**Roseicyclus mahoneyensis** gen. nov., sp. nov., an aerobic phototrophic bacterium isolated from a meromictic lake

Christopher Rathgeber,1 Natalia Yurkova,1 Erko Stackebrandt,2 Peter Schumann,2 J. Thomas Beatty3 and Vladimir Yurkov1

1The University of Manitoba, Department of Microbiology, 422 Buller Building, Winnipeg, MB, Canada R3T 2N2
2DSMZ – Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Mascheroder Weg 1b, D-38124, Braunschweig, Germany
3The University of British Columbia, Department of Microbiology and Immunology, 300-6174 University Boulevard, Vancouver, BC, Canada V6T 1Z3

Eight strains of Gram-negative bacteria able to form ring-like cells were isolated from Mahoney Lake, a meromictic lake in south-central British Columbia, Canada. All strains were pink–purple and contained bacteriochlorophyll a incorporated into the light-harvesting 1 and 2 and reaction-centre pigment–protein complexes. Growth did not occur anaerobically under illuminated conditions; these strains were obligately aerobic, prompting their designation as members of the aerobic phototrophic bacteria. Physiological characterization revealed that these isolates share a similar tolerance to high levels of salinity and pH, as would be expected of bacteria from a highly saline lake; however, the strains exhibited marked differences in their ability to utilize organic substrates for aerobic heterotrophic growth. 16S rRNA sequence analysis showed that the strains are closely related to members of the non-phototrophic genera *Octadecabacter* (92±0–92±9 %) and *Ketogulonicigenium* (92±2–92±6 %), as well as to aerobic phototrophs of the genera *Roseivivax* (92±2–92±9 %) and *Roseovarius* (91±7–92±4 %) within the ‘Alphaproteobacteria’. The DNA G+C content was 66±2 mol%. The unusual light-harvesting complex 2, the distinct morphological features and physiological traits of these strains as well as the phylogenetic data support the proposal of the novel genus and species *Roseicyclus mahoneyensis* gen. nov., sp. nov., with ML6T (= DSM 16097T = VKM B-2346T) as the type strain.

**INTRODUCTION**

Mahoney Lake is a meromictic saline lake located in the south-central region of British Columbia, Canada. Interesting features of this lake include a sharp chemical discontinuity at the chemocline and high concentrations of Na⁺, Ca²⁺, Mg²⁺ and SO₄²⁻, leading to Mahoney Lake’s classification as a sodium sulfate-dominated lake (Northcote & Halsey, 1969; Hall & Northcote, 1986). The primary focus of most previous microbiological investigations of Mahoney Lake has been on the extremely dense population of the purple sulfur bacterium *Amoebobacter purpureus* (Overman et al., 1991, 1994, 1996). However strains of the purple sulfur bacterium *Thiocapsa roseopersicina*, the purple non-sulfur bacterium *Rhodobacter capsulatus* and the green sulfur bacteria *Chloroherpeton thalassum* and *Prosthecochloris aestuarii* have also been isolated from the chemocline (Overman et al., 1991). In 1997, 33 aerobic bacteriochlorophyll (Bchl)-containing strains were isolated from the oxic mixolimnion, between the surface and a depth of 5 m. These strains included both purple non-sulfur bacteria and aerobic anoxygenic phototrophic bacteria, and exhibited a variety of interesting spectral absorption properties and morphologies (Yurkova et al., 2002).

Aerobic bacteria that contain Bchl, commonly known as aerobic phototrophic bacteria (APB), are a relatively recently discovered and taxonomically diverse group. The primary distinguishing features of the APB are the presence of Bchl incorporated into light-harvesting (LH) and reaction-centre complexes, the relatively low level of photosynthetic units per cell, the inhibition of Bchl synthesis by light, the inability to grow phototrophically under anaerobic conditions, the high mid-point potential of the

**Abbreviations:** APB, aerobic phototrophic bacteria; Bchl, bacteriochlorophyll; LH, light-harvesting.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain ML6T is AJ 315682.
reaction-centre primary electron carrier and the abundance of carotenoid pigments (Yurkov & Beatty, 1998; Rathgeber et al., 2004).

The first-reported member of the APB, Erythrobacter longus, is an orange-pigmented rod-shaped bacterium that was isolated from the Bay of Tokyo some 20 years ago (Shiba et al., 1979; Shiba & Simidu, 1982). Since that time, other APB displaying a wide range of morphologies have been described. Members of the APB have been shown to produce typical rod shapes, elongated rods displaying thread-like cells and branching, ovoid cells and coccioid cells (Yurkov & Beatty, 1998); in addition, a highly pleomorphic member of this group, ‘Citromicrobium bathyomarinum’ (Yurkov et al., 1999), has been described. Although several vibrioid and spirillum-shaped genera and species have been described for the purple non-sulfur bacteria (Imhoff, 2001), no vibrioid species that are members of the APB have been identified. Here, we describe eight closely related vibrioid strains from Mahoney Lake as novel members of the APB.

**RESULTS AND DISCUSSION**

**Isolation**

The strains examined in this taxonomic description were isolated from the meromictic Mahoney Lake in southwestern British Columbia, Canada, in October 1997. Details of the isolation and enumeration of these bacteria were given by Yurkova et al. (2002).

**Culture properties**

All strains formed small, ~2 mm-diameter pink–purple to purple colonies on the surface of agar media. In liquid media under aerobic conditions, cultures appear pink–purple after 24 h, becoming more purple with age.

