strain | CECT 7116<br>CGMCC 1.5338<br>DSM 17691<br>JCM 13463 | CECT 7631<br>JCM 16592 | CECT 7536<br>DSM 22427<br>JCM 16110 | CGMCC 1.11001<br>IBRC-M 10015 | CECT 7098<br>CGMCC 1.4248<br>JCM 14624 | CGMCC 1.6204<br>DSM 18193<br>JCM 13892 |
| Cell shape | Pleomorphic rods | Pleomorphic rods | Pleomorphic rods | Pleomorphic: rods to triangles, squares or disc-shaped | Pleomorphic rods | Pleomorphic rods and irregular cells |
| Cell size (μm) | 0.5–1.0 × 1.0–3.0 | 0.8–1.0 × 2.0–2.5 | 0.8–1.0 × 2.0–2.5 | 0.6–1.3 × 4.9–10.7 | 0.4–0.5 × 4.0–5.0 | 0.6–0.8 × 3.5–4.5 |
| Motility | – | + | + | – | – | – |
| Colony color | Pink | White-pink | White, later pink | Red | Pale pink | Red |
| NaCl range for growth and optimum (%) | 15–30 (Opt. 20) | 20–30 (Opt. 25) | 10–30 (Opt. 15) | 15–30 (Opt. 23) | 15–25 (Opt. 20) | >15 (Opt. 20) |
| Lysis in distilled water | + | + | + | + | + | + |
| Magnesium requirement and optimum (M) | – | NR | – (Opt. 0.06) | 0.2–1.0 (Opt. 0.5) | – | >0.005 (Opt. 0.15) |
| pH range for growth and optimum | Opt. 7.0–8.0 | 8.0–10.0 (Opt. 8.5–9.0) | 6.0–9.0 (Opt. 6.5–7.0) | 6.0–8.0 (Opt. 7.5) | 6.0–9.0 (Opt. 7.0–7.5) | 6.0–9.0 (Opt. 7.0–7.5) |
| Temperature range for growth and optimum (°C) | <50 (Opt. 37) | 20–55 (Opt. 37) | 20–45 (Opt. 30) | 25–50 (Opt. 40) | 25–45 (Opt. 37) | 25–45 (Opt. 37) |
| Organic substrates used | Acet Arab Fruc Gala Gluc Glyc Lacto Malt Prop Ribo Star Treh Xylo | Fruc Fuma Gala Gluc Glyc Lact Malt Mann Prop Pyru Sucr Treh Xylo | Acet Arab Gala Gluc Glyc Lacto Mala Malt Mann Prop Treh | Gala Gluc | Acet Lacto Prop Raff Treh Xylo | Fuma Lacto Mann Prop Raff Ribo Starc Treh Xylo |
| Acid produced from | Sucr | NR | Arab Mann | Gluc | Xylo | NR |
| Organic substrates not used | Fuma Mala Raff Sorbi Succ | Acet Arab Cell Citr Lacto Mala Manni Ribo Raff Succ | Cell Fruc Fuma Manni Ribo Sorbi Succ Sucr Xylo | Lacto | Arab Fruc Fuma Gala Gluc Glyc Mala Malt Manni Ribo Sorbi Star Succ Sucr | Acet Arab Fruc Gala Gluc Glyc, Mala Malt Manni Sorbi Succ |
| Indole from typtophan | – | – | + | – | – | – |
| Starch hydrolysis | + | – | – | – | – | – |
| Gelatin liquefaction | – | – | – | – | + | + |

**Table 7.15 (continued)**

| Genus | *Halostagnicola* | | | *Halovenus* | *Halovivax* | |
|---|---|---|---|---|---|---|
| **Species** | ***Hst. larsenii***[a] | ***Hst. alkaliphila***[b] | ***Hst. kamekurae***[c] | ***Hvn. aranensis***[d] | ***Hvx. asiaticus***[e] | ***Hvx. ruber***[f] |
| Nitrate reduction | + | + | + | − | − | − |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, 2 unidentified glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me | PG, PGP-Me, 2 major unknown glycolipids, several minor unknown glycolipids | PG, PGP-Me, 2 minor phospholipids | PG, PGP-Me, 2 major and 1 minor glycolipids, 1 unidentified glycolipid | PG, PGP-Me, 2 major and 1 minor glycolipids, 1 unidentified glycolipid |
| Respiratory quinones | NR | NR | NR | MK-8(II-$H_2$) | NR | NR |
| Sensitivity to antibiotics | Sensitive: Bac Nov | Sensitive: Ani Bac Ery Nov Rif | Sensitive: Ani Bac Nov Rif | Sensitive: Ani Bac Nov Rif Str | Sensitive: Bac Nov | Sensitive: Amp Bac Gen Neo Nov Rif |
| | Resistant: Amp Chl Ery Neo Pen Rif Str Tet | Resistant: Amp Chl Ery Kan Neo Pen Str Tet Van | Resistant: Amp Chl Ery Gen Kan Neo Pen Str Tet | Resistant: Amp Chl Ery Gen Kan Neo Pen Tet | Resistant: Amp Chl Ery Gen Neo Pen Rif Str Tet | Resistant: Chl Ery Pen |
| G + C content of DNA (mol %) | 61.0 | 60.7 | 59.8 | 61.0 | 60.3 | 65.0 |
| Sample source and site | Salt lake, Inner Mongolia | Rock salt imported to Japan from China | Solar salt important to Japan from the Philippines | Salt lake, Iran | Salt lake, Inner Mongolia | Salt lake, Inner Mongolia |

Data taken from:
[a] Castillo et al. (2006d)
[b] Nagaoka et al. (2011)
[c] Nagaoka et al. (2010)
[d] Makhdoumi-Kakhki et al. (2012a)
[e] Castillo et al. (2006b)
[f] Castillo et al. (2007b)
Additional data on growth substrates and other properties can be found in the original species descriptions

examples being *Har. hispanica*, *Hfx. volcanii*, *Hmn. pharaonis*, and *Hrd. utahensis* (Feng et al. 2012). The list of organic compounds given here is limited to sugars, sugar alcohols, and organic acids. Some species descriptions give information on the use of different amino acids as well. Properties such as the Gram stain are not listed in the tables as, with very few exceptions, all members of the *Halobacteriaceae* stain Gram negative, when using the special modification of the Gram stain protocol developed for halophilic prokaryotes. Exceptions are *Hrr. vacuolatum* and *Htg. daquinensis*, reported as Gram variable. Nearly all members of the family were reported to display catalase activity, exceptions being *Hla. acidiphilum*, *Hns. pteroides*, *Hst. alkaliphila*, *Hst. kamekurae*, and *Nac. mannanilyticum*. The oxidase reaction is also generally positive, but in some species, no oxidase activity could be detected: *Hbt. noricense*, *Hac. jeotgali*, *Hla. acidiphilum*, *Hcc. hamelinensis*, *Hcc. qingdaonensis*, *Hfx. mucosum*, *Hns. pteroides*, *Hrd. tiamatea* (a rare case of a member of the *Halobacteriaceae* with an anaerobic life style), *Hrr. aquaticum*, *Hrr. cibi*, *Hst. kamekurae*, *Nnm. pellirubrum*, *Nac. mannanilyticum*, and *Ncc. jeotgali*. When evaluating such results, it should be taken into account that different protocols may have been used in different laboratories. A comparative study using comparable methods and culture of similar age was never yet performed.

A critical evaluation of the tables shows some problematic data published in the species descriptions. For example, the growth of *Hmr. oriensis*, *Hrr. aquaticum*, *Hrr. kocurii*, *Hrr. orientale*, *Hrr. tibetense*, *Htg. salina*, and *Hvx. ruber* was reported to be stimulated by starch, but amylase activity could not be detected in these species. Also some of the published data on sensitivity to antibiotics need a renewed evaluation. For example, the described sensitivity of *Hvx. ruber* to ampicillin, an antibiotic that inhibits the formation of the bacterial cell wall but not of the wall of the Archaea, needs to be reassessed.

The short descriptions of the different genera given below only list their distinctive phenotypic and chemotaxomic properties. Since in recent years many new genera have been proposed mainly on the basis of 16S rRNA gene sequences, it has become

**Table 7.16**

**Comparison of selected characteristics of the members of the genus *Natrialba***

| Genus | *Natrialba*[a] | | | | | |
|---|---|---|---|---|---|---|
| Species | *Nab. asiatica*[b] | *Nab. aegyptiaca*[c] | *Nab. chagannaoensis*[d] | *Nab. hulunbeirensis*[d] | *Nab. magadii*[e,f] | *Nab. taiwanenis*[c] |
| Older names | | *Nab. aegyptia* | | | Basonym: *Natronobacterium magadii* | *Natrialba asiatica* B1T |
| Type strain | ATCC 700177<br>CIP 105332<br>DSM 12278<br>JCM 9576<br>NBRC 102637 | DSM 13077<br>JCM 11194<br>NBRC 102636 | AS 1.1977<br>JCM 10990<br>NBRC 102638 | AS 1.1986<br>JCM 10989<br>NBRC 102639 | ATCC 43099<br>CIP 104546<br>JCM 8861<br>NBRC 102185<br>NCIMB 2190 | DSM 12281<br>JCM 9577<br>NBRC 102640 |
| Cell shape | Rods-coccobacilli | Rods, cocci, tetrads | Rods | Rods | Rods | Rods-coccobacilli |
| Cell size (μm) | 0.5–1.0 × 1.0–5.0 | 0.5–1.2 × 1.5–6 | 0.4–0.6 × 1.0–2.5 | 0.4–0.6 × 1.0–2.5 | 0.7–0.9 × 2–4 | 0.3–0.5 × 1.0–1.5 |
| Motility | + | + (rods) | – | – | + | + |
| Colony color | Non-pigmented | Non-pigmented to slightly pigmented | Red | Red | Orange-red | Non-pigmented |
| NaCl range for growth and optimum (%) | 12–30 (Opt. 23) | 10–30 (Opt. 15–18) | 10–30 (Opt. 15) | 12–30 (Opt. 20) | 12–30 (Opt. 20) | 12–30 (Opt. 20) |
| Lysis in distilled water | + | + | + | + | + | + |
| Magnesium requirement and optimum (M) | – | – | NR | NR | NR | – |
| pH range for growth and optimum | 6.0–8.0 (Opt. 6.6–7.0) | 6.0–9.0 (Opt. 7.0–8.0) | 8.5–10.5 (Opt. 9.0) | 8.5–10.0 (Opt. 9.0) | 8.5–11.0 (Opt. 9.5) | 5–10 (Opt. 7.5–7.8) |
| Temperature range for growth and optimum (°C) | <50 (Opt. 30–40) | <60 (Opt. 37–42) | 20–55 (Opt. 45) | 20–55 (Opt. 50) | 20–50 (Opt. 37–40) | Up to 55 (Opt. 35–40) |
| Organic substrates used | NR | NR | Acet Fruc Gluc Malt | Fruc Malt | Acet | NR |
| Acid produced from | NR | Arab Gluc Lacto (w) Malt Sucr Star Xylo | NR | NR | NR | Arab Gluc (w) Malt (w) Sucr Star Xylo |
| Organic substrates not used | NR | NR | Lacto Manni Sucr | Acet Gluc Lacto Manni Sucr | Carbohydrates | NR |
| Indole from typtophan | + | + | NR | NR | NR | + |
| Starch hydrolysis | – | + | + | – | NR | + |
| Gelatin liquefaction | + | + | + | + | – | – |
| Nitrate reduction | + | + | + | + | – | + |

**Table 7.16** (continued)

| Genus | *Natrialba*[a] | | | | | |
|---|---|---|---|---|---|---|
| Species | *Nab. asiatica*[b] | *Nab. aegyptiaca*[c] | *Nab. chagannaoensis*[d] | *Nab. hulunbeirensis*[d] | *Nab. magadii*[e,f] | *Nab. taiwanenis*[c] |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$–DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, 1 uncharacterized lipid | NR | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD |
| Respiratory quinones | NR | NR | NR | NR | MK-8, MK-8($H_2$) | NR |
| Sensitivity to antibiotics | Sensitive: Ani Bac Nov Rif | Sensitive: Ani Bac Rif Nov | Sensitive: Bac Ery Rif | Sensitive: Bac Ery Rif | Sensitive: Ani Bac Ery Nov | Sensitive: Ani Bac Rif Nov |
| | Resistant: Chl Ery Pen Str Tet | Resistant: Chl Ery Pen Str Tet | Resistant: Tet | Resistant: Tet | Resistant: Amp Chl Pol Str Tet | Resistant: Chl Ery Pen Str Tet |
| G + C content of DNA (mol%) | 60.3–63.1 | 61.5 | 63.7 | 64.3 | 63.0 (major component) 49.5 (minor component) | 62.3 |
| Sample source and site | Beach sand, Japan | Salt soil, Egypt | Soda lake, China | Soda lake, China | East-African alkaline lakes | Solar salt, Taiwan |

Data taken from:

[a] Kamekura (2001a)

[b] Kamekura and Dyall-Smith (1995)

[c] Hezayen et al. (2001)

[d] Xu et al. (2001b)

[e] Tindall et al. (1984)

[f] Kamekura et al. (1997)

Additional data on growth substrates and other properties can be found in the original species descriptions

more difficult to find morphological, physiological, or chemotaxonomic traits that can be used to unequivocally assign a strain to one of these genera. An example can be found in the description below of the genus *Halomicrobium*, a genus established only on the basis of 16S rRNA gene comparisons, which now contains organisms with greatly different G+C contents of their DNA, with some species possessing and some lacking phosphatidylglycerol sulfate in their polar lipids. Full descriptions of the genera can be found in the original descriptions as cited. A number of emended genus descriptions were given by Oren et al. (2009).

## Genus *Halobacterium* Elazari-Volcani 1957, 207$^{AL}$; emend. Kamekura and Dyall-Smith 1995, 344; emend. Oren, Arahal, and Ventosa 2009, 638

*Ha.lo.bac.te'ri.um.* Gr. n. *hals, halos*, salt; L. neut. n. *bacterium*, a small rod; N.L. neut. n. *Halobacterium*, salt (-requiring) bacterium.

Cells are motile rods of varying length and lyse in distilled water. 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. Magnesium requirement is moderate (5–50 mM). Amino acids are required for growth. Many strains grow anaerobically in the dark by fermentation of arginine. Sugars are poorly used, and no acid is formed in the presence of sugars. The optimum salt concentration for growth is 3.5–4.5 M NaCl. Neutrophilic. Characteristic lipids are PG, PGP-Me, PGS, and sulfated triglycosyl- and tetraglycosyl diethers.

The mol% G+C of the DNA is 54.3–70.9.

The genus *Halobacterium* currently contains three species: *Hbt. salinarum* (type species), *Hbt. jilantaiense*, and *Hbt. noricense.*

The main features of the members of the genus are summarized in ➔ *Table 7.1*.

Additional comments:

- *Hbt. piscisalsi* (Yachai et al. 2008) is not included in the table, as it is now considered a later heterotypic synonym of *H. salinarum* (Minegishi et al. 2012b).
- *Hbt. cutirubrum, Hbt. halobium*, and *Hbt. salinarium* were renamed as *Hbt. salinarium* nom. corrig. (Ventosa and Oren 1996).

**Table 7.17**

**Comparison of selected characteristics of the members of the genus *Natrinema***

| Genus | *Natrinema*[a] | | | | | |
|---|---|---|---|---|---|---|
| Species | *Nnm. pellirubrum*[b] | *Nnm. altunense*[c] | *Nnm. ejinorense*[d] | *Nnm. gari*[e] | *Nnm. pallidum*[b] | *Nnm. versiforme*[f] |
| Type strain | CIP 106293<br>JCM 10476<br>NCIMB 786 | AS 1.31731<br>JCM 12890 | CECT 7144<br>CGMCC 1.6202<br>JCM 13890 | BCC 24370<br>JCM 14663<br>PCU 303 | CIP 106292<br>JCM 8980<br>NCIMB 777 | ANMR 0149<br>AS 1.2365<br>JCM 10478 |
| Cell shape | Rods | Rods | Pleomorphic | Rods | Rods | Pleomorphic |
| Cell size (μm) | 0.6–1.0 × 1–4 | 0.8–1.2 × 3–7 | 0.8–2.0 × 1.5–4.0 | 0.5–0.8 × 2.0–3.0 | 0.7–1.0 × 1.5–6 | 0.6–1.5 × 1–5 |
| Motility | + | + | – | + | + | – |
| Colony color | Pale orange | Orange-red | Pale red | Pale orange | Pale orange | Light red |
| NaCl range for growth and optimum (%) | >12 (Opt. 20–25) | > 10 (Opt. 18–25) | >10 (Opt. 20) | Opt. 15–20 | >10 (Opt. 20–25) | > 9 (Opt. 20–25) |
| Lysis in distilled water | + | + | + | + | + | + |
| Magnesium requirement and optimum (M) | 0.1–0.2 | >0.005 (Opt. 0.050–0.2) | – | – (Opt. 0.1–0.2) | 0.1–0.2 | >0.005 (Opt. 0.15) |
| pH range for growth and optimum | 6.0–8.6 (Opt. 7.2–7.8) | 6.0–8.0 (Opt. 7.0–7.7) | 6.0–8.5 (Opt. 7.0) | 5.5–8.5 (Opt. 6.0–6.5) | 6.0–8.4 (Opt. 7.2–7.6) | 6.0–8.0 (Opt. 6.5–7.0) |
| Temperature range for growth and optimum (°C) | 20–45 | 20–40 | 25–50 (Opt. 37) | 20–60 (Opt. 37–40) | 25–60 (Opt. 37–40) | 20–53 (Opt. 37–46) |
| Organic substrates used | Fruc Gluc Lacto Ribo | Acet Fuma Gluc Glyc, Mala Malt Prop Pyru Succ | Acet Fruc Fuma Gluc Glyc Malt Prop Treh | Arab Gluc Glyc | Fruc Gluc Lacto | Fruc Gala Gluc Glyc Malt Mann Ribo Sucr Xylo |
| Acid produced from | NR | Gluc Glyc Malt Mann | NR | Arab, Glyc | NR | Glyc |
| Organic substrates not used | NR | Fruc Gala Lacto Ribo Sucr Xylo | Arab Gala Mala Mann Lacto Manni Raff Ribo, Sorbi Succ Xylo | Citr Lacto Malt Manni Mann, Meli Rham Ribo Sorbi Sucr Xylo | Ribo | Lacto |
| Indole from typtophan | – | – | – | – | – | + |
| Starch hydrolysis | – | – | + | – | – | w |
| Gelatin liquefaction | + | + | + | + | + | – |
| Nitrate reduction | + | + | + | – | + | + |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, PGS (trace), unidentified glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, PGS, unidentified glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, $S_2$-DGD-1 | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, PGS, 2 glycolipids, 1 unidentified lipid | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, PGS, unidentified glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, PGS, 2 unidentified glycolipids |

**Table 7.17 (continued)**

| Genus | *Natrinema*[a] | | | | | |
|---|---|---|---|---|---|---|
| Species | *Nnm. pellirubrum*[b] | *Nnm. altunense*[c] | *Nnm. ejinorense*[d] | *Nnm. gari*[e] | *Nnm. pallidum*[b] | *Nnm. versiforme*[f] |
| Respiratory quinones | MK-8, MK-8($H_2$) | NR | NR | MK-8 | MK-8, MK-8($H_2$) | NR |
| Sensitivity to antibiotics | Sensitive: Ani Bac Nov | Sensitive: NR | Sensitive: Bac Nov | Sensitive: Bac Nov Rif | Sensitive: Ani Bac Nov Rif (w) | Sensitive: Ani Bac Nov Rif |
| | Resistant: Amp Chl Rif Str Tet | Resistant: Amp Cip Ery Kan Neo Str | Resistant: Amp Chl Ery Pen Rif Str Tet | Resistant: Amp Chl Kan Neo. Str Tet | Resistant: Amp Chl Str Tet | Resistant: Amp Chl Ery Neo Pen |
| G + C content of DNA (mol %) | 69.9 (major component), 60.0 (minor component) | 65.6 | 64.7 | 65.4 | NR | 64.2 |
| Sample source and site | Salted hides | Salt lake, China | Salt lake, Inner Mongolia | Fermented fish sauce, Thailand | Salted fish, hides | Salt lake, China |

Data taken from:
[a] McGenity et al. (2001)
[b] McGenity et al. (1998)
[c] Xu et al. (2005b)
[d] Castillo et al. (2006c)
[e] Tapingkae et al. (2008)
[f] Xin et al. (2000)
Additional data on growth substrates and other properties can be found in the original species descriptions

- *Hbt. denitrificans* (Tomlinson et al. 1986) was reclassified as *Hfx. denitrificans* comb. nov. (Tindall et al. 1989).
- *Hbt. distributum* (Zvyagintseva et al. 1987) was reclassified as *Hrr. distributum* comb. nov. (Oren and Ventosa 1996).
- *Hbt. lacusprofundi* (Franzmann et al. 1988) was reclassified as *Hrr. lacusprofundi* comb. nov. (McGenity and Grant 1995; Validation List 57, 1996).
- *Hbt. mediterranei* (Rodriguez-Valera et al. 1983) was reclassified as *Hfx. mediterranei* (Torreblanca et al. 1986).
- *Hbt. pharaonis* (Soliman and Trüper 1982) was reclassified first as *Nbt. pharaonis* comb. nov. (Tindall et al. 1984) and later as *Nmn. pharaonis* comb. nov. (Kamekura et al. 1997).
- *Hbt. saccharovorum* (Tomlinson and Hochstein 1976) was reclassified as *Hrr. saccharovorum* comb. nov. (McGenity and Grant 1995; Validation List 57, 1996).
- *Hbt. sodomense* (Oren 1983) was reclassified as *Hrr. sodomense* comb. nov. (McGenity and Grant 1995; Validation List 57, 1996).
- *Hbt. trapanicum* (Petter 1931) (Elazari-Volcani 1957) was reclassified as *Hrr. trapanicum* comb. nov. (McGenity and Grant 1995).
- *Hbt. vallismortis* (Gonzalez et al. 1978) was reclassified as *Har. vallismortis* comb. nov. (Torreblanca et al. 1986).

## Genus *Haladaptatus* Savage, Krumholz, Oren, and Elshahed 2007, 23$^{VP}$; emend. Cui, Sun, Gao, Dong, Xu, Zhou, Liu, Oren, and Zhou 2010a, 1087; emend. Roh, Lee, and Bae 2010, 1189

*Hal.a.dap.ta'tus.* Gr. n. *hals, halos*, salt; L. part. adj. *adaptatus*, adapted to a thing; N.L. masc. n. *Haladaptatus*, a bacterium adapted to salt.

Cells are cocci or coccobacilli occurring singly or in pairs and do not lyse in distilled water. Some species possess more than one different 16S rRNA gene sequences. Grow on a wide range of substrates, including single and complex carbon sources. Acid is produced from carbohydrates. Grow at a wide range of NaCl concentrations. Cells contain PG and PGP-Me and two or three glycolipids may be present, one of which is chromatographically identical to S-DGD-1. The presence of PGS is variable.

The mol% G+C of the DNA is 54.0–60.5.

The genus *Haladaptatus* currently contains three species: *Hap. paucihalophilus* (type species), *Hap. cibarius*, and *Hap. litoreus.*

The main features of the members of the genus are summarized in *Table 7.1*.

**Table 7.18**

**Comparison of selected characteristics of the members of the genera *Natronoarchaeum*, *Natronobacterium*, and *Natronococcus***

| Genus | *Natronoarchaeum* | *Natronobacterium*[b] | *Natronococcus*[d] | | |
|---|---|---|---|---|---|
| Species | *Nac. mannanilyticum*[a] | *Nbt. gregoryi*[c] | *Ncc. occultus*[b] | *Ncc. amylolyticus*[e] | *Ncc. jeotgali*[f] |
| Type strain | CECT 7565 JCM 16328 | ATCC 43098 CIP 104747<br>DSM 3393 JCM 8860<br>NBRC 102187 NCIMB 2189<br>VKM B-1750 | ATCC 43101 CIP 104548<br>DSM 3396 JCM 8859<br>NBRC 102186 NCIMB 2192<br>VKM B-1752 | ATCC 51971<br>CIP 10533<br>DSM 10524<br>JCM 9655 | CECT 7216<br>DSM 18795<br>JCM 14583<br>KCTC 4018 |
| Cell shape | Extremely pleomorphic | Rods | Cocci | Cocci | Cocci |
| Cell size (μm) | 1–5 | 0.5–1.0 × 2–15 | 1.0–2.0 | 1.0–2.0 | 1.0–2.0 |
| Motility | − | − | − | − | − |
| Colony color | Red | Red | Pale brown | Orange-red | Orange-red |
| NaCl range for growth and optimum (%) | 12–30 (Opt. 23–26) | 12–30 (Opt. 17.5) | 8–30 (Opt. 20–22) | 8–30 (Opt. 15–20) | 7.5–30 (Opt. 23–25) |
| Lysis in distilled water | + | + | − | − | − |
| Magnesium requirement and optimum (M) | + (Opt. 0.005) | − | − | − | − |
| pH range for growth and optimum | 5.8–9.5 (Opt.8.0–9.0) | >8.5 (Opt. 9.5) | 8.5–11.0 (Opt. 9.5) | 8.0–10.0 (Opt. 9.0) | 7.0–9.5 (Opt. 7.5) |
| Temperature range for growth and optimum (°C) | 20–55 (Opt. 37) | 25–40 (Opt. 37) | 20–50 (Opt. 35–40) | 22–50 (Opt. 40–45) | 21–50 (Opt. 37–45) |
| Organic substrates used | Cell Gluc Lacto Mann Pyru Raff | Fruc Gluc Mann Ribo Sucr | Gluc Ribo Sucr | Citr Lacto | Acet Fruc Gluc Lacto Sucr |
| Acid produced from | NR | NR | NR | NR | NR |
| Organic substrates not used | NR | NR | Citr Lacto | NR | Citr |
| Indole from typtophan | + | NR | NR | NR | NR |
| Starch hydrolysis | + | − | − | + | NR |
| Gelatin liquefaction | − | + | + | − | NR |
| Nitrate reduction | − | − | + | + | + |
| Polar lipids | PG, PGP-Me, $S_2$–DGD, 1 unknown glycolipid | PG, PGP-Me, minor unidentified phospholipids | PG, PGP-Me, a phosphatidylglycero-(cyclo-)-phosphate (PL2) | PG, PGP-Me | PG, PGP-Me |
| Respiratory quinones | NR | MK-8, MK-8(VIII-$H_2$), MMK-8, MMK-8(VIII-$H_2$), DMMK-8, DMMK-8(VIII-$H_2$) | MK-8, MK-8($H_2$) | NR | NR |
| Sensitivity to antibiotics | Sensitive: Bac Nov Rif | Sensitive: Ani Bac Cip Ery Nov | Sensitive: Ani Bac Eri Nov | Sensitive: Ani Bac Eri Nov Tet | Sensitive: Ani Aph Bac (w) Nov |
| | Resistant: Amp Chl Ery Gen Kan Neo Pen Str Tet Van | Resistant: Amp Chl Pol Str Tet | Resistant: Amp Chl Pol Str Tet | Resistant: Amp Chl Pol Str | Resistant: Amp Chl Ery Pen |

**Table 7.18** (continued)

| Genus | *Natronoarchaeum* | *Natronobacterium*[b] | *Natronococcus*[d] | | |
|---|---|---|---|---|---|
| Species | *Nac. mannanilyticum*[a] | *Nbt. gregoryi*[c] | *Ncc. occultus*[b] | *Ncc. amylolyticus*[e] | *Ncc. jeotgali*[f] |
| G + C content of DNA (mol%) | 63 | 63.2–65.0 | 64.0 (major component)<br>55.7 (minor component) | 63.5 | NR |
| Sample source and site | Commercial salt, Japan | East-African soda lakes | Soda lakes, East Africa | Lake Magadi, Kenya | Shrimp jeotgal, Korea |

Data taken from:
[a]Shimane et al. (2010)
[b]Tindall (2001a)
[c]Tindall et al. (1984)
[d]Tindall (2001b)
[e]Kanai et al. (1995)
[f]Roh et al. (2007b)
Additional data on growth substrates and other properties can be found in the original species descriptions

## Genus *Halalkalicoccus* Xue, Fan, Ventosa, Grant, Jones, Cowan, and Ma 2005, 2504$^{VP}$

*Hal.al.ka.li.coc'cus.* Gr. n. *hals, halos*, salt; Arabic n. alkali (al-qaliy), the ashes of saltwort; N.L. masc. *coccus* (from Gr. masc. n. *kokkos*, grain, seed), coccus; N.L. masc. n. *Halalkalicoccus*, coccus existing in salted and alkaline environment.

Cells are cocci occurring singly, in pairs, or irregular clusters. Stain mainly Gram negative with some cells Gram positive in young cultures. Cells do not lyse in distilled water. Alkaliphilic. Possesses $C_{20}C_{20}$ and $C_{20}C_{25}$ diethers. No glycolipids or PGS detected. Isoprenoid quinones are MK-8 and MK-8($H_2$).

The mol% G+C of the DNA is 61.5–63.2.

The genus *Halalkalicoccus* currently contains two species: *Hac. tibetensis* (type species) and *Hac. jeotgali.*

The main features of the members of the genus are summarized in ➋ *Table 7.1*.

## Genus *Halarchaeum* Minegishi, Echigo, Nagaoka, Kamekura, and Usami 2010, 2515$^{VP}$

*Hal.ar.chae'um.* Gr. n. *hals, halos*, salt; N.L. neut. n. *archaeum* (from Gr. adj. *archaios*, ancient), ancient one, archaeon; N.L. neut. n. *Halarchaeum*, a saline archaeon.

Cells are nonmotile, pleomorphic, with triangular and disk morphology. Lipids are $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG and PGP-Me, and four unidentified glycolipids. Cells lyse in distilled water. Cells grow on a wide range of substrates, including simple and complex carbon sources.

The mol% G+C of the DNA is 61.4.

Type species and currently only species: *Hla. acidiphilum.*

The main features of the members of the genus are summarized in ➋ *Table 7.2*.

## Genus *Haloarchaeobius* Makhdoumi-Kakhki, Amoozegar, Bagheri, Ramezani, and Ventosa 2012, 1024$^{VP}$

*Ha.lo.ar.chae.o'bi.us.* Gr. n. *hals, halos*, salt; N.L. adj. *archaeos* from Gr. adj. *archaios* ancient; N.L. masc. n. *bius* from Gr. masc. n. *bios* life; N.L. masc. n. *Haloarchaeobius*, halophilic ancient (archaeal) life.

Cells are motile strictly aerobic rods, pigmented orange-red. Neutrophilic and mesophilic. Magnesium is not required for growth. Polar lipids include PG, PGP-Me, PGS, three unidentified glycolipids, and one minor phospholipid. MK-8(II-$H_2$) is the only respiratory lipoquinone present.

The mol% G+C of the DNA is 67.7.

Type species and currently only species: *Hab. iranensis.*

The main features of the members of the genus are summarized in ➋ *Table 7.2*.

## Genus *Haloarcula* Torreblanca, Rodriguez-Valera, Juez, Kamekura, and Kates 1986b, 573$^{VP}$ (Validation list 22); Effective Publication: Torreblanca, Rodriguez-Valera, Juez, Kamekura, and Kates 1986a, 98; emend. Oren, Arahal, and Ventosa 2009, 638

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

**Table 7.19**

**Comparison of selected characteristics of the members of the genera *Natronolimnobius*, *Natronomonas*, and *Salarchaeum***

| Genus | *Natronolimnobius* | | *Natronomonas*[b] | | *Salarchaeum* |
|---|---|---|---|---|---|
| Species | *Nln. baerhuensis*[a] | *Nln. innermongolicus*[a] | *Nmn. pharaonis*[c,d] | *Nmn. moolapensis*[e] | *Sar. japonicum*[f] |
| Older names | | | Basonym: *Halobacterium pharaonis* Other synonym: *Natronobacterium pharaonis* | | |
| Type strain | CGMCC 1.3597<br>JCM 12253 | CGMCC 1.2124<br>JCM12255 | ATCC 35678<br>CIP 103997<br>DSM 2160<br>IFO (now NBRC) 14720<br>JCM 8858<br>NCIMB 2260<br>VKM B-1749 | CECT 7526<br>DSM 18674<br>JCM 14361 | CECT 7563<br>JCM 16327 |
| Cell shape | Rods | Pleomorphic, flat | Rods | Short rods, flat tetragonal shapes, cocci | Short rods |
| Cell size (μm) | 0.5 × 3.0–5.0 | 0.6 × 3.0–6.0 | 0.8 × 2–3 | 0.7–1.7 | 0.5–1.0 × 0.5–2.0 |
| Motility | + | − | + | + | + |
| Colony color | Red | Light red | Red | Red | Red |
| NaCl range for growth and optimum (%) | >15 (Opt. 20) | >10 (Opt. 15–20) | 12–30 (Opt. 20) | 14–36 (Opt. 18–20) | 9–30 (Opt. 15–18) |
| Lysis in distilled water | + | + | + | + | + |
| Magnesium requirement and optimum (M) | NR | NR | − | Opt. 0.2–0.4 | + (Opt. 0.2–0.3) |
| pH range for growth and optimum | 7.0–10.0 (Opt. 9.0) | 7.5–10.0 (Opt. 9.5) | Opt. 8.5–9.0 | 5.5–8.5 (Opt. 7.0–7.5) | 5.0–8.8 (Opt. 5.2–6.3) |
| Temperature range for growth and optimum (°C) | 30–46 (Opt. 37) | 19–54 (Opt. 45) | 25–50 (Opt. 45) | 25–45 | 20–55 (Opt. 40) |
| Organic substrates used | Acet Arab Fruc Fuma Gala Gluc Glyc Lacto Malt Mann Pyru Rham Raff Xylo | Acet Arab Fuma Gala Gluc Glyc Lact Mala Prop Pyru Raff Sorbi | Buty Fuma Pyru | Acet Buta Buty Etha Gluc (v) Glyc Lact Prop Pyru | Fuma Mala Succ |
| Acid produced from | NR | NR | NR | − | NR |
| Organic substrates not used | Citr Prop Sorbi | Fruc Lacto Malt Mann Rham Succ Sucr Xylo | Sugars | Arab, Benz Cell Citr Fruc Fuma Gala Gluc (v) Lacto Mala Manni Mann Ribo Succ Sucr Xylo | Acet Arab Cell Citr Fruc Gala Gluc Glyc Lact Lacto Malt Mann Pyru Raff Ribo Sorbi Sucr Treh Xylo |
| Indole from typtophan | + | + | + | − | − |
| Starch hydrolysis | − | − | − | − | − |

**Table 7.19 (continued)**

| Genus | *Natronolimnobius* | | *Natronomonas*[b] | | *Salarchaeum* |
|---|---|---|---|---|---|
| Species | *Nln. baerhuensis*[a] | *Nln. innermongolicus*[a] | *Nmn. pharaonis*[c,d] | *Nmn. moolapensis*[e] | *Sar. japonicum*[f] |
| Gelatin liquefaction | – | + | + | NR | – |
| Nitrate reduction | – | + | – | v | – |
| Polar lipids | PG, PGP-Me, 1 minor unidentified phospholipid | PG, PGP-Me | PG, PGP-Me, phosphatidic acid, 1 unknown phospholipid | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, 1 unknown glycolipid, 1 other unknown lipid | PG, PGP-Me, S-DGD-1, 5 unidentified glycolipids |
| Respiratory quinones | NR | NR | MK-8, MK-8($H_2$) | NR | NR |
| Sensitivity to antibiotics | Sensitive: Aph Ani Bac Ery Nov Rif | Sensitive: Aph Ani Bac Ery Nov Rif | Sensitive: Ani Bac Nov Tet | Sensitive: Nov Rif | Sensitive: Nov |
| | Resistant: Amp Chl Neo Pen | Resistant: Amp Chl Neo Pen | Resistant: Amp Chl Ery Str | Resistant: Amp Ani Bac Chl Ery Kan Neo Str Tet | Resistant: Amp Ani Bac Chl Ery Gen Kan Neo Pen Rif Str Tet Van |
| G + C content of DNA (mol %) | 59–60 | 63 | 61.2–64.3 (major component); 51.9 (minor component) | 63.4–63.8 | 64 |
| Sample source and site | Soda lake, Inner Mongolia | Soda lake, Inner Mongolia | Alkaline lake, Wadi Natrun, Egypt | Saltern, Australia | Marine salt, Japan |

Data taken from:
[a] Itoh et al. (2005)
[b] Kamekura (2001b)
[c] Soliman and Trüper (1982)
[d] Kamekura et al. (1997)
[e] Burns et al. (2010a)
[f] Shimane et al. (2011)
Additional data on growth substrates and other properties can be found in the original species descriptions

Cells are extremely pleomorphic and lyse in distilled water. Irregular disks, flat triangles, and other irregular shapes are commonly found. Some species are motile. Magnesium requirement is moderate (5–50 mM). Amino acids are not required for growth. The optimum salt concentration for growth is 2–3 M NaCl. Neutrophilic. Characteristic lipids are PG, Me-PGP, and a triglycosyl diether lipid (S-TGD-2).

The mol% G+C of the DNA is 60.1–64.7.

The genus *Haloarcula* currently contains 9 species: *Har. vallismortis* (type species), *Har. amylolytica*, *Har. argentinensis*, *Har. hispanica*, *Har. japonica*, *Har. marismortui*, *Har. quadrata*, *Har. salaria*, and *Har. tradensis*.

The main features of the members of the genus are summarized in ➲ *Table 7.3.*

Additional comments:

- *Har. mukohataei* (Ihara et al. 1997) has been transferred to the genus *Halomicrobium* as *Hmc. mukohataei* comb. nov. (Oren et al. 2002).

## Genus *Halobaculum* Oren, Gurevich, Gemmell, and Teske 1995, 752$^{VP}$

*Ha.lo.ba'cu.lum.* Gr. n. *hals, halos*, salt; L. neut. n. *baculum* stick; N.L. neut. n. *Halobaculum*, salt stick.

Cells are motile rods of varying length and lyse in distilled water. Magnesium requirement is moderate (5–50 mM). Amino acids are required for growth. The optimum salt concentration for growth is 3.5–4.5 M NaCl. Neutrophilic. Characteristic lipids are PG, Me-PGP, and a sulfated diglycosyl diether. PGS is absent.

The mol% G+C of the DNA is 70.

Type species and currently only species: *Hbl. gomorrense.*

The main features of the members of the genus are summarized in ➲ *Table 7.2.*

Additional comment:

- The description of *Hbl. magnesiiphilum*, a species that grows optimally at 5 % NaCl only and can grow at salt concentrations as low as 1 % is currently in press (Shimoshige et al. 2012).

**Table 7.20**

**Comparison of selected characteristics of the members of the genus *Natronorubrum***

| Genus | *Natronorubrum*[a] | | | | |
|---|---|---|---|---|---|
| Species | *Nrr. bangense*[b] | *Nrr. aibiense*[c] | *Nrr. sediminis*[d] | *Nrr. sulfidifaciens*[e] | *Nrr. tibetense*[b] |
| Type strain | AS 1.1984<br>CIP 107015<br>JCM 10635 | CGMCC 1.4299<br>JCM 13488 | CECT 7487<br>CGMCC 1.8981<br>JCM 15982 | CGMCC 1.6307<br>JCM 14089 | AS 1.2123<br>CIP 107016<br>JCM 10636 |
| Cell shape | Pleomorphic flat | Rods | Pleomorphic rods | Pleomorphic rods, triangular disc-shaped | Pleomorphic flat |
| Cell size (μm) | NR | 0.8–1.0 × 1.4–3.6 | 0.8–1.0 × 4.0–6.0 | NR | NR |
| Motility | – | + | – | + | – |
| Colony color | Red | Red | Pink | Red | Red |
| NaCl range for growth and optimum (%) | 12–25 (Opt. 22.5) | 12–25 (Opt. 15–18) | 15–30 (Opt. 20) | 12–28 (Opt. 18) | 12–30 (Opt. 20) |
| Lysis in distilled water | + | + | + | NR | + |
| Magnesium requirement and optimum (M) | NR | 0–0.5 (Opt. 0.05) | – | – | NR |
| pH range for growth and optimum | 8.0–11 (Opt. 9.0–9.5) | 6.5–9.5 (Opt. 8.0) | 8.0–11.0 (Opt. 9.0) | 8.0–1.0 (Opt. 8.7–9.2) | 8.5–11 (Opt. 9.0) |
| Temperature range for growth and optimum (°C) | 25–55 (Opt. 45) | 20–50 (Opt. 45) | 25–50 (Opt. 37) | 20–55 (Opt. 44–47) | 25–55 (Opt. 45) |
| Organic substrates used | Acet Fruc Gluc Malt Sucr | Gala Gluc Malt Sucr | Arab Fruc Gluc Mann Xylo | Acet Fuma Gluc Glyc Lact Mala Malt Pyru Succ Sucr | Acet Fruc Gluc Lacto Malt, Sucr |
| Acid produced from | NR | Gala Gluc Malt Sucr | NR | NR | NR |
| Organic substrates not used | Manni | Fruc Lacto Mann Manni Ribo Sorb Sorbi Xylo | Acet Fuma Gala Glyc Lacto Mala Malt Manni Prop Raff Ribo Sorbi Succ Treh | Citr Fruc Gala Lacto Mann Manni Ribo Sorb Sorbi Xylo | Manni |
| Indole from typtophan | + | + | – | + | + |
| Starch hydrolysis | – | – | – | – | – |
| Gelatin liquefaction | – | – | – | – | + |
| Nitrate reduction | – | + | + | + | – |
| Polar lipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, 2 minor uncharacterized phospholipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, TGD-1, 2 unidentified glycolipids | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me | PG, PGP-Me | $C_{20}C_{20}$ and $C_{20}C_{25}$ derivatives of PG, PGP-Me, 2 minor uncharacterized phospholipids |
| Respiratory quinones | NR | NR | NR | NR | NR |

**Table 7.20 (continued)**

| Genus | *Natronorubrum*[a] | | | | |
|---|---|---|---|---|---|
| Species | *Nrr. bangense*[b] | *Nrr. aibiense*[c] | *Nrr. sediminis*[d] | *Nrr. sulfidifaciens*[e] | *Nrr. tibetense*[b] |
| Sensitivity to antibiotics | Sensitive: Ery | Sensitive: Nov Rif | Sensitive: Nov | Sensitive: Cip Ery Nov Rif Tet | Sensitive: Ery |
| | | Resistant: Amp Bac Chl Cip Ery Kan Neo Pen Tet | Resistant: Amp Bac Chl Ery Neo Pen Rif Str Tet | Resistant: Amp Bac Chl Neo Pen Str | |
| G + C content of DNA (mol%) | 59.9 | 61.2 | 61.9–62.5 | 60.9 | 60.1 |
| Sample source and site | Soda lake, Tibet | Salt lake, China | Salt lake, Inner Mongolia | Salt Lake, China | Soda lake, Tibet |

Data taken from:
[a] Xu et al. (2001a)
[b] Xu et al. (1999)
[c] Cui et al. (2006b)
[d] Gutiérrez et al. (2010)
[c] Cui et al. (2007b)
Additional data on growth substrates and other properties can be found in the original species descriptions

## Genus *Halobellus* Cui, Yang, Gao, and Xu 2011d, 2687$^{VP}$

*Ha.lo.bel'lus.* Gr. n. *hals, halos*, salt; L. masc. adj. *bellus*, beautiful; N.L. masc. n. *Halobellus*, beautiful salt organism.

Cells are rod shaped under optimal growth conditions and lyse in distilled water. Sugars are metabolized, in some cases with formation of acids. The major polar lipids are PG, PGP-Me, PGS, and one major glycolipid chromatographically identical to S-DGD-1.

The mol% G+C of the DNA is 61.5–69.2.

The genus *Halobellus* currently contains three species: *Hbs. clavatus* (type species), *Hbs. limi*, and *Hbs. salinus*.

The main features of the members of the genus are summarized in ➋ *Table 7.2*.

## Genus *Halobiforma* Hezayen, Tindall, Steinbüchel, and Rehm 2002, 2278$^{VP}$; emend. Oren, Arahal, and Ventosa 2009, 640

*Ha.lo.bi.for'ma.* Gr. n. *hals, halos*, salt; L. adv. num. *bis*, twice; L. fem. n. *forma*, form; N.L. fem. n. *Halobiforma*, the halophile with two different shapes.

Cells are rod shaped, coccoid or pleomorphic, motile. Cells are red or pink and lyse in distilled water. Neutrophilic or alkaliphilic with growth up to pH 10.5. Grow by aerobic respiration; some species grow also by anaerobic respiration in the presence of nitrate. No growth on single substrates. Some 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 PGP-Me. Glycolipids may be present in some species; when present, the glycolipids are a triglycosyl diether and its sulfated derivative.

The mol% G+C of the DNA is 63.8–66.9.

The genus *Halobiforma* currently contains three species: *Hbf. haloterrestris* (type species), *Hbf. lacisalsi*, and *Hbf. nitratireducens.*

The main features of the members of the genus are summarized in ➋ *Table 7.4*.

## Genus *Halococcus* Schoop 1935, 817$^{AL}$; emend. Oren, Arahal, and Ventosa 2009, 639

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

Cells are coccoid, nonmotile, occurring in pairs, tetrads, or irregular clusters. Most cells stain Gram negative. Do not lyse in distilled water. Oxidase positive or negative. Magnesium requirement is moderate (1–40 mM). The optimum salt concentration for growth is 3.5–4.5 M NaCl. Neutrophilic. Some species require amino acids for growth. Possess both $C_{20}C_{20}$ and sometimes $C_{20}C_{25}$ core lipids. Characteristic lipids are PG, Me-PGP, and a sulfated diglycosyl diether.

The mol% G+C of the DNA is 59.5–66.

The genus *Halococcus* currently contains seven species: *Hcc. morrhuae* (type species), *Hcc. dombrowskii*, *Hcc. hamelinensis*, *Hcc. qingdaonensis*, *Hcc. saccharolyticus*, *Hcc. salifodinae*, and *Hcc. thailandensis*.

**Table 7.21**

**Properties of the sequenced genomes of members of the *Halobacteriaceae* (as of August 2012)**

| Species, strain | Length | G + C content | Predicted protein genes | Predicted RNA genes | 16S rRNA genes | Accession no. | References |
|---|---|---|---|---|---|---|---|
| *Halalkalicoccus jeotgali* B3$^{T}$ | 3,698,650 (chromosome)<br>2,809,118<br>406,285<br>363,534<br>44,576<br>23,727<br>6,951 (plasmids) | 65.0<br>55.3<br>54.2<br>58.9<br>54.9<br>47.6<br>60.0 | 3860 | 52 | 1 | CP002062.1–CP002068.1 | Roh et al. (2010b) |
| "Haloarcula californiae" ATCC 22799 | 4,420,514 | 60.8 | 4627 | 69 | NR | PubSEED 662475.4 | Lynch et al. (2012) |
| *Haloarcula hispanica* ATCC 33869 | 2,995,271 (chromosome I)<br>488,918 (minichromosome II<br>405,816 (megaplasmid) | 63.7<br>57.0<br>59.9 | 3859 | 58 | 3 | CP002921–CP002923 | Liu et al. (2011) |
| *Haloarcula marismortui* ATCC 43049 | 3,131,724<br>288,050 (chromosomes)<br>410,554<br>155,300<br>132,678<br>50,060<br>39,521<br>33,452<br>33,303 (plasmids) | 61.1 | 4242[a]; 4348[b] | 62 | 3 | AY596290.1 – AY596298.1 | Baliga et al. (2004)[a], Anderson et al. (2011)[b] |
| "Haloarcula sinaiiensis" ATCC 33800 | 4,525,388 | 60.8 | 4538 | 55 | NR | PubSEED 662478.5 | Lynch et al. (2012) |
| *Haloarcula vallismortis* ATCC 29715 | 3,930,055 | 61.8 | 4084 | 84 | NR | PubSEED 662477.4 | Lynch et al. (2012) |
| *Halobacterium salinarum* R1 | 2,000,962 (chromosome)<br>147,963<br>194,963<br>284,332<br>40,894 (plasmids) | 68.0<br>57.4<br>58.6<br>59.8<br>57.9 | 2878 | 52 | NR | AM774415.1–AM774419.1 | Pfeifer et al. (2008)a |
| *Halobacterium* sp. NRC–1 | 2,014,239 (chromosome)<br>191,346<br>365,425 (minichromosomes) | 67.9<br>57.9<br>59.2 | 2630 | 52 | 1 | AE004437.1,<br>AF016485.1<br>AE004438.1 | Ng et al. (2000) |
| *Halobiforma lacisalsi* AJ5 | 4,398,155 (draft) | 65.4 | 4682 | 49 | 2 | AGFZ01000000 | Jiang et al. (2011) |
| *Halococcus hamelinensis* strain 100A6$^{T}$ | 3,133,046 | 60.1 | 3150 | 48 | 1 | PRJNA80845 | Burns et al. (2012) |

**Table 7.21 (continued)**

| Species, strain | Length | G + C content | Predicted protein genes | Predicted RNA genes | 16S rRNA genes | Accession no. | References |
|---|---|---|---|---|---|---|---|
| *Haloferax denitrificans* ATCC 35960 | 3,848,468 | 66.3 | 3809 | 58 | NR | PubSEED 662478.4 | Lynch et al. (2012) |
| *Haloferax mediterranei* ATCC 33500 | 2,948,884<br>129,210<br>321,908<br>504,705<br>3,905,749 | 61.1<br>57.6<br>57.9<br>57.5<br>60.3 | 3864<br>3942 | 63<br>63 | 2 | CP001868–CP001871<br>PubSEED 523841.6 | Han et al. (2012), Lynch et al. (2012) |
| *Haloferax mucosum* ATCC BAA-1512 | 3,371,699 | 61.8 | 3455 | 61 | NR | PubSEED 662479.5 | Lynch et al. (2012) |
| *Haloferax sulfurifontis* ATCC BAA-897 | 3,816,558 | 66.3 | 3856 | 59 | NR | PubSEED 662480.4 | Lynch et al. (2012) |
| *Haloferax volcanii* DS2$^T$ | 2,847,757 (main chromosome)<br>635,786 (small chromosome)<br>437,906<br>85,092<br>6,359 (plasmids) | 66.6<br>61.7<br>65.5<br>55.5<br>56<br>65 | 4063 | 57 | 2 | CP001953–1–CP001957.1 | Hartman et al. (2010) |
| *Halogeometricum borinquense* DSM 11551 | 3,944,467 (chromosome and 5 plasmids) | 59.9 | 3937 | 57 | 2 | CP01690.1–CP01695.1 | Malfatti et al. (2009) |
| *Halomicrobium mukohataei* DSM 12286 | 3,332,349 (chromosome of 3.11 Mbp and one 219kbp plasmid) | 65.5 | 3416 | 56 | 3 | CP001688.1<br>CP001689.1 | Tindall et al. (2009) |
| *Halopiger xanaduensis* SH-6 | 3,668,009 (chromosome)<br>436,718<br>181,778<br>68,763 (plasmids) | 65.2 | 4310 | 60 | 3 | CP002839.1–CP002842.1 | Anderson et al. (2012) |
| *Haloquadratum walsbyi* DSM 16790 | 3,132,949 (chromosome)<br>46,867 (plasmid) | 47.9<br>47.7 | 2738 + 39 | 51 | 2 | AM180088.1<br>AM180089.1 | Bolhuis et al. (2006) |
| *Halorhabdus tiamatea* strain SARL4B$^T$ | NR | 62 | 4034 | NR | NR | 66979 – AFNT00000000 | Antunes et al. (2011) |
| *Halorhabdus utahensis* DSM 12940 | 3,129,561 | 62.9 | 3027 (or 3097, 2898 or 3254, depending on the annotation service used) | 48 | 1 | CP001687.1 | Anderson et al. (2009), Bakke et al. (2009) |
| *Halorubrum lacusprofundi* | 2,735,295<br>525,943<br>431,338 | NR | 3665 | NR | 3 | CP001365.1–CP001367.1 | Anderson et al. (2011), Shukla et al. (2006) |

**Table 7.21 (continued)**

| Species, strain | Length | G + C content | Predicted protein genes | Predicted RNA genes | 16S rRNA genes | Accession no. | References |
|---|---|---|---|---|---|---|---|
| *Haloterrigena turkmenica* DSM 5511 | 5,540,782 (3,889,038 [chromosome] and 6 plasmids of 15.8–698.5 kbp) | 64.3 | 5287 | 63 | 3 | CP001860–CP001866 | Saunders et al. (2010) |
| *Natrialba magadii* ATCC 43099$^T$ | 3,751,858 (large chromosome)<br>378,348 (small chromosome)<br>254,950 (plasmid)<br>58,487 (virus ΦCh1) | 61.4<br>60.1<br>56.8<br>61.9 | 4212 | 60 | 3 | CP001932.1–CP001935.1 | Sidderamappa et al. (2012) |
| *Natrinema pellirubrum* DSM 15624 (Draft) | NR | NR | 4555 | NR | NR | AGIN01000000 | Feng et al. (2012) |
| *Natrinema* sp. J7-2 | 3,687,626 (chromosome)<br>95,989 (plasmid) | 64<br>59 | 4302 | 56 | 3 | CP003412<br>CP003413 | Feng et al. (2012) |
| *Natronomonas pharaonis* DSM 2160 | 2,595,221 (chromosome)<br>130,989<br>23,486 (plasmids) | 63.4<br>57.2<br>60.6 | 2843 | 51 | 1 | CR936257.1–CR936259.1 | Falb et al. (2005) |

The main features of the members of the genus are summarized in *Table 7.5*.

Additional comments:

- *Hcc. turkmenicus* (Zvyagintseva and Tarasov 1987; Validation List 31, 495, 1989) was reclassified as *Htg. turkmenica* comb. nov. (Ventosa et al. 1999).

## Genus *Haloferax* Torreblanca, Rodriguez-Valera, Juez, Kamekura, and Kates 1986b, 573$^{VP}$ (Validation list 22); Effective Publication: Torreblanca, Rodriguez-Valera, Juez, Kamekura, and Kates 1986a, 98; emend. Oren, Arahal, and Ventosa 2099, 639

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

Cells are extremely pleomorphic and lyse in distilled water. Flat disks and pleomorphic rods are commonly found. Colonies have a mucoid appearance. Pigmentation often depends on the salinity of the medium. Some species are motile; some possess gas vesicles. Most species are oxidase positive, but oxidase-negative and oxidase-variable species have been reported. Magnesium requirement is high (20–50 mM). Amino acids are not required for growth. Acids are produced from sugars. The optimum salt concentration for growth is 2–3 M NaCl. Neutrophilic. Characteristic lipids are PG, Me-PGP, and a sulfated diglycosyl diether. PGS is absent.

The mol% G+C of the DNA is 59.5–66.3.

The genus *Haloferax* currently contains 11 species: *Hfx. volcanii* (type species), *Hfx. alexandrinus*, *Hfx. denitrificans*, *Hfx. elongans*, *Hfx. gibbonsii*, *Hfx. larsenii*, *Hfx. lucentense*, *Hfx. mediterranei*, *Hfx. mucosum*, *Hfx. prahovense*, and *Hfx. sulfurifontis*.

The main features of the members of the genus are summarized in *Tables 7.6* and *7.7*.

Additional comments:

- The name *Hfx. alexandrinus* is illegitimate because the epithet must be in the neuter gender (*alexandrinum*).
- The original spelling of the specific epithet *lucentensis* (Gutierrez et al. 2002) has been corrected to *lucentense* on validation.

**Table 7.22**

**List of Haloviruses described as of August (2010)[a]**

| Name | Host organism | Morphology | Classification | Nucleic acid type | Genome size | Life style | Reference |
|---|---|---|---|---|---|---|---|
| B10 | *Halobacterium* sp. | Head -tail | Myovirus | NR | NR | NR | Torsvik (1982), Dyall-Smith et al. (2003) |
| BJ1 | *Halorubrum saccharovorum* | Head-tail | Siphovirus | C dsDNA | 42,271 | Virulent | Pagaling et al. (2007) |
| HATV-1 | *Haloarcula* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HATV-2 | *Haloarcula* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HCTV-1 | "Haloarcula californiae" | Head-tail | Siphovirus | NR | NR | NR | Kukkaro and Bamford (2009) |
| HCTV-2 | "Haloarcula californiae" | Head-tail | Siphovirus | NR | NR | NR | Atanasova et al. (2012) |
| HCTV-5 | "Haloarcula californiae" | Head-tail | Siphovirus | NR | NR | NR | Atanasova et al. (2012) |
| HGPV-1 | *Halogeometricum* sp. | Pleomorphic | "Pleolipovirus" | C dsDNA with short stretches of ssDNA | 9,694 | Released without cell lysis | Atanasova et al. (2012), Senčilo et al. (2012), Pietilä et al. (2012a) |
| HF1 | *Halorubrum saccharovorum*, *Haloferax volcanii* | Head-tail | Myovirus | L dsDNA | 75,898 | Virulent | Nuttall and Dyall-Smith (1993a), Tang et al. (2002) |
| HF2 | *Halorubrum coriense* | Head-tail | Myovirus | L dsDNA | 77,670 | Virulent | Nuttall and Dyall-Smith (1993a), Tang et al. (2002) |
| HGTV-1 | *Halogranum* sp. | Head-tail | *Myoviridae* | NR | NR | NR | Atanasova et al. (2012) |
| Hh-1 | *Halobacterium salinarum* | Head-tail | Siphovirus | dsDNA | 37.6 kpb | Temperate | Rohrmann et al. (1983), Pauling (1982), Dyall-Smith et al. (2003) |
| Hh-3 | *Halobacterium salinarum* | Head-tail | Siphovirus | dsDNA | 29.6 kpb | Temperate | Rohrmann et al. (1983), Pauling (1982), Dyall-Smith et al. (2003) |
| HHIV-2 | *Haloarcula hispanica* | Icosaedral with inner membrane | Unclassified | L dsDNA | 30,578 | Virulent | Jaakkola et al. (2012) |
| HHPV-1 | *Haloarcula hispanica* | Pleomorphic | "Pleolipoviruses" | C dsDNA | 8,082 | Released without cell lysis | Roine et al. (2010), Pietilä et al. (2012a) |
| HHTV-1 | *Haloarcula hispanica* | Head-tail | Siphovirus | NR | NR | NR | Kukkaro and Bamford (2009) |
| HHTV-2 | *Haloarcula hispanica* | Head-tail | Siphovirus | NR | NR | NR | Atanasova et al. (2012) |
| His1 | *Haloarcula hispanica* | Lemon-shaped | Salterprovirus (*Fuselloviridae*) | L dsDNA | 14.9 kbp | Released without cell lysis | Bath and Dyall-Smith (1998), Pietilä et al. (2012b) |
| His2 | *Haloarcula hispanica* | Pleomorphic | Salterprovirus ("Pleolipovirus") | L dsDNA | 16,067 | Released without cell lysis | Bath et al. (2006), Pietilä et al. (2012a) |
| HJTV-1 | *Haloarcula japonica* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HJTV-2 | *Haloarcula japonica* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRPV-1 | *Halorubrum* sp. | Pleomorphic | "Pleolipovirus" | C ssDNA | 7,048 nt | Released without cell lysis, persistent in host cells | Pietilä et al. (2009, 2010, 2012a); Senčilo et al. (2012) |

**Table 7.22 (continued)**

| Name | Host organism | Morphology | Classification | Nucleic acid type | Genome size | Life style | Reference |
|---|---|---|---|---|---|---|---|
| HRPV-2 | *Halorubrum* sp. | Pleomorphic | "Pleolipovirus" | C ssDNA | 10,656 | Released without cell lysis | Senčilo et al. (2012), Pietilä et al. (2012a) |
| HRPV-3 | *Halorubrum* sp. | Pleomorphic | "Pleolipovirus" | C dsDNA with short stretches of ssDNA | 8,770 | Released without cell lysis | Senčilo et al. (2012), Pietilä et al. (2012a) |
| HRPV-6 | *Halorubrum* sp. | Pleomorphic | "Pleolipovirus" | C ssDNA | 8,549 | Released without cell lysis | Senčilo et al. (2012), Pietilä et al. (2012a) |
| HRTV-1 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Kukkaro and Bamford (2009) |
| HRTV-2 | *Halorubrum* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-3 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-4 | *Halorubrum* sp. | Head-tail | Siphovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-5 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-6 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-7 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-8 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-9 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-10 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-11 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HRTV-12 | *Halorubrum* sp. | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| Hs1 | *Halobacterium salinarum* | Head-tail | Bradley Gp A (Myovirus) | NR | NR | Temperate? | Torsvik and Dundas (1974, 1980), Torsvik (1982) |
| HSTV-1 | "Haloarcula sinaiiensis" | Head-tail | Podovirus | NR | NR | NR | Atanasova et al. (2012) |
| HSTV-2 | *Halorubrum sodomense* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HSTV-3 | *Halorubrum sodomense* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HTV-1 | NR | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HVTV-1 | *Haloarcula vallismortis* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| HVTV-2 | *Haloarcula vallismortis* | Head-tail | Myovirus | NR | NR | NR | Atanasova et al. (2012) |
| Ja. 1 | *Halobacterium salinarum* | Head-tail | Bradley Gp A (Myovirus) | dsDNA | NR | Virulent | Wais et al. (1975) |
| S41 | *Halobacterium salinarum (curtirubrum)* | Head-tail | Bradley A1 (Myovirus) | NR | NR | Virulent | Daniels and Wais (1998) |
| S4100 | *Halobacterium salinarum (curtirubrum)* | Head-tail | Bradley A1 (Myovirus) | NR | NR | Virulent | Daniels and Wais (1998) |
| S45 | *Halobacterium salinarum* | Head-tail Group B1 | Siphovirus | dsDNA | NR | Virulent | Daniels and Wais (1984) |
| S50.2 | *Halobacterium salinarum (curtirubrum)* | Head-tail | Bradley A1 (Myovirus) | NR | NR | Virulent | Daniels and Wais (1998) |

**Table 7.22** (continued)

| Name | Host organism | Morphology | Classification | Nucleic acid type | Genome size | Life style | Reference |
|---|---|---|---|---|---|---|---|
| S5100 | *Halobacterium salinarum* | Head- tail | Bradley A1 (Myovirus) | NR | NR | Temperate | Daniels and Wais (1990) |
| SH1 | *Haloarcula hispanica* | Icosahedral, with inner membrane | Unclassified | L dsDNA | 30,898 | Virulent | Porter et al. (2005), Kivelä et al. (2006), Bamford et al. (2005), Jäälinoja et al. (2008) |
| SNJ1 | *Natrinema* sp. | (Head-tail), icosahedral with inner mambrane | Unclassified | C dsDNA | 16,341 | Temperate | Mei et al. (2007), Zhang et al. (2012) |
| ΦCh1 | *Natrialba magadii* | Head-tail | Myovirus | L, dsDNA, RNA | 58,498 Several RNA of 80–700 nt | Temperate | Witte et al. (1997), Klein et al. (2002, 2012) |
| ϕH | *Halobacterium salinarum* | Head-tail isometric head, contractile tail | *Myoviridae* | L | 59 | Temperate | Schnabel et al. (1982), Dyall-Smith et al. (2003) |
| ΦN | *Halobacterium salinarum* | Head-tail isometric head, contractile tail | Siphovirus | L dsDNA | 56 kbp | Not critically tested, most probably lytic | Vogelsang-Wenke and Oesterhelt (1988) |

[a]The author thanks Dr. Elina Roine, University of Helsinki, Finland, for valuable comments

## Genus *Halogeometricum* Montalvo-Rodríguez, Vreeland, Oren, Kessel, Betancourt, and López-Garriga 1998, 1310$^{VP}$; emend. Cui, Yang, Gao, Li, Xu, Zhou, Liu, and Zhou 2010f, 2615

*Ha.lo.ge.o.me'tri.cum.* Gr. n. *hals, halos*, salt; L. neut. adj. *geometricum* geometrical; N.L. neut. n. *Halogeometricum*, salty geometrical shape.

Cells are extremely pleomorphic (short and long rods, squares, triangles, ovals, and irregular cocci) under optimal growth conditions, motile, and lyse in distilled water. Sugars are metabolized, in some cases with formation of acids. Neutrophilic. Cells contain PG and Me-PGP. In some species, a yet unidentified non-sulfate-containing glycolipid and S-DGD-1 may be present as a minor component. In other species, the major glycolipid is chromatographically identical to S-DGD-1, and DGD-1 may be present as a minor component. PGS is absent.

The mol% G + C of the DNA is 59.9–64.9

The genus *Halogeometricum* currently contains two species: *Hgm. borinquense* (type species), and *Hgm. rufum.*

The main features of the members of the genus are summarized in ➋ *Table 7.4*.

## Genus *Halogranum* Cui, Gao, Sun, Dong, Xu, Zhou, Liu, Oren, and Zhou 2010b, 1369$^{VP}$, emend. Cui, Yang, Gao, and Xu 2011e, 913

*Ha.lo.gra'num.* Gr. n. *hals, halos*, salt; L. neut. n. *granum*, granule; N.L. neut. n. *Halogranum*, salty granule shape.

Cells are pleomorphic under optimal growth conditions and lyse in distilled water. Sugars are metabolized with the formation of acids. The polar lipids are PG, PGP-Me, traces of PGS, and one major glycolipid and one minor glycolipid chromatographically identical to S-DGD-1 and DGD-1, respectively. Other minor glycolipids may be present.

The mol% G + C of the DNA is 55.7–64.4.

The genus *Halogranum* currently contains 4 species: *Hgn. rubrum* (type species), *Hgn. amylolyticum*, Hgn. *gelatinilyticum*, and *Hgn. salarium.*

The main features of the members of the genus are summarized in ➋ *Table 7.4*.

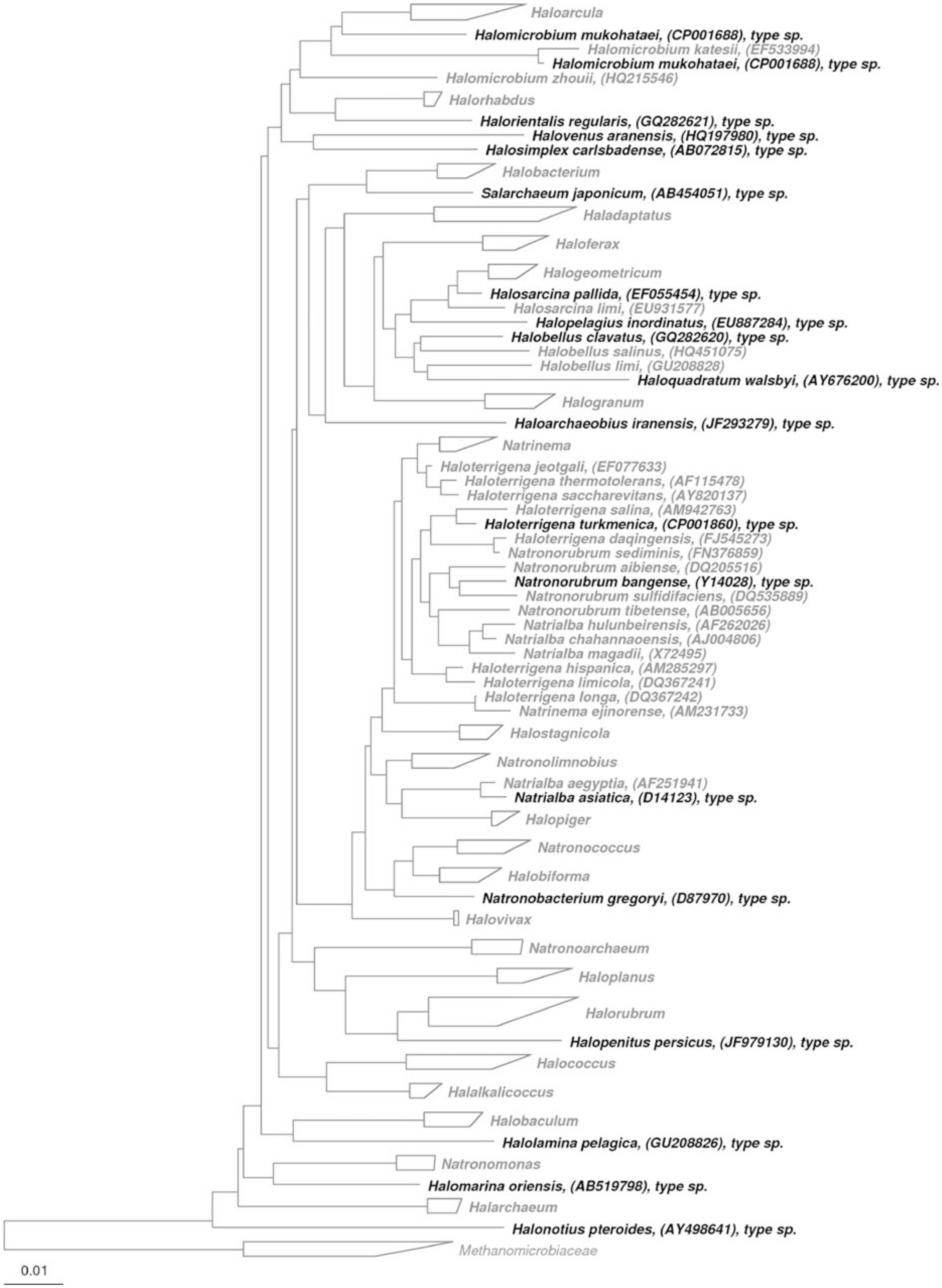

**Fig. 7.1 (continued)**

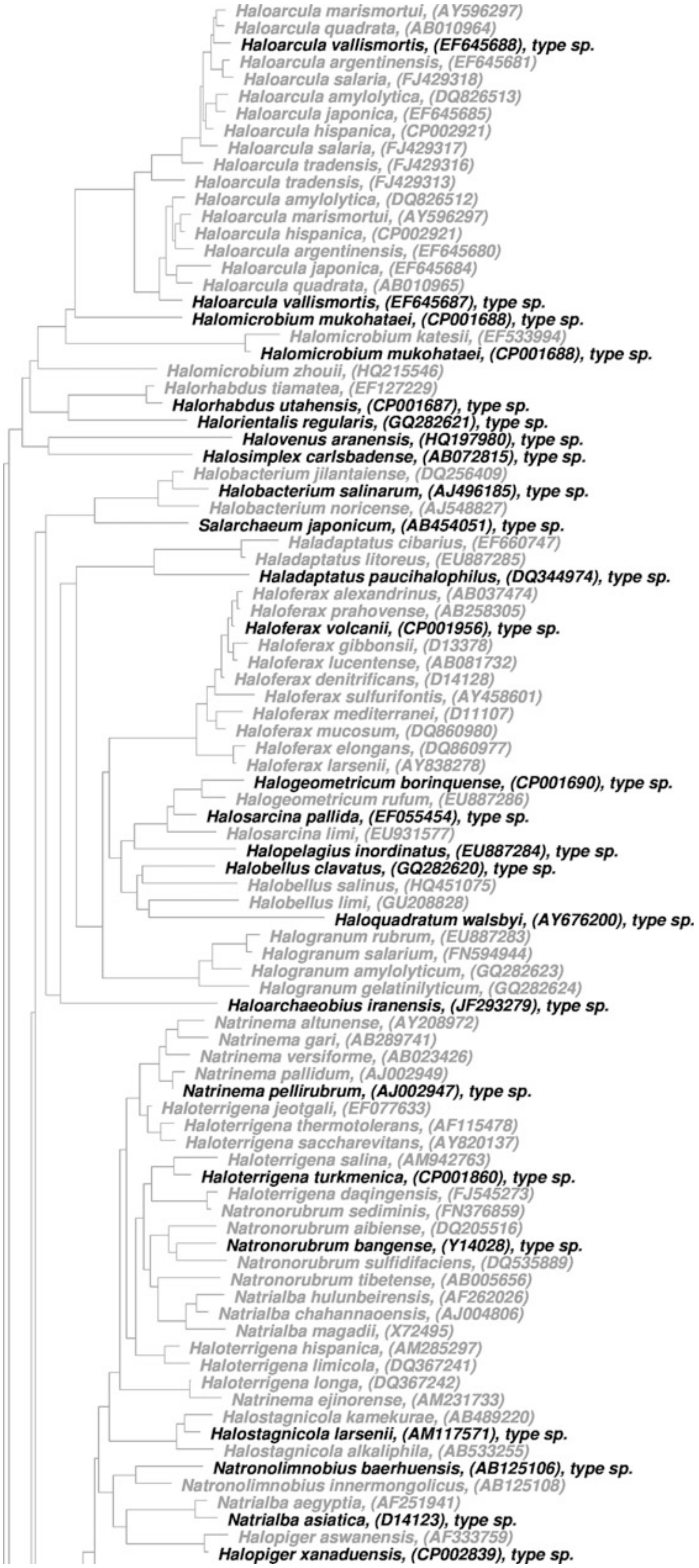

**Fig. 7.1 (continued)**

## Genus *Halolamina* Cui, Gao, Yang, and Xu 2011b, 1619$^{VP}$

*Ha.lo.la'mi.na.* Gr. n. *hals, halos*, salt; L. fem. n. *lamina*, a thin slice; N.L. fem. n. *Halolamina*, thin-slice-shaped salt (organism).

Cells are pleomorphic and thin-slice-shaped. Sugars are metabolized, sometimes with the formation of acids. Polar lipids include PGS and 8 yet uncharacterized glycolipids.

The mol% G + C of the DNA is 64.8.

Type species and currently only species: *Hlm. pelagica.*

The main features of the members of the genus are summarized in ➋ *Table 7.7.*

## Genus *Halomarina* Inoue, Itoh, Ohkuma, and Kogure 2011, 944$^{VP}$

*Ha.lo.ma.ri'na.* Gr. n. *hals, halos*, salt; L. adj. *marinus*, marine; N. L. fem. n. *Halomarina*, a halophile existing in the marine environment.

Cells are mesophilic and neutrophilic. Lipids are $C_{20}C_{20}$ and $C_{20}C_{25}$ diether derivatives of PG, PGP-Me, triglycosyl diether, and at least one unidentified glycolipid. Grows on a wide range of substrates, including single and complex carbon sources. Survives at low salt concentrations and can recover after prolonged exposure to distilled water.

The mol% G + C of the DNA is 67.7.

Type species and currently only species: *Hmr. oriensis.*

The main features of the members of the genus are summarized in ➋ *Table 7.8.*

## Genus *Halomicrobium* Oren, Elevi, Watanabe, Tamura, Ihara, and Corcelli 2002, 1834$^{VP}$

*Ha.lo.mi.cro'bi.um.* Gr. n. *hals, halos*, salt; N.L. neut. n. *microbium* (from Gr. adj. *micros*, small and Gr. n. bios, life), a microbe; N.L. neut. n. *Halomicrobium*, small, salt life-form.

Cells are rod shaped or pleomorphic, aerobic, or facultatively anaerobic in the presence of nitrate. Some species are motile.

The mol% G + C of the DNA is 52.4–69.1.

The genus *Halomicrobium* currently contains three species: *Hmc. mukohataei* (type species), *Hmc. katesii*, and *Hmc. zhouii.*

The main features of the members of the genus are summarized in ➋ *Table 7.8.*

Additional comment:

- *Har. mukohataei* (Ihara et al. 1997) has been transferred to the genus *Halomicrobium* as *Hmc. mukohataei* comb. nov. (Oren et al. 2002).

## Genus *Halonotius* Burns, Janssen, Itoh, Kamekura, Echigo, and Dyall-Smith 2010, 1198$^{VP}$

*Ha.lo.no'ti.us.* Gr. n. *hals, halos*, salt; L. masc. n. *notius*, southern; N.L. masc. n. *Halonotius*, a salty southern one.

Cells are flat rods, often with rounded ends. Oxidase and catalase tests are negative.

The mol% G + C of the DNA is 58.4–58.7.

Type species and currently only species: *Hns. pteroides.*

The main features of the members of the genus are summarized in ➋ *Table 7.8.*

## Genus *Halopelagius* Cui, Li, Gao, Xu, Zhou, Liu, Oren, and Zhou 2010g, 2092$^{VP}$

*Ha.lo.pe.la'gi.us.* Gr. n. *hals, halos*, salt; L. masc. adj. *pelagius*, of or pertaining to the sea; N.L. masc. n. *Halopelagius*, salt organism from the sea.

Cells are pleomorphic under optimal growth conditions and lyse in distilled water. Sugars are metabolized, in some cases with formation of acid. Lipids are PG, PGP-Me, and two main glycolipids chromatographically identical to S-DGD-1 and DGD-1. PGS is absent.

The mol% G + C of the DNA is 59.9–61.0.

Type species and currently only species: *Hpl. inordinatus.*

The main features of the members of the genus are summarized in ➋ *Table 7.8.*

## Genus *Halopenitus* Amoozegar, Makhdoumi-Kakhki, Shahzedeh Fazeli, Azarbaijani, and Ventosa 2012, 1935$^{VP}$

*Ha.lo.pe'ni.tus.* Gr. n. *hals, halos*, salt; L. masc. adj. *penitus* inner, interior; N.L. masc. n. *Halopenitus*, intended to mean an archaeon isolated from an inland salt lake.

Cells are pleomorphic rods, triangular, or disk-shaped, nonmotile. Neutrophilic. Polar lipids include PG, PGP-Me, one unidentified glycolipid, and three minor phospholipids.

The mol% G + C of the DNA is 66.0.

**Fig. 7.1**

**Phylogenetic reconstruction of the family *Halobacteriaceae* based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. (a) presents the genera in a grouped tree, and (b) is an unfolded tree showing the type strains of species of the family. The sequence datasets and alignments were used according to the All-Species Living Tree Project (LTP) database (Yarza et al. 2010; http://www.arb-silva.de/projects/living-tree). The tree topology was stabilized with the use of a representative set of nearly 750 high-quality type strain sequences proportionally distributed among the different bacterial and archaeal phyla. In addition, a 40 % maximum frequency filter was applied in order to remove hypervariable positions and potentially misplaced bases from the alignment. Scale bar indicates estimated sequence divergence**

Type species and currently only species: *Hpt. persicus*.

The main features of the members of the genus are summarized in ➋ Table 7.9.

## Genus *Halopiger* Gutiérrez, Castillo, Kamekura, Xue, Ma, Cowan, Jones, Grant, and Ventosa 2007, 1404$^{VP}$

*Ha.lo.pi'ger*. Gr. n. *hals, halos*, salt; L. masc. adj. *piger*, lazy; N.L. masc. n. *Halopiger*, lazy halophile, referring to the slow growth under laboratory conditions.

Cells are strictly anaerobic pleomorphic rods. Polar lipids include $C_{20}C_{20}$ and $C_{20}C_{25}$ glycerol diethers of PG, PGP-Me, and the bis-sulfated glycolipid $S_2$-DGD-1. PGS is absent.

The mol% G + C of the DNA is 65.2–67.1.

The genus *Halopiger* currently contains two species: *Hpg. xanaduensis* (type species) and *Hpg. aswanensis*.

The main features of the members of the genus are summarized in ➋ Table 7.9.

## Genus *Haloplanus* Elevi Bardavid, Mana, and Oren 2007, 782$^{VP}$; emend. Cui, Gao, Li, Xu, and Zhou 2010c, 1826

*Ha.lo.pla'nus*. Gr. n. *hals, halos*, salt; L. adj. *planus*, flat; N.L. masc. n. *Haloplanus*, flat salt-life form.

Cells are pleomorphic and flat and contain gas vesicles. In static liquid culture, cells float to the surface. Strictly aerobic. Cells lyse in distilled water. Cells contain PG, PGP-Me, PGS, and one major glycolipid that is chromatographically identical to S-DGD-1.

The mol% G + C of the DNA is 62.1–66.4.

The genus *Haloplanus* currently contains three species: *Hpn. natans* (type species), *Hpn. aerogenes*, and *Hpn. vescus*.

The main features of the members of the genus are summarized in ➋ Table 7.9.

## Genus *Haloquadratum* Burns, Janssen, Itoh, Kamekura, Li, Jensen, Rodríguez-Valera, Bolhuis, and Dyall-Smith 2007, 391$^{VP}$

*Ha.lo.qua.dra'tum*. Gr. n. *hals, halos*, salt; L. neut. n. *quadratum*, square; N.L. neut. n. *Haloquadratum*, salt square.

Cells are flat and square and usually contain gas vesicles and PHA storage granules. Oxidase and catalase tests are negative.

The mol% G + C of the DNA is 46.9–47.9.

Type species and currently only species: *Hqr. walsbyi*.

The main features of the members of the genus are summarized in ➋ Table 7.9.

## Genus *Halorhabdus* Wainø, Tindall, and Ingvorsen 2000, 188$^{VP}$; emend. Antunes, Taborda, Huber, Moissl, Nobre, and Da Costa 2008, 218

*Ha.lo.rhab.dus*. Gr. n. *hals, halos*, salt; Gr. fem. n. *rhabdos*, rod, stick; N.L. fem. n. *Halorhabdus*, salt (-loving) rod.

Cells are extremely pleomorphic, although most are rod shaped. Pigmented red or unpigmented. Motile by a single flagellum or nonmotile. Cells lyse in distilled water. Ferments glucose. Amino acids are not required for growth; grows under aerobic or anaerobic conditions in defined media; some species prefer anaerobic conditions. PHA is produced. Acid is produced from carbohydrates. A limited number of organic substrates are used for growth. The polar lipids are PG, PGP-Me, TGD, S-TGD, and an unknown component. PGS is absent. MK-8 and MK-8(VIII-$H_2$) are the respiratory lipoquinones.

The mol% G + C of the DNA is 62.0–64.0.

The genus *Halorhabdus* currently contains two species: *Hrd. utahensis* (type species), and *Hrd. tiamatea*.

The main features of the members of the genus are summarized in ➋ Table 7.10.

## Genus *Halorientalis* Cui, Yang, Gao, and Xu 2011d, 2687$^{VP}$

*Hal.o.ri.en.ta'lis*. Gr. n. *hals, halos*, salt; L. fem. adj. *orientalis*, of the east; N.L. fem. n. *Halorientalis*, salt-loving organism from the orient.

Cells are pleomorphic and rod shaped under optimal growth conditions and lyse in distilled water. Sugars are metabolized, in some cases with the formation of acids. The polar lipids are PG, PGP-Me, one major glycolipid, chromatographically identical to S-DGD-1, and 3–4 minor unidentified glycolipids.

The mol% G + C of the DNA is 61.5–61.9.

Type species and currently only species: *Hos. regularis*.

The main features of the members of the genus are summarized in ➋ Table 7.10.

## Genus *Halorubrum* McGenity and Grant 1996, 362$^{VP}$; Effective Publication: McGenity and Grant 1995, 241; emend. Oren, Arahal, and Ventosa 2009, 639

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

Cells are rod shaped or pleomorphic under optimal growth conditions, motile or nonmotile, and lyse in distilled water. Short and long rods, triangles, squares, and oval cells are found. Some species may be almost colorless. Some species possess gas vesicles. Magnesium requirement is moderate (5–50 mM) or low. Amino acids are not required for growth.

Some species grow on single carbon sources. Most species use sugars, some with the production of acids. The optimum salt concentration for growth is 2.5–4.5 M NaCl. Neutrophilic and alkaliphilic species exist. The major polar lipids are $C_{20}C_{20}$ or $C_{20}C_{20}$ and $C_{20}C_{25}$ glycerol diether derivatives of PG, PGP-Me, PGS, and a sulfated diglycosyl diether. Alkaliphilic species lack PGS and glycolipids.

The mol% G + C of the DNA is 60.2–71.2.

The genus *Halorubrum* currently contains 26 species: *Hrr. saccharovorum* (type species), *Hrr. aidingense, Hrr. alkaliphilum, Hrr. aquaticum, Hrr. arcis, Hrr. californiense, Hrr. chaoviator, Hrr. cibi, Hrr. coriense, Hrr. distributum, Hrr. ejinorense, Hrr. ezzemoulense, Hrr. kocurii, Hrr. lacusprofundi, Hrr. lipolyticum, Hrr. litoreum, Hrr. luteum, Hrr. orientale, Hrr. sodomense, Hrr. tebenquichense, Hrr. terrestre, Hrr. tibetense, Hrr. trapanicum, Hrr. vacuolatum*, and *Hrr. xinjiangense.*

The main features of the members of the genus are summarized in ➲ *Table 7.10*.

Additional comments:

- *Halorubrobacterium* (Kamekura and Dyall-Smith 1995) (Validation list 57, 1996) is a later synonym of *Halorubrum* (McGenity and Grant 1995). *Halorubrobacterium coriense, Halorubrobacterium* distributum, and *Halorubrobacterium sodomense* were transferred to *Halorubrum* (Oren and Ventosa 1996).
- Strain VKM B-1733 was originally designated as the type strain of *Hrr. distributum* (Zvyagintseva and Tarasov 1987). Zvyagintseva et al. (1996) later proposed VKM B-1739 as the new type. However, strain VKM B-1733 and JCM 9100 which was derived from it must remain the type strain of the species (Oren et al. 1997).
- NCIMB 13488 was proposed as a neotype of *Hrr. trapanicum* (basonym: *Hbt. trapanicum*) as the original isolate is no longer available (Grant et al. 1998). However, the Judicial Commission of the ICSP ruled that strain NCIMB 13488 is derived from strain NRC 34021, which in turn is derived from Petter's original isolate (Judicial Commission 2003). Therefore NCIMB 13488 may serve as the type strain of the species.
- The name *Hrr. sfaxense* (Trigui et al. 2011) has been effectively but not yet validly published. The species was therefore not included in ➲ *Table 7.11*, ➲ *7.12*, and ➲ *7.13*.

## Genus *Halosarcina* Savage, Krumholz, Oren, and Elshahed 2008, 859$^{VP}$; emend. Cui, Gao, Li, Xu, Zhou, Liu, and Zho 2010d, 2464

*Ha.lo.sar.ci'na.* Gr. n. *hals, halos*, salt; L. fem. n. *sarcina* a package; N.L. fem. n. *Halosarcina*, a salt (-loving) package.

Cells are cocci (sarcina-like clusters) or pleomorphic (rods and deformed cocci) under optimal growth conditions. Cells are motile or nonmotile and lyse in distilled water. Sugars are metabolized, sometimes with formation of acids. Polar lipids are PG and PGP-Me; PGS is absent. The major glycolipid is chromatographically identical to S-DGD-1. DGD-1 or another glycolipid may be present in some species as a minor component.

The mol% G + C of the DNA is 61.2–65.4.

The genus *Halosarcina* currently contains two species: *Hsn. pallida* (type species) and *Hsn. limi.*

The main features of the members of the genus are summarized in ➲ *Table 7.10*.

## Genus *Halosimplex* Vreeland, Rosenzweig, Straight, Krammes, Dougherty, and Kamekura 2002, 450 (Validation list 92, 2003, 936$^{VP}$)

*Ha.lo.sim'plex.* Gr. n. *hals, halos*, salt; L. adj. *simplex*; simple, uncomplicated; N.L. neut. n. *Halosimplex*, the simple halophile.

Cells are rod shaped or pleomorphic, pink to red. Cannot use nitrate or other alternate electron acceptors. Neutrophilic and mesophilic. Extremely fastidious: grows only on pyruvate, pyruvate plus glycerol, or glycerol plus acetate as carbon sources in defined medium. Unable to grow on any other organic carbon compounds tested. Lipids are PG, PGP-Me, and four sulfated glycolipids, two of which have been identified as TeGD and $S_2$-DGD.

The mol% G + C of the DNA is 64.4.

Type species and currently only species: *Hsx. carlsbadense.*

The main features of the members of the genus are summarized in ➲ *Table 7.10*.

## Genus *Halostagnicola* Castillo, Gutiérrez, Kamekura, Xue, Ma, Cowan, Jones, Grant, and Ventosa 2006, 1521$^{VP}$

*Ha.lo.stag.ni'co.la.* Gr. n. *hals, halos*, salt; L. neut. n. *stagnum*, a piece of standing water, pond, lake; L. suff. –*cola* (from L. n. *incola*), inhabitant, dweller; N.L. fem. n. *Halostagnicola*, a dweller of a saline lake.

Cells are pleomorphic, although most are rod shaped. Strictly aerobic. Polar lipids include $C_{20}C_{20}$ and $C_{20}C_{25}$ diethers of PG, PGP-Me, and two unidentified glycolipids.

The mol% G + C of the DNA is 59.8–61.0.

The genus *Halostagnicola* currently contains three species: *Hst. larsenii* (type species), *Hst. alkaliphila*, and *Hst. kamekurae.*

The main features of the members of the genus are summarized in ➲ *Table 7.15*.

## Genus *Haloterrigena* Ventosa, Gutiérrez, Kamekura, and Dyall-Smith 1999b, 135$^{VP}$; emend. Oren, Arahal, and Ventosa 2009, 640

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

Cells are coccoid or oval or rod shaped under optimal growth conditions. Some species become coccoid in stationary cultures. Cells lyse in distilled water. The optimum salt concentration for growth is 3.5–4.5 M NaCl. Magnesium requirement is moderate (5–50 mM) or low. Amino acids are required for growth. Some species grow on single carbon sources. Most species use sugars, some with the production of acids. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids. Characteristic lipids are PG, Me-PGP, and a glycolipid ($S_2$-DGD in most species or S-DGD). PGS is absent.

The mol% G + C of the DNA is 59.3–67.0.

Type species: *Haloterrigena turkmenica.*

The genus *Haloterrigena* currently contains nine species: *Htg. turkmenica* (type species), *Htg. daqingensis, Htg. hispanica, Htg. jeotgali, Htg. limicola, Htg. longa, Htg. saccharevitans*, and *Htg. salina.*

The main features of the members of the genus are summarized in ➋ *Table 7.14*.

Additional comment:

- Phylogenetically the genera *Haloterrigena* and *Natrinema* are not well separated (Tindall 2003; see also ➋ *Fig. 7.1*). Based on other phylogenetic markers such as the RNA polymerase subunit B′ (*rpoB*′) gene, the genera *Natrinema* (McGenity et al. 1998) and *Haloterrigena* (Ventosa et al. 1999) might constitute a single genus (Minegishi et al. 2010a).

## Genus *Halovenus* Makhdoumi-Kakhki, Amoozegar, and Ventosa 2012a, 1334$^{VP}$

*Ha.lo.ve'nus.* Gr. n. *hals, halos*, salt; L. fem. n. *venus* beauty, grace, elegance; N.L. fem. n. *Halovenus*, a salt-loving beauty, reflecting the attractive appearance of colonies.

Cells are nonmotile and pleomorphic (rods to triangles, squares, or disk shaped) and lyse in distilled water. Strictly aerobic, growing on a wide range of substrates, including single and complex carbon sources. Polar lipids are PG, PGP-Me, and two minor phospholipids. MK-8(II-$H_2$) is the only lipoquinone present.

The mol% G + C of the DNA is 61.0.

Type species and currently only species: *Hvn. aranensis.*

The main features of the members of the genus are summarized in ➋ *Table 7.15*.

## Genus *Halovivax* Castillo, Gutiérrez, Kamekura, Ma, Cowan, Jones, Grant, and Ventosa 2006, 767$^{VP}$

*Ha.lo.vi'vax.* Gr. n. *hals, halos*, salt; L. adj. *vivax*, long-lived, tenacious of life; N.L. masc. n. *Halovivax*, long-living halophile.

Cells are extremely pleomorphic, although most are rod shaped. Colonies are pale pink pigmented. Strictly aerobic. Polar lipids include PG, PGP-Me, two major and one minor glycolipids similar to those of *Nnm. pellirubrum*, and an unidentified glycolipid.

The mol% G + C of the DNA is 60.3–65.0.

The genus *Halovivax* currently contains two species: *Hvx. asiaticus* (type species) and *Hvx. ruber.*

The main features of the members of the genus are summarized in ➋ *Table 7.15*.

## Genus *Natrialba* Kamekura and Dyall-Smith 1996, 625$^{VP}$; Effective Publication: Kamekura and Dyall-Smith 1995, 347 (Validation list 57); emend. Oren, Arahal, and Ventosa 2009, 640

*Na.tri.al'ba.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; L. fem. adj. *alba*, white; N.L. fem. n. *Natrialba*, sodium white, referring to the high sodium ion requirement and the pigmentless colonies of the type species.

Cells are rods, cocci, or coccobacilli, sometimes occurring in tetrads. Some species lack pigmentation, while others are pigmented red by bacterioruberin carotenoids. Cells lyse in distilled water. Salt concentration for growth is 1.6–5.3 M NaCl. Neutrophilic or alkaliphilic with growth up to pH 10.5–11. Magnesium requirement is moderate (5–50 mM) or low. No growth on single substrates. Neutrophilic species produce acids from sugars. Amino acids are required for growth. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids. Polar lipids are PG and PGP-Me. Neutrophilic species contain $S_2$-DGD in addition. Unidentified phospholipids found in alkaliphilic species. Glycolipids are absent in alkaliphilic species.

The mol% G + C of the DNA is 61.5–64.3 CHECK.

The genus *Natrialba* currently contains six species: *Nab. asiatica* (type species), *Nab. aegyptiaca, Nab. chagannaoensis, Nab. hulunbeirensis, Nab. magadii*, and *Nab. taiwanensis.*

The main features of the members of the genus are summarized in ➋ *Table 7.16*.

Additional comments:

- *Nab. taiwanensis* was originally described as a strain of *Nab. asiatica* (Hezayen et al. 2001).
- The name *Nab. aegyptiaca* was changed to *Nab. aegyptia* by the List Editor of Int. J. Syst. Evol. Microbiol. (Notification List, Int. J. Syst. Evol. Microbiol. 51, 1233, 2001), but *Nab. aegyptiaca* is correct as well. The International Committee on Systematics of Prokaryotes Subcommittee on the Taxonomy of *Halobacteriaceae* recommends use of *Nab. aegyptiaca.*

## Genus *Natrinema* McGenity, Gemmell, and Grant 1998, 1194$^{VP}$

*Na.tri.ne'ma.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; Gr. neut. n. *nema*, a thread; N.L. neut. n. *Natrinema*, sodium (-requiring) thread.

Cells are rods of varying length that lyse in distilled water. The optimum salt concentration for growth is 3.4–4.3 M NaCl. Magnesium requirement is moderate (5–50 mM) or low. Amino acids are required for growth. Neutrophilic and slightly alkaliphilic species exist. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids, as well as several unidentified glycolipids.

The mol% G + C of the DNA is 64.2–69.9.

The genus *Natrinema* currently contains 6 species: *Nnm. pellirubrum* (type species), *Nnm. altunense, Nnm. ejinorense, Nnm. gari, Nnm. pallidum, Nnm. pellirubrum*, and *Nnm. versiforme*.

The main features of the members of the genus are summarized in ➋ *Table 7.17*.

Additional comments:

– Phylogenetically the genera *Haloterrigena* and *Natrinema* are not well separated (Tindall 2003; see also ➋ *Fig. 7.1*). Based on other phylogenetic markers such as the RNA polymerase subunit B′ (*rpoB*′) gene, the genera *Natrinema* (McGenity et al. 1998) and *Haloterrigena* (Ventosa et al. 1999) might constitute a single genus (Minegishi et al. 2010a).

## Genus *Natronoarchaeum* Shimane, Hatada, Minegishi, Mizuki, Echigo, Miyazaki, Ohta, Usami, Grant, and Horikoshi 2010, 2532$^{VP}$

*Na.tro.no.ar.chae'um.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; N.L. neut. n. *archaeum* (from Gr. adj. *archaios*, ancient), ancient one, archaeon; N.L. neut. n. *Natronoarchaeum*, the soda archaeon.

Cells are nonmotile and extremely pleomorphic. Aerobic and slightly alkaliphilic. The major polar lipids are PG, PGP-Me, and a disulfated diglycosyl diether ($S_2$-DGD).

The mol% G + C of the DNA is 63.

Type species and currently only species: *Nac. mannanilyticum*.

The main features of the members of the genus are summarized in ➋ *Table 7.18*.

## Genus *Natronobacterium* Tindall, Ross, and Grant 1984b, 355$^{VP}$; Effective Publication: Tindall, Ross, and Grant 1984a, 41 (Validation list 15)

*Na.tro.no.bac.te'ri.um.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; N.L. pref. *natrono-*, pertaining to soda; L. neut. n. *bacterium*, a small rod; N.L. neut. n. *Natronobacterium*, soda rod.

Cells are rods of varying length that lyse in distilled water. Motile or nonmotile. The optimum salt concentration for growth is 3.5–4.5 M NaCl. Alkaliphilic, with a very low magnesium requirement. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids. Unidentified phospholipids are present; glycolipids and PGS are absent.

The mol% G + C of the DNA is 65.

Type species and currently only species: *Nbt. gregoryi*.

The main features of the members of the genus are summarized in ➋ *Table 7.18*.

Additional comments:

– *Nbt. magadii* (Tindall et al. 1984) was transferred to the genus *Natrialba* as *Nab. magadii* comb. nov. (Kamekura et al. 1997).
– *Nbt. nitratireducens* (Xin et al. 2001) was transferred to the genus *Halobiforma* as *Hbf. nitratireducens* comb. nov. (Hezayen et al. 2002).
– *Nbt. pharaonis* (Soliman and Trüper 1982) was transferred to the genus *Natronomonas* as *Nmn. pharaonis* comb. nov. (Kamekura et al. 1997).
– *Nbt. vacuolatum* (Mwatha and Grant 1993) was transferred to the genus *Halorubrum* as *Hrr. vacuolatum* comb. nov. (Kamekura et al. 1997).

## Genus *Natronococcus* Tindall, Ross, and Grant 1984b, 355$^{VP}$; Effective Publication: Tindall, Ross, and Grant 1984a, 41

*Na.tro.no.coc'cus.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; N.L. pref. *natrono-*, pertaining to soda; N.L. masc. n. *coccus* (from Gr. n. *kokkos*, grain, seed), coccus; N.L. masc. n. *Natronococcus*, soda berry.

Cells are coccoid, nonmotile, occurring in pairs, tetrads, or irregular clusters, and do not lyse in distilled water. Alkaliphilic, with a very low magnesium requirement. The optimum salt concentration for growth is 3.0–4.0 M NaCl. Neutrophilic. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids. Unidentified phospholipids are present; glycolipids and PGS are absent.

The mol% G + C of the DNA is 63.5–64.0

Type species: *Natronococcus occultus*.

The genus *Natronococcus* currently contains three species: *Ncc. occultus* (type species), *Ncc. amylolyticus*, and *Ncc. jeotgali*.

The main features of the members of the genus are summarized in ➋ *Table 7.18*.

## Genus *Natronolimnobius* Itoh, Yamaguchi, Zhou, and Takashina 2005, 1744$^{VP}$ (Validation list no. 105); Effective Publication: Itoh, Yamaguchi, Zhou, and Takashina 2005, 114

*Na.tro.no.lim.no'bi.us.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; N.L. pref. *natrono-*, pertaining to soda; Gr. n. *limnos*, a pool of standing water, lake; Gr. masc. n. *bios*, life; N.L. masc. n. *Natronolimnobius*, organism living in a soda lake.

Cells are rod shaped or pleomorphic flat shaped and strictly aerobic. Cells lyse in distilled water. Mesophilic or thermotolerant. $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids are present; glycolipids are not detected.

The mol% G + C of the DNA is 59–63.

The genus *Natronolimnobius* currently contains two species: *Nln. baerhuensis* (type species) and *Nln. innermongolicus*.

The main features of the members of the genus are summarized in ➋ Table 7.19.

## Genus *Natronomonas* Kamekura, Dyall-Smith, Upasani, Ventosa, and Kates 1997, 856$^{VP}$, emend. Burns, Janssen, Itoh, Minegishi, Usami, Kamekura, and Dyall-Smith 2010, 1175

*Na.tro.no.mo'nas.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; N.L. pref. *natrono-*, pertaining to soda; L. fem. n. *monas*, monad, unit; N.L. fem. n. *Natronomonas*, the soda unit.

Cells are rods or pleomorphic shapes of varying length, motile, and lyse in distilled water. Amino acids are required for growth. Alkaliphilic or non-alkaliphilic. Alkaliphilic strains grow at pH 7–10, while non-alkaliphilic strains grow at pH 5.5–8.5. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids. PG, PGP-Me, and phosphatidic acid. Unidentified phospholipids or glycolipids are present; PGS are absent, and alkaliphilic strains lack glycolipids.

The mol% G + C of the DNA is 61.2–64.3.

The genus *Natronomonas* currently contains two species: *Nmn. pharaonis* (type species) and *Nmn. moolapensis*.

The main features of the members of the genus are summarized in ➋ Table 7.19.

Additional comment:

- *Nbt. pharaonis* (Soliman and Trüper 1982) was transferred to the genus *Natronomonas* as *Nmn. pharaonis* comb. nov. (Kamekura et al. 1997).

## Genus *Natronorubrum* Xu, Zhou, and Tian 1999, 265$^{VP}$; emend. Cui, Tothy, Feng, Zhou, and Liu 2006, 1517; emend. Oren, Arahal, and Ventosa 2009, 641

*Na.tro.no.ru'brum.* N.L. neut. n. *natron* (arbitrarily derived from the Arabic n. *natrun* or *natron*) soda, sodium carbonate; N.L. pref. *natrono-*, pertaining to soda; L. neut. adj. *rubrum*, red; N.L. neut. n. *Natronorubrum*, the red of soda.

Cells are pleomorphic nonmotile rods or pleomorphic flat shaped, which lyse in distilled water. Cells are nonmotile or motile. Amino acids are required for growth. The optimum salt concentration for growth is 3.4–3.8 M NaCl. Alkaliphilic, with a very low magnesium requirement, or neutrophilic. Many sugars are utilized, sometimes with acid production. Possess both $C_{20}C_{20}$ and $C_{20}C_{25}$ core lipids. Unidentified phospholipids are present; glycolipids absent in some species; others may contain TGD-1 and additional unidentified glycolipids. PGS is absent.

The mol% G + C of the DNA is 59.9–62.5.

The genus *Natronorubrum* currently contains 5 species: *Nrr. bangense* (type species), *Nrr. aibiense, Nrr. sediminis, Nrr. sulfidifaciens*, and *Nrr. tibetense.*

The main features of the members of the genus are summarized in ➋ Table 7.20.

## Genus *Salarchaeum* Shimane, Hatada, Minegishi, Echigo, Nagaoka, Miyazaki, Ohta, Maruyama, Usami, Grant, and Horikoshi 2011, 2269$^{VP}$

*Sal.ar.chae'um.* L. n. *sal*, salt; N.L. neut. n. *archaeum* (from Gr. adj. *archaios*, ancient), ancient one, archaeon; N.L. neut. n. *Salarchaeum*, salt-requiring archaeon.

Cells are motile short rods. Does not use sugars as a single carbon source. Slightly acidophilic. The major polar lipids are PG, PGP-Me, S-DGD-1, and five unidentified glycolipids.

The mol% G + C of the DNA is 64.

Type species and currently only species: *Sar. japonicum.*

The main features of the members of the genus are summarized in ➋ Table 7.19.

## Isolation, Enrichment, and Maintenance Procedures

A variety of media have been recommended for the growth of different members of the *Halobacteriaceae.* Useful information can be found in the original papers with the species descriptions and in earlier reviews (Tindall 1991; Oren 2006). The web site of the Deutsche Sammlung von Mikroorganismen und Zellkulturen mbH (DSMZ, http://www.dmsz.de) lists many protocols for the preparation of media. Another useful online resource providing descriptions of growth media and laboratory procedures for use with the halophilic Archaea is the "Halohandbook" prepared by Dyall-Smith (2008) http://www.haloarchaea.com/resources/halohandbook/halohandbook_2008_v7.pdf). For solid media, higher than usual agar concentrations should be used as the high salt concentration of the medium interferes with the solidification of the agar. A concentration of 20 g agar/l generally gives satisfactory results. For the preparation of agar media for the haloalkaliphiles, the agar should be sterilized separately from the sodium carbonate and the other alkaline components of the media.

Media used differ greatly in total salt concentration, ionic composition (e.g., high magnesium concentrations of up to 0.8 M for species isolated from the Dead Sea), and pH (9.5 and higher for the alkaliphilic species, using media very low in divalent cation concentrations). Members of the *Halobacteriaceae* are generally grown in complex media containing high concentrations of yeast extract, casamino acids, and similar rich sources of nutrients. The use of media with high concentrations of peptides and amino acids reflects environments such as salted fish and hides from which many isolates were obtained. Not all members of the family prefer such rich media; the use of low-nutrient media and a restricted range of organic compounds has in the past decade led to the isolation of a number of interesting species such as *Hqr. walsbyi* and *Hsx. carlsbadense*. Notably the use of pyruvate, whether or not combined with the use of agarose instead of agar, has enabled the isolation of the elusive square flat *Haloquadratum* (Bolhuis et al. 2004; Burns et al. 2004a; Walsby 1980, 2005) and is one of the few substrates that enable growth of *Hsx. carlsbadense* (Vreeland et al. 2002).

Several brands of peptone, notably Bacto peptone (Difco), are unsuitable for the cultivation of members of the *Halobacteriaceae* as they cause lysis of the cells. The toxic factor present in Bacto peptone was identified as bile acids (Kamekura et al. 1988), known since 1956 to cause lysis of halophilic Archaea when present at very low concentrations (Dussault 1956a, b). Sugars may stimulate growth of many species. When adding sugars, proper buffering may be required to avoid acidification of the medium to values inhibitory for growth. Though light can be used as an energy source in species containing bacteriorhodopsin, no absolute requirement for light has been demonstrated for any strain, and all known members of the *Halobacteriaceae* grow well in the dark.

One of the key factors important when trying to recover as many species of *Halobacteriaceae* as possible as colonies on agar plates is the incubation time. Combined use of cultivation-dependent and cultivation-independent methods showed that members of most haloarchaeal groups in an Australian crystallizer pond are cultivable. Out of the $1.2 \times 10^7$ cells/ml detected by microscopy, up to $1.9 \times 10^6$ were recovered as colonies on plates containing 0.01 % nutrient broth and salts after 8 weeks of incubation (Burns et al. 2004b). Drying out of agar plates with the formation of salt crystals on the surface of the agar may present a serious problem in view of the often long incubation times required for colonies to appear. Incubation and storage of petri dishes in plastic bags is then recommended.

Recovery of colonies of halophilic Archaea from samples collected from nature may sometimes be enhanced by the addition of natural brine from the sampling site and a whole cell extract of *Halobacterium salinarum* as a source of stimulatory growth factors (Wais 1988). For the selective isolation of Archaea from natural sources, inclusion of antibiotics such as penicillin or ampicillin has been recommended.

Few procedures have been described for the selective isolation of specific genera and species belonging to the family *Halobacteriaceae*. *Halobacterium* can be selectively enriched under anaerobic conditions in medium containing L-arginine (Oren and Litchfield 1999). *Halococcus* species may possibly be selectively isolated by suspension of the sample in medium with a salt concentration sufficiently low to kill other neutrophilic halophilic Archaea, followed by cultivation in a suitable high-salinity medium. Viable *Halococcus* cells could even be recovered from seawater: 2–35 *Halococcus* colonies were obtained from 5 l portions of Mediterranean seawater sampled 5 km off the coast of Spain (Rodriguez-Valera et al. 1979). Members of the genera *Haloferax* and *Haloarcula* grow on inorganic media amended with a suitable single carbon and energy source (Rodriguez-Valera et al. 1980).

### Maintenance

Cold maintenance at −20 C to −70 C in 10–15 % glycerol + salts in stab cultures kept under liquid paraffin at 4–8 C are sometimes used for preservation of cultures of *Halobacteriaceae*. For long-term preservation, suspensions can be frozen in liquid nitrogen in salt solutions + 5 % DMSO or by lyophilization with the pre-dried milk method (Tindall 1991).

## Chemotaxonomic Properties

The *Halobacteriaceae* show many interesting chemotaxonomic traits, part of which are connected to their phylogenetic affiliation with the archaeal domain.

### Surface Layers

The non-coccoid representatives of the *Halobacteriaceae* possess an S-layer cell wall, whose main constituent is a high-molecular-weight glycoprotein. This glycoprotein cell wall is responsible for maintaining the native cell shape. The S-layer glycoprotein of *Hbt. salinarum* (molecular mass ~120 kDa) consists of a 87 kDa core protein rich in acidic amino acids, containing attached acidic and neutral saccharide chains. The primary structure of the protein backbone and the mode of glycosylation vary among the species. The glycoprotein cell wall requires high NaCl concentrations for stability. Similar to most other proteins of halophilic Archaea (see below), the wall protein denatures when suspended in distilled water, and as a result, the cells of most species lyse in the absence of salt due to the denaturation and dissolution of the cell wall. In some species, relatively high concentrations of magnesium or other divalent cations are required in addition to high NaCl concentrations to maintain the structural stability of the glycoprotein cell wall.

*Halococcus* species possess a thick sulfated heteropolysaccharide cell wall that does not require high salt concentrations to maintain its rigidity. The polysaccharide wall of *Hcc. morrhuae* contains glucose, galactose, mannose, N-acetylglucosamine, N-acetylgalactosamine, and different uronic acids; part of the sugar residues are sulfated (Schleifer et al. 1982). The coccoid *Ncc. occultus* also has a thick cell wall that retains its shape in the absence of salt. Its structure is unlike that of the cell wall polymer of *Halococcus*, and it consists of repeating units of a poly(L-glutamine) glycoconjugate (Niemetz et al. 1997).

Some species excrete exopolysaccharides that form a slime layers around the cells. This feature is especially prominent in some *Haloferax* species. The *Hfx. mediterranei* exopolysaccharide is built of glucose, mannose, and sulfated glucose units; the *Hfx. gibbonsii* polymer is composed of mannose, galactose, glucose, and rhamnose. *Hfx. denitrificans* has an exopolysaccharide composed of 2,3-diacetamido-2,3-dideoxy-D-glucopyranosiduronic acid and galactose (Parolis et al. 1999). Further information about the structure of these polysaccharides was reviewed by Oren (2006). Other types of extracellular polymers may occur as well; an interesting example is the poly-(γ-glutamate) layer found outside the cell wall of *Nab. aegyptiaca* (Hezayen et al. 2001).

## Polar Lipids, Neutral Lipids, and Pigments

The *Halobacteriaceae* possess lipids based on branched 20-carbon (phytanyl) and in some genera also 25-carbon (sesterterpanyl) chains, bound to glycerol by ether bonds. This unusual lipid structure was elucidated long before the Archaea were recognized as the third domain of life (Sehgal et al. 1962; Kates et al. 1966). A variety of polar lipids, including phospholipids, sulfolipids, and glycolipids, can be encountered in the different representatives of the group. The types of polar lipids present are an important characteristic in the taxonomic classification of genera and species (see ➲ *Tables 7.1*, ➲ *7.2*, ➲ *7.3*, ➲ *7.4*, ➲ *7.5*, ➲ *7.6*, ➲ *7.7*, ➲ *7.8*, ➲ *7.9*, ➲ *7.10*, ➲ *7.11*, ➲ *7.12*, ➲ *7.13*, ➲ *7.14*, ➲ *7.15*, ➲ *7.16*, ➲ *7.17*, ➲ *7.18*, ➲ *7.19*, ➲ *7.20*, ➲ *7.21*, and ➲ *7.22*). The diether core lipid that forms the basis for most of the polar lipid structures is 2,3-di-*O*-phytanyl-*sn*-glycerol ($C_{20}$,$C_{20}$). Many genera (*Halalkalicoccus, Halarchaeum, Halobiforma, Halococcus, Halomarina, Haloterrigena, Natrialba, Natrinema*, and others) contain in addition 2-O-sesterterpanyl-3-O-phytanyl-sn-glycerol ($C_{25}$,$C_{20}$). Sometimes 2,3-di-O-sesterterpanyl-sn-glycerol ($C_{25}$,$C_{25}$) is encountered as a minor component as well (De Rosa et al. 1982, 1983). The ratio between $C_{20}$,C $_{20}$ and $C_{25}$,$C_{20}$ lipids may depend on growth conditions: increasing medium salinity leads to an increased proportion of $C_{25}$,$C_{20}$ in the alkaliphiles *Nbt. gregoryi* and *Nab. magadii* (Morth and Tindall 1985). In most cases, the hydrophobic chains are fully saturated, but the occurrence of unsaturated phytanyl ("phytenyl") side chains was documented in *Hrr. lacusprofundi* isolated from Deep Lake, Antarctica, and able to grow at temperatures down to 4 C (Franzmann et al. 1988). Introduction of double bonds in the carbon chains is important in the regulation of membrane fluidity in this cold-adapted species. When grown at 25 C, the polar lipids (PG, PGP-Me, PGS, sulfated and non-sulfated glycolipids; see below) have fully saturated hydrophobic chains; cells grown at 12 C have unsaturated analogues with up to six double bonds (Gibson et al. 2005).

All *Halobacteriaceae* contain diether derivatives of phosphatidyl glycerol (PG) and the methyl ester of phosphatidyl glycerophosphate (PGP-Me) (Kates et al. 1993). The diether derivatives of phosphatidyl glycerosulfate (PGS) is present in many species. Its presence or absence is an important chemotaxonomic property that can be used to discriminate between different genera and species. Cardiolipins (bis-phosphatidyl glycerol) with different combinations of $C_{20}$ and $C_{25}$ isopranoid chains were found in the membranes of the haloalkaliphiles *Ncc. occultus* and *Ncc. amylolyticus* (Angelini et al. 2012). Other yet unidentified phospholipids have been detected in the genus *Natrinema* (McGenity et al. 1998). In *Ncc. occultus*, a phospholipid with a cyclic phosphate group has been identified: 2,3-di-*O*-phytanyl-*sn*-glycero-1-phosphoryl-3′-*sn* glycerol-1,2-cyclic phosphate (Lanzotti et al. 1989).

Glycolipids are present in most neutrophilic species, but are generally absent in the alkaliphilic members of the family. Di-, tri-, and tetraglycosyl diether lipids occur, part of them carrying one or more sulfate groups bound to the sugar moieties. Not all have yet been fully characterized. Some of the better known and widespread glycolipids are:

- S-DGD-1 (1-*O*-[α-D-mannose-(6′-$SO_3H$)-(1′ → 2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), the major glycolipid in the genus *Haloferax*. Chromatographically identical sulfated diglycosyl diether lipids have been identified in many other genera.
- DGD-1 (1-*O*-[α-D-mannose-(1′ → 2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), found in minor amounts in *Haloferax* species.
- DGD-2, a minor diglyceride lipid of unknown structure, containing mannose and glucose, found as a minor component in *Haloarcula* species.
- S-DGD-3 (1-*O*-[α-D-mannose-(2′-$SO_3H$)-α-D-(1 → 4)-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), the glycolipid of some *Halorubrum* species.
- $S_2$-DGD-1, a bis-sulfated glycolipid (1-*O*-[α-D-mannose-(2′,6′-$SO_3H$)-α-D-(1′ → 2′)-glucose]-2,3-di-*O*-phytanyl- or phytanyl sesterterpenyl-*sn*-glycerol), first characterized from *Natrialba asiatica.*
- TGD-1 (1-*O*-[β-D-galactose-(1′ → 6′)-α-D-mannose-(1′ → 2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), a minor glycolipid of *Hbt. salinarum.*
- TGD-2 (1-*O*-[β-D-glucose-(1′ → 6′)-α-D-mannose-(1′ → 2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), the sole or major glycolipid of most *Haloarcula* species.
- S-TGD-1 (1-*O*-[β-D-galactose-(3′-$SO_3H$)-(1′ → 6′)-α-D-mannose-(1′ → 2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), found in the genus *Halobacterium.*
- TeGD (1-*O*-[β-D-galactose-(1′ → 6′)-α-D-mannose-(3′ ← 1′)-α-D-galactofuranose-(1′ → 2′)-α-D-glucose]-2,3-di-*O*-phytanyl-*sn*-glycerol), a minor glycolipid of *Hbt. salinarum.*
- S-TeGD (1-*O*-[β-D-galactose-(3′-$SO_3H$)-(1′ → 6′)-α-D-mannose-(3′ ← 1′)-α-D-galactofuranose)-(1′ → 2′)-α-D-glucose]-2,3-di-O-phytanyl-*sn*-glycerol), found in *Halobacterium.*

The chemical structures of many of the above-listed lipids were given by Kamekura and Kates (1999) and Oren (2006).

Neutral lipids may represent about 10 % of the total lipid content of the *Halobacteriaceae* (Kamekura and Kates 1988; Kushwaha and Kates 1979). They include:

- $C_{20}$ isoprenoid lipids: geranylgeraniol.
- Neutral phytanyl ethers of glycerol: DL-*O*-phytanyl-*sn*-glycerol and 2,3-di-*O*-phytanyl-*sn*-glycerol.
- $C_{30}$-isoprenoid compounds: squalene, dihydrosqualene, tetrahydrosqualene, and dehydrosqualene.
- Carotenoids. Most species are pigmented red-orange due to a high content of carotenoid pigments in their cell membrane. Rare exceptions are *Nab. asiatica* and *Hrb. tiamatea*, which lack substantial amounts of carotenoids. The pigment content of the cells may depend on their nutritional status (Gochnauer et al. 1972; Kushwaha and Kates 1979) and on the salinity of the growth medium: certain *Haloferax* species are pigmented when grown at low salinity (e.g., 15 %), while at higher salt concentrations (e.g., 25 %), they may be almost colorless (Kushwaha et al. 1982; Rodriguez-Valera et al. 1980). The most abundant carotenoids of the *Halobacteriaceae* are the 50-carbon compounds α-bacterioruberin and its derivatives monoanhydrobacterioruberin and bis-anhydrobacterioruberin (Kelly et al. 1970; Kushwaha et al. 1974, 1975). $C_{40}$ carotenoids may be present in small amounts, lycopene and β-carotene being the most abundant (Kushwaha et al. 1982; Tindall 1992). Accumulation of canthaxanthin, in addition to bacterioruberin carotenoids, was reported in *Hfx. alexandrinus* (Asker and Ohta 2002b). Carotenoid pigments protect the cells against photodamage as shown in competition experiments in which wild-type cells of *Hbt. salinarum* and a carotenoid-less mutant were incubated at high light intensities (Dundas and Larsen 1962).

### Respiratory Quinones and Polyamines

The major respiratory quinones in the *Halobacteriaceae* are MK-8 and MK-8(VIII-$H_2$) (Collins et al. 1981; Tindall and Collins 1986). Quinones may amount to about 9 % of the total neutral lipid content of the cells (Kamekura and Kates 1988). The relative abundance of MK-8 and MK-8(VIII-$H_2$) depend on the growth conditions (Tindall 1992; Tindall et al. 1991). *Nbt. gregoryi* also contains monomethylated and dimethylated menaquinones (Collins and Tindall 1987).

Polyamines are found in the *Halobacteriaceae* in very small amounts, if at all. If present, agmatine appears to be the most common polyamine (Hamana et al. 1995; Kamekura et al. 1987).

## Physiological Properties

To provide osmotic balance of the cytoplasm with the extremely high salt concentrations in their environment, the *Halobacteriaceae* accumulate molar concentrations of KCl. Organic osmotic solutes are generally not used. An exception is the accumulation of 2-sulfotrehalose in *Ncc. occultus* (Martin et al. 1999). Most proteins require high salt for structural stability and activity and are characterized by an exceptionally high content of the acidic amino acids glutamate and aspartate. Accordingly they have a large net negative charge at the physiological pH (Mevarech et al. 2000; Lanyi 1974; Reistad 1970). In addition to the high salinity required by all species, many are obligate alkaliphiles. Some have temperature optima above 50 °C (Bowers and Wiegel 2011; Robinson et al. 2005).

Most species lead an aerobic heterotrophic life style (Tindall and Trüper 1986). They generally prefer complex media with amino acids as main organic nutrient. *Hbt. salinarum*, the type species of the type genus of the family, is unable to grow on sugars, but carbohydrates can be used by a variety of other species. Carbohydrate utilization was first demonstrated in *Hrr. saccharovorum* (Tomlinson and Hochstein 1972a, b; Tomlinson and Hochstein 1976). Breakdown of glucose follows a modified Entner-Doudoroff pathway in which the phosphorylation step is postponed: glucose is oxidized via gluconate to 2-keto-3-deoxygluconate, followed by phosphorylation to 2-keto-3-deoxy-6-phosphogluconate, which is then split into pyruvate and glyceraldehyde-3-phosphate (Tomlinson et al. 1974). Use of carbohydrates is often associated with the production of acids, as oxidation of such substrates is incomplete. When grown on glucose, *Hrr. saccharovorum* excretes acetic acid and pyruvic acid; galactose, lactose, and other sugars are converted to the corresponding aldonic acids (Tomlinson and Hochstein 1972b; Tomlinson et al. 1978). Acetate, pyruvate, and D-lactate were identified in cultures of several *Haloferax* and *Haloarcula* species grown in the presence of glycerol (Oren and Gurevich 1994).

While the species of *Halobacterium* and many other genera require complex media for growth, other members of the family can grow on defined media with single organic compounds (simple sugars, organic acids, amino acids) as carbon and energy source (Rodriguez-Valera et al. 1980). Many species produce exoenzymes (proteases, amylases, lipases, nucleases) enabling them to use proteins, starch, lipids, and nucleic acids as sources of nutrients.

Recent advances in genomic and systems biology have enabled an in-depth reconstruction of the metabolism of model organisms, notably strains of *Hbt. salinarum*, *Har. marismortui*, *Hqr. walsbyi*, and *Nmn. pharaonis* (Falb et al. 2008; Gonzalez et al. 2008). Recently a novel anaplerotic pathway for the incorporation of acetate into cellular carbon was identified in *Har. marismortui* and *Hfx. volcanii*: rather than the classic glyoxylate cycle, a methylaspartate cycle is operative (Khomyakova et al. 2011).

Some isolates can degrade aliphatic hydrocarbons (tetradecane, hexadecane, heptadecane, eicosane, heneicosane), aromatic hydrocarbons (acenaphthene, phenanthrene, anthracene, 9-methylanthracene), and other aromatic compounds (benzoate, cinnamate, 3-phenylpropionate, *p*-hydroxybenzoate). Most hydrocarbon and aromatic compounds degrading isolates belong to the genera *Haloferax* and *Haloarcula* (Bertrand et al. 1990; Cuadros-Orellana et al. 2006.; Emerson et al. 1994; Fu and Oriel 1999; Kulichevskaya et al. 1991; Tapilatu et al. 2010).

Due to the low solubility of oxygen in salt-saturated brines, oxygen may easily become a limiting factor for development of halophilic Archaea. One possible strategy to avoid oxygen limitation is the use of gas vesicles to buoy the cells toward the surface of the brine. *Hbt. salinarum*, *Hfx. mediterranei*, *Hgm. borinquense*, *Hpn. aerogenes*, *Hpn. natans*, *Hpn. vescus*, *Hqr. walsbyi*, and *Hrr. vacuolatum* can form gas vesicles. How effective gas vacuoles are to enable the cells to reach layer richer in oxygen is uncertain; for a critical discussion of this topic, see Oren et al. (2006).

One member of the family preferentially leads an anaerobic life style: *Hrd. tiamatea*, found in deep brines near the bottom of the Red Sea. It probably obtains its energy by fermentation (Antunes et al. 2008). Many other species have limited possibilities to survive and even grow in the absence of molecular oxygen, strategies based on anaerobic respiration with different electron acceptors, fermentation, or the use of light as an energy source when respiration cannot supply sufficient energy.

The ability to reduce nitrate is widespread among the members of the *Halobacteriaceae*. A few species (e.g., *Hfx. denitrificans*, *Har. marismortui*, *Har. vallismortis*, *Hgm. borinquense*) can grow anaerobically using nitrate as electron acceptor. Nitrate is generally reduced to $N_2$, but $N_2O$ formation has also been observed in several cases (Hochstein and Tomlinson 1985; Mancinelli and Hochstein 1986; Tomlinson et al. 1986). The ecological relevance of anaerobic growth on nitrate has never yet been ascertained.

Other alternative electron acceptors for respiration are dimethylsulfoxide (DMSO), trimethylamine *N*-oxide (TMAO), and fumarate. Reduction of DMSO and TMAO is coupled with growth in several species. *Hbt. salinarum*, *Hfx. mediterranei*, *Har. marismortui*, and *Har. vallismortis* grew anaerobically in the presence of DMSO or TMAO; in *Hfx. volcanii*, DMSO supported anaerobic growth, while TMAO did not (Oren and Trüper 1990). The genes enabling *Halobacterium* strain NRC-1 to grow on DMSO and TMAO have been characterized (Müller and DasSarma 2005). Fumarate-driven anaerobic growth was reported in some *Hbt. salinarum* strains, in *Hfx. denitrificans*, and in *Hfx. volcanii* (Oren 1991). The ecological relevance of anaerobic growth of members of the *Halobacteriaceae* on DMSO, TMAO, or fumarate is unknown. However, TMAO may be available as an electron acceptor in salted fish, a well-known habitat for species of *Halobacterium* and *Halococcus*. TMAO can be present in high concentrations within fish tissues as an osmotic solute. A recent addition to the list of electron acceptors that can drive anaerobic respiration in members of the *Halobacteriaceae* is thiosulfate. It is used by the pleomorphic rod-shaped strain HG, isolated from hypersaline lakes in the Kulunda steppe, Altai, Russia, phylogenetically affiliated with the genus *Natronorubrum*. It grows on acetate with reduction of thiosulfate to tetrathionate (Sorokin et al. 2005).

An entirely different strategy for anaerobic energy generation is fermentation of L-arginine to citrulline, ammonia, and $CO_2$. This process can drive anaerobic growth in *Hbt. salinarum* (Hartmann et al. 1980; Ruepp and Soppa. 1996). Anaerobic growth on arginine is not widespread among the haloarchaea; a wide variety of neutrophilic strains tested belonging to genera other than *Halobacterium* gave negative results (Oren 1994; Oren and Litchfield 1999). A specific enrichment procedure for members of the genus *Halobacterium* could thus be developed, based on their ability to grow anaerobically in the presence of L-arginine (Oren and Litchfield 1999).

Light can be used as an energy source to drive anaerobic growth in *Hbt. salinarum*, provided the cells contain the light-driven proton pump bacteriorhodopsin, a membrane-bound 27 kDa protein carrying retinal as a prosthetic group (Hartmann et al. 1980; Oesterhelt 1982; Oesterhelt and Krippahl 1983). As the biosynthesis of retinal from β-carotene is oxygen-dependent, either trace concentrations of oxygen must still be present, or retinal or retinaloxime should be supplied to the medium to enable sustained light-driven anaerobic growth (Oesterhelt and Krippahl 1983). Four retinal-containing proteins have been identified in members of the family: bacteriorhodopsin, an outward light-driven proton pump; halorhodopsin, an inward light-driven chloride pump; and two sensory rhodopsins, involved in light sensing for phototaxis. Bacteriorhodopsin was first identified in *Hbt. salinarum*, where it is localized in specialized patches of the cell membrane ("purple membrane") (Oesterhelt and Stoeckenius 1971; for a historic overview, see also Grote and O'Malley 2011). Upon excitation by light (absorption maximum 570 nm), protons are extruded from the cytoplasm to the outside of the cell (for a review, see Lanyi 2004). The proton gradient thus formed is used to drive energy-requiring processes in the cell, including the phosphorylation of ADP to ATP (Danon and Stoeckenius 1974). Not all members of the family produce bacteriorhodopsin; among those that do are *Hrr. sodomense* and *Hqr. walsbyi*. Studies of the bacteriorhodopsin gene cluster of *Hbt. salinarum* have shown that expression of the protein is induced by low oxygen tension and by light (Betlach et al. 1986; Shand and Betlach 1991). A second retinal protein, also first discovered in *Hbt. salinarum*, is halorhodopsin. The structure of this protein is similar to that of bacteriorhodopsin, but it acts as a chloride pump: excitation by light (absorption maximum 580 nm) causes the inward transport of chloride ions (Schobert and Lanyi 1982). Chloride transport is important to maintain the proper ionic balance and is essential for cell growth. Halorhodopsin was also found in several haloalkaliphilic Archaea, and the halorhodopsin of *Nmn. pharaonis* has been studied in detail (Lanyi et al. 1990). *Hbt. salinarum* contains two sensory rhodopsins, involved in light sensing for phototaxis. Sensory rhodopsin I is a green light receptor (light to which the cells are attracted), and sensory rhodopsin II, also termed phoborhodopsin, is a blue light receptor (light that acts as a repellent).

## Sensitivity to Antibiotics

Members of the *Halobacteriaceae* typically are resistant to such Bacteria-specific antibiotics as penicillin, ampicillin, cycloserine, kanamycin, neomycin, polymyxin, and streptomycin (Bonelo et al. 1984; Hilpert et al. 1981; Pecher and Böck 1981). Sensitivity to chloramphenicol is variable (see also ➲ *Tables 7.1*, ➲ *7.2*, ➲ *7.3*, ➲ *7.4*, ➲ *7.5*, ➲ *7.6*, ➲ *7.7*, ➲ *7.8*, ➲ *7.9*, ➲ *7.10*, ➲ *7.11*, ➲ *7.12*, ➲ *7.13*, ➲ *7.14*, ➲ *7.15*, ➲ *7.16*, ➲ *7.17*, ➲ *7.18*, ➲ *7.19*, ➲ *7.20*, ➲ *7.21*, and ➲ *7.22*). Most species are sensitive to novobiocin and bacitracin. Novobiocin is a DNA gyrase inhibitor (Gadelle and Forterre 1994, Sioud et al. 1988) and acts on the same target in the Archaea as in sensitive Bacteria. Bacitracin inhibits incorporation of the high-molecular-weight saccharide into the cell wall glycoprotein of non-coccoid halophilic Archaea and may also inhibit lipid biosynthesis in these organisms.

Members of the *Halobacteriaceae* are sensitive to a number of additional antibiotics and other antibacterial compounds:

- Anisomycin, a protein synthesis inhibitor of ribosomes of eukaryotes, also inhibits protein synthesis of nearly all members of the *Halobacteriaceae* tested, both in vivo and in vitro (Pecher and Böck 1981). Four species were reported as resistant: *Hrr. chaoviator*, *Hsx. carlsbadense*, *Nmm. moolapensis*, and *Sar. japonicum*.
- Cerulenin, an inhibitor of the synthesis of the straight-chain fatty acids by the fatty acid synthetase complex, inhibits *Hbt. salinarum* (and possibly other members of the order as well) (Dees and Oliver 1977). This finding suggests that the production of straight-chain fatty acids is essential even in an organism possessing archaeal type lipids. It is now known that fatty acids are used to acylate certain membrane proteins (Pugh and Kates 1994).
- Rifampicin inhibits many members of the *Halobacteriaceae* (Bonelo et al. 1984; Hilpert et al. 1981; Pecher and Böck 1981). The target of rifampicin action in the halophilic Archaea is probably not the DNA-dependent RNA polymerase, but the inhibition may be due to its detergent effect on the cell membrane, causing cell lysis.
- The DNA polymerase inhibitor aphidicolin prevents cell division and often causes the formation of elongated cells (Forterre et al. 1984, 1986; Schinzel and Burger 1984).
- Inhibition of halophilic Archaea by coumarin and quinolone antibacterial compounds presented evidence for the presence of DNA gyrase-like enzymes (Sioud et al. 1988). The quinolone compound ciprofloxacin inhibited most *Haloferax* and *Haloarcula* species at concentrations between 25 and 60 μg/ml. *Halobacterium* cells proved less sensitive. Sensitivity to ciprofloxacin and other quinolone derivatives (norfloxacin, perfloxacin) was decreased at increased magnesium concentrations (Oren 1996; Sioud et al. 1988). *Hfx. volcanii* became more resistant when the magnesium concentration in the growth medium was increased. Alkaliphiles such as *Nmn. pharaonis* are very sensitive (Oren 1996).
- Bile acids at low concentrations cause lysis of the cell envelopes of non-coccoid halophilic Archaea and are potent growth inhibitors (Dussault 1956a, b; Kamekura et al. 1988).

## Halocins

Many species of *Halobacteriaceae* excrete "halocins," protein antibiotics that inhibit the growth of other related species (Meseguer and Rodriguez-Valera 1986; Meseguer et al. 1986; Rodriguez-Valera et al. 1982; Torreblanca et al. 1989, 1990, 1994). Different modes of action have been suggested for different halocins (Shand et al. 1999). Halocin H4, excreted by the type strain of *Hfx. mediterranei* and halocin H1 of *Hfx. mediterranei* strain Xai3 cause membrane permeability changes and ionic imbalance in *Hbt. salinarum* (Meseguer and Rodriguez-Valera 1986; Meseguer et al. 1991; O'Connor and Shand 2002). Halocin H7, excreted by *Hfx. gibbonsii*, targets the $Na^+/H^+$ antiporter activity of sensitive strains (Alberola et al. 1998; Meseguer et al. 1995). More than 10 halocins have been wholly or partially characterized (Li et al. 2003; O'Connor and Shand 2002). The size of the mature proteins (after cleavage of signal sequence of the pre-protein) varies between 3.6 kDa, the 36-amino acid long "microhalocin" S8 excreted by a further uncharacterized strain isolated from Great Salt Lake, Utah (Price and Shand 2000), and 34.9 kDa—halocin H4 of *Hfx. mediterranei* (Cheung et al. 1997). Although the ability to excrete halocins may be expected to be of considerable ecological advantage, no data are available as yet that prove that halocins are excreted by natural communities of halophilic Archaea in concentrations sufficient to inhibit the development of competitor strains, thus substantiating their ecological role (see Kis-Papo and Oren 2000).

# Ecology

Members of the *Halobacteriaceae* can be found worldwide in hypersaline environments with salt concentrations above 10–15 % (Norton 1992; Oren 1994, 2011). As most species lyse when exposed to lower salinities even for short times, a stable high-salt environment is a prerequisite for their development. We find selected species at high pH in soda lakes, and an acidophilic species (*Hla. acidiphilum*) that grows optimally at pH 4.4 was recently characterized (Minegishi et al. 2008). Curiously, it was isolated from a sample of Chinese salt imported to Japan, that in saturated solution yielded an alkaline pH. Some can grow at low temperatures (*Hrr. lacusprofundi* from Deep Lake, Antarctica) (Franzmann et al. 1988), and temperatures up to 55 °C are tolerated by many species. Thus, as long as the salinity is suitably high, members of the *Halobacteriaceae* can be expected to grow.

Lakes with salt concentrations approaching saturation may show red hues, such as documented for the north arm of the

Great Salt Lake, the Dead Sea, and hypersaline alkaline lakes such as Lake Magadi, Kenya. Red-colored brines are also typically present during the final stages of the evaporation of seawater in solar saltern ponds (Oren 1994). Archaea are generally responsible for most of the color of the saltern brines. Numbers of $10^7$ to $10^8$ cells and higher per ml of brine are not unusual. Members of the *Halobacteriaceae* have also been recovered from saline and hypersaline soils (Zvyagintseva and Tarasov 1987).

The concentration of divalent cations, especially magnesium and calcium, in the environment is of considerable ecological importance. Thus, the Dead Sea is dominated by divalent cations (presently around 2 M $Mg^{2+}$ and 0.5 M $Ca^{2+}$, in addition to about 1.5 M $Na^+$ and 0.2 M $K^+$). Halophilic Archaea isolated from the Dead Sea are characterized by a relatively low requirement for $Na^+$ and an extraordinarily high tolerance toward and often also a requirement for high $Mg^{2+}$ concentrations, such as was shown for *Hfx. volcanii* (Mullakhanbhai and Larsen 1975), *Hrr. sodomense* (Oren 1983), and *Hbc. gomorrense* (Oren et al. 1995).

Alkaliphilic members of the family such as *Hrr. vacuolatum* (Mwatha and Grant 1993), *Nmn. pharaonis* (Soliman and Trüper 1982), *Nab. magadii*, *Nbt. gregoryi*, *Ncc. occultus* (Tindall et al. 1984), and *Ncc. amylolyticus* (Kanai et al. 1995) are characteristic inhabitants of hypersaline soda lakes in which the pH reaches 9–10 and higher. In accordance with the low solubility of the divalent cations $Mg^{2+}$ and $Ca^{2+}$ at high pH, the alkaliphilic halophiles do not require significant concentrations of magnesium for growth (Tindall et al. 1980).

*Halobacteriaceae* were also recovered from rock salt deposited millions of years ago. Such isolates include the type strains of *Hsx. carlsbadense*, *Hcc. dombrowskii*, *Hcc. salifodinae*, and *Nbt. noricense*. Much has been speculated about the longevity of such organisms within salt crystals. Sequences of haloarchaeal 16S rRNA fragments have been retrieved from salt samples as ancient as the Permian or the Triassic era (Fish et al. 2002; McGenity et al. 2000; Radax et al. 2001).

The first isolates of *Halobacteriaceae* described—strains of *Hbt. salinarum* and *Hcc. morrhuae*—were obtained from red growth on salted food products (fish, meat) and salted hides, nutrient-rich environments where colonization by haloarchaea may cause economic damage.

In view of the extremely high salt requirement of most species of *Halobacteriaceae*, it is somewhat surprising to find reports of their isolation (and/or the recovery of their 16S rRNA genes in culture-independent studies) from low-salt environments. The isolation of *Halococcus* sp. from seawater (Rodriguez-Valera et al. 1979) was possible due to the fact that in contrast to most other genera that lyse at low salt concentrations, *Halococcus* has a rigid cell wall. *Halococcus* cells may be dispersed by birds: strains of *Hcc. morrhuae* and *Hcc. dombrowskii* could be cultivated from the salt-excreting glands in the nostrils of the seabird *Calonectris diomedea* (Brito-Echeverría et al. 2007). A strain related to *Haladaptatus*, isolated from a traditional Japanese-style salt field, showed a high survival rate after 9 days incubation in 0.5 % seawater salts (Fukushima et al. 2007). In recent years, several reports were published on the existence of strains of *Halobacteriaceae* with a relatively low salt requirement for growth. Isolates of haloarchaea were obtained from a salt marsh in Essex, UK, an environment containing ~2.5 % salt only. One isolate designated strain HA Gp1 (unfortunately not characterized further) was reported to grow optimally at 10 % salt with growth being even possible at 2.5–3 % salt (Purdy et al. 2004). *Hap. paucihalophilus* was isolated from a low-salt sulfur spring in Oklahoma, and it grows at salt concentrations as low as 4.7 % NaCl with an optimum at 15–18 % (Savage et al. 2007). The recovery of *Haloarcula* sp. 16S rRNA gene sequences from a deep-sea black smoker chimney at a hydrothermal vent area near Papua New Guinea (Takai et al. 2001) is interesting as well. Whether hypersaline areas may be present within such chimney structures remains to be ascertained. An intriguing environment from which *Haloarcula*-related strains were recovered is the geothermal steam vent aerosols emerging from fumaroles in Kamchatka, Hawaii, New Mexico, California, and Wyoming. A single fumarole was estimated to emit $>10^9$ cells of haloarchaea per year (Ellis et al. 2008). The finding of 16S rRNA gene sequences of *Halobacteriaceae* within the intestine of humans is discussed in the next section.

## Pathogenicity: Clinical Relevance

As the *Halobacteriaceae* require high salt concentrations for growth, much higher than the physiological salt concentration of ~9 g/l of the body fluids, members of the family cannot be expected to be associated with the human body. Still there are two interesting observations showing that some species may indeed colonize humans. A culture-independent study of the intestinal microflora of Korean people yielded 16S rRNA gene sequences related to *Halorubrum* and *Halococcus* (Nam et al. 2008). The finding may be related to the local diet: species such as *Hrr. alimentarium* and *Hrr. koreense* were isolated from salt-fermented seafood based on shrimps. Haloarchaeal 16S rRNA gene sequences were also recovered from the intestinal mucosa of patients with inflammatory bowel disease in the UK. Eight out of the 39 biopsy samples gave positive PCR results. Some phylotypes were affiliated to the genera *Halobacterium* and *Halorubrum*; others belonged to a new lineage not yet represented by cultures. Thus, members of the *Halobacteriaceae* may under certain conditions be present in the mucosal microbiota (Oxley et al. 2010).

## Application

Members of the *Halobacteriaceae* have a number of useful applications, and potential new applications in biotechnological processes are being investigated (Galinski and Tindall 1992; Litchfield 2011; Margesin and Schinner 2001; Oren 2010;

Rodriguez-Valera 1992; Ventosa and Nieto 1995). The following list presents some of the current and potential future applications of the group:

- The positive effect of the presence of dense communities of red halophilic Archaea in saltern crystallizer ponds has been recognized for a long time. By trapping solar radiation, they raise the temperature of the brine and the rate of evaporation, thereby increasing salt production. To improve salt production in salterns that do not develop a sufficiently dense archaeal community, fertilization with nutrients may increase the red color of the ponds (Jones et al. 1981).
- Production of fermented fish sauce in the Far East (e.g., nam pla in Thailand) involves participation of halophilic Archaea. The product is traditionally made by adding two parts of fish and one part of marine salts. The mixture is covered with concentrated brine (4.4–5.1 M NaCl) and left to ferment for about a year. Red halophilic Archaea (identified as *Halobacterium* and *Halococcus*) reach their maximum density in the liquor after 3 weeks and persist throughout the fermentation period. The halobacterial proteases probably take part in the fermentation process (Thongthai and Siriwongpairat 1990; Thongthai and Suntinanalert 1991; Thongthai et al. 1992). Addition of starter cultures of *Halobacterium* sp. SP1(1) may accelerate fish sauce fermentation (Akolkar et al. 2010). Use of different strains of halophilic Archaea could improve the safety and quality of salted anchovies by reducing the content of histamine (Aponte et al. 2010). Immobilized cells of *Natrinema gari* strain BCC 24369 may be highly effective for the removal of histamine from salted food products (Tapingkae et al. 2010a, b).
- Different species of halophilic Archaea synthesize potentially useful products such as bacteriorhodopsin, exopolysaccharides, and poly-β-hydroxyalkanoate (PHA). Halophilic Archaea have distinct advantages in biotechnological processes as they are relatively easy to grow, danger of contamination is minimal, and culture size can be upscaled to the use of large fermenters (Kushner 1966). However, because of the low solubility of gases in concentrated brines, the supply of sufficient amounts of oxygen may cause problems. In addition, the aggressive nature of the salts should be taken into account when planning the construction of large fermenters with metal parts exposed to the medium. A corrosion-resistant bioreactor made of polyetheretherketone was developed for the production of PHA and poly(γ-glutamic acid) by *Natrialba* sp. (Hezayen et al. 2000).
- Bacteriorhodopsin, the light-driven proton pump of *Hbt. salinarum*, has considerable biotechnological potential (Oesterhelt et al. 1991). It may be used as a biological material for information processing. Other suggested uses include conversion of sunlight to electricity, ATP generation, desalination of seawater, use in chemo- and biosensors, and ultrafast light detection. The photochromic effect—shifts between the purple ground state of the molecule (the "B state") and the yellow "M state"—may be used for information storage, including holographic storage, and may enable development of powerful computer memories and processors (Birge et al. 1999). Bacteriorhodopsin offers many advantages since it is a very stable molecule, functioning well between 0 °C and 45 °C and pH 1–11 (Chen and Birge 1993), is easy to immobilize on solid substrates, and produces very reproducible photoelectric signals. Holographic bacteriorhodopsin films are suitable for the construction of computer memories enabling parallel processing, and the developing technology may lead to a new generation of computers (Hong 1986). To turn bacteriorhodopsin into a light sensor, it is spread in a thin film sandwiched between an electrode and an electrically conductive gel. Changes in the shape of the molecule create a displacement of charge, generating an electrical signal. The suitability of bacteriorhodopsin for all these applications can be greatly enhanced by mutation; using genetically engineered bacteriorhodopsin, up to 700-fold improvement has been realized in volumetric data storage (Hampp 2002a, b; Wise et al. 2002). Bacteriorhodopsin-based photo-electrochemical cells can be constructed (Chu et al. 2010). Use of *Hbt. salinarum* for light-driven hydrogen production was also explored (Lata et al. 2007; Zabut et al. 2006).
- A microbial fuel cell operating at high ionic strength conditions was designed, using *Nab. magadii* or *Hfx. volcanii* as biocatalyst at the fuel cell anode. Such a system may be favorable as high-salt media have a high electrical conductivity so that the internal resistance is diminished (Abrevaya et al. 2011).
- The extracellular polysaccharide produced by *Haloferax* has considerable biotechnological potential (Antón et al. 1988; Rodriguez-Valera et al. 1991). The bacterium produces up to 3–8 g/l of an acidic heteropolysaccharide with a high apparent viscosity at relatively low concentrations and resistance to extremes of salts, temperature, and pH. The structure of this polymer was elucidated (Parolis et al. 1996). *Hfx. volcanii* and *Hfx. gibbonsii* also produce exopolysaccharides. Such polymers may be used to modify rheological properties of aqueous systems, for viscosity stabilization as thickening agents, gelling agents, and emulsifiers, and may find applications in microbially enhanced oil recovery (Ventosa and Nieto 1995). Here, a salt-resistant surfactant is advantageous as high-salinity brines are often encountered associated with oil deposits. Whole cell preparations may be used, as the lipids liberated upon lysis of halophilic Archaea may also act as surfactants to improve the oil-carrying properties (Post and Al-Harjan 1988).
- Use of *Haloferax* species (*Hfx. mediterranei*, *Hfx. denitrificans*) was proposed for the bioremediation of saline and hypersaline waters containing nitrate (Cyplik et al. 2007, 2010) or chlorate and perchlorate (Martinez-Espinosa and Bonete 2007). *Hbt. salinarum* ATCC 43214 (misnamed as *Halobacter* (sic) *halobium*) was used to supplement activated sludge in a rotating biological disk system for COD removal

from saline wastewater (Dinçer and Kargi 2001; Kargi 2002; Kargi and Dinçer 1996). However, the salinity of the wastewater treated (up to 5 % or 10 % salt) is too low for growth or even for survival of the halophilic Archaea, and therefore, the mechanism of the reported improvement in performance of the system is not clear.

- *Hfx. mediterranei* cells may contain considerable amounts of poly-β-hydroxyalkanoate (PHA) (Fernandez-Castillo et al. 1986; Rodriguez-Valera et al. 1991). PHA is used for the production of biodegradable plastics. Though halophilic Archaea are not yet being used commercially for PHA production, they have certain obvious advantages over an organism such as *Alcaligenes eutrophus*, which is already being exploited for the purpose. *Hfx. mediterranei* can be grown on a cheap substrate such as starch. Moreover, downstream processing and purification of the product should be relatively simple as the cells are easily lysed in water (Ventosa and Nieto 1995). Also the high genomic stability of the organism and the reduced danger of contamination are clear assets. PHA production is maximal when grown on sugars (glucose or starch) and in the presence of low phosphate concentrations (Lillo and Rodriguez-Valera 1990; Rodriquez-Valera and Lillo 1992). PHA production was demonstrated in certain other halophilic Archaea as well, such as *Hfx. volcanii* and *Har. marismortui*. It has been argued that *Hfx. mediterranei* is economically better than several non-halophilic producers for the production of PHA from whey: the strain is robust and stable, and danger of contamination is minimal (Koller et al. 2007). Processes for the use of crude oil, petrochemical wastewater, or glycerol for the production of PHA by *Haloarcula* sp. IRU1 were recently described (Taran 2011a, b, c). However, the proposed addition of 0.8 % tryptone or 0.4 or 0.8 % yeast extract as source of nitrogen and other nutrients will make such a process economically unfeasible.
- Exoenzymes such as amylases, amyloglucosidases, proteases, and lipases that function at high salinity may be useful in biotechnological processes requiring degradation of macromolecules in the presence of high salt concentrations (Chaga et al. 1993; Eichler 2001; Ventosa and Nieto 1995).
- Canthaxanthin can be produced using *Hfx. alexandrinus* (Asker and Ohta 1999, 2002b).
- Halophilic Archaea degrading aliphatic and aromatic hydrocarbons may prove useful for the reduction of the chemical oxygen demand of hypersaline petroleum-produced water and the bioremediation of oil spills (Bertrand et al. 1990; Bonfá et al. 2011; Kulichevskaya et al. 1991).
- Members of the *Halobacteriaceae* growing on brine-cured hides (a phenomenon known as "red heat") negatively affect the quality of the product (Bailey and Birbir 1996). To prevent damage of brine-cured hides by growth of proteolytic halophilic Archaea, gelatinase-negative halocin producers could be applied against damaging proteolytic strains (Birbir et al. 2004).
- A 84 kDa protein from *Hbt. salinarum* has been used as an antigen to detect antibodies against the human c-*myc* oncogene product in the sera of cancer patients, and therefore, the protein may be useful for the detection of certain forms of cancer (Ben-Mahrez et al. 1988, 1991).
- Gas vesicles of *Halobacterium* can be used as a *Chlamydia* vaccine display and delivery system. Haptenes incorporated in recombinant GvpC protein showed strong antibody response in mice in the absence of further adjuvants (Childs and Webley 2012; Stuart et al. 2001). Lipid vesicles ("archaeosomes") made of *Hrr. tebenquichense* total polar lipids can be developed into vaccine delivery vehicles (Gonzalez et al. 2009).
- Site-specific endonucleases of halophilic Archaea (Schinzel and Burger 1986) may find uses in molecular biological research.

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