Growth did not occur anaerobically in either light or dark conditions, and light was not required for growth under aerobic conditions, which led us to designate them as APB (Yurkov & Beatty, 1998).

**Morphology and cytolgy**

Morphology was examined in exponential-phase cells grown in rich organic medium (described above) under aerobic conditions. Strains ML6, ML16, ML18, ML33, ML38, ML39, ML40 and ML44 shared a similar morphology, which varied from elongated rods to slightly curved rods to vibrioid, almost cyslindrical cells (Fig. 1a). Elongated rods were 0.6–2.6 μm in size, while vibrioid cells were 0.6–0.7 × 2.7–3.0 μm. This morphology is similar to that of the purple non-sulfur bacterium Rhodococcus purpureus (Pfenning, 1978), except that our isolates had pointed ends rather than flat to rounded ends.

Transmission electron microscopy (using Zeiss 10C equipment) of negatively stained cells showed the pointed regions at the poles to be electron dense (Fig. 1b), while electron microscopy of thin sections indicated that these polar zones are actually due to an enlarged periplasmic space found in...
both rod-shaped and vibrioid cells (Fig. 1c, d). The appearance is similar to that seen in *Rhodospirillum tenue* (Pfennig, 1969), although the significance of these polar, periplasmic structures is unclear. Polar localization of proteins critical for cell division, chromosome partitioning and cell-cycle control in *Escherichia coli*, *Bacillus subtilis* and *Caulobacter crescentus* have been described. Bacterial polarity seems to play a critical role in cell structure and life cycles (Lybarger & Maddock, 2001).

The above-mentioned strains are all non-motile. Cell division in strain ML6<sup>T</sup> occurs by way of symmetric and asymmetric constrictions.

The Gram-negative structure of the cell wall was confirmed by the electron-microscopic thin sections, but intracytoplasmic membrane formations, of the type usually found in true anoxygenic phototrophs, were not observed, which is typical of the APB (Fig. 1c, d). Cells contained electron-clear inclusions presumably due to storage of poly-β-hydroxyalkanoates.

The unusual morphological characteristics of these strains, ranging from rod shapes through vibrioid shapes to cyclical shapes, as well as the pointed periplasmic space, have not been previously reported in the APB (Yurkov & Beatty, 1998). Thus, these isolates are an exciting new addition to this already morphologically diverse group.

**Photosynthetic apparatus**

Absorption spectra for the representative strain ML6<sup>T</sup> are shown in Fig. 2. As for all the strains in the present study, the spectra showed *in vivo* Bchl a peaks at 805–806 nm and at 870–871 nm. The 870–871 nm peak is indicative of the LH1 complex, and the peak at 805–806 nm is indicative of a peripheral LH2 complex. This unusual organization of the

![Fig. 2. Absorption spectra of intact cells of strain ML6<sup>T</sup> grown aerobically in the dark (solid line), showing peaks at 805 and 870 nm corresponding to Bchl incorporated into the LH2 and LH1 complexes, respectively. These peaks are reduced or absent in cells grown aerobically in the presence of continuous illumination (broken line).](http://ijs.sgmjournals.org)
photosynthetic apparatus, where the LH2 complex has only
one peak at approximately 805 nm, has been found in only
two genera of the APB so far, namely *Roseobacter* (Shiba,
1991) and *Rubrimonas* (Suzuki *et al*., 1999), both of which
have morphological and physiological characteristics quite
distinct from those of our isolates. The presence of a

**Table 1.** Comparative physiological characteristics of the aerobic phototrophic strains isolated from Mahoney Lake and close phylogenetic relatives

Symbols: +, substrate is utilized, substrate is hydrolysed or antibiotic-sensitive; ++, substrate is utilized for very good growth; −, substrate is not utilized, substrate is not hydrolysed or antibiotic-resistant; W, very weak growth; NG, no growth; NA, not available. Reference strains were *Roseobacter litoralis* (Och 149^T*), *Roseivivax halodurans* (Och 239^T*); and *Roseovarius tolerans* (EL-172^T*). None of the strains shown utilized methanol and all were sensitive to chloramphenicol.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Mahoney Lake strains</th>
<th>Reference strains</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ML6^T</td>
<td>ML16</td>
</tr>
<tr>
<td>Growth at:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 °C</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>10 °C</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>28 °C</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>37 °C</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>45 °C</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Growth at pH:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-5</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>6-0</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>7-0</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>8-0</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>9-5</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>10-0</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>11-0</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>Utilization of:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acetate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Pyruvate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Glutamate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Butyrate</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Citrate</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Malate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Succinate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Lactate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Formate</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Fructose</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Glucose</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ethanol</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Yeast extract</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hydrolysis of:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Starch</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Gelatin</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Tween 60</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Antibiotic sensitivity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Penicillin G</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Streptomycin</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Polymixin B</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Tetracycline</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ampicillin</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Kanamycin</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Nalidixic acid</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

*Only optimum temperature and pH have been published (Suzuki *et al*., 1999).
relatively small reaction-centre peak located in the region of 800 nm is masked by the strong LH2 peak at 805 nm, as indicated in other experiments in which the reaction centre and LH complexes were purified from the photosynthetic membranes of ML6\(^T\) (C. Rathgeber, J. Afric, A. Vermeglio and V. Yurkov, unpublished).

These isolates lack absorption peaks in both the 805 and 870 nm regions when grown aerobically in the presence of continuous illumination (as shown for strain ML6\(^T\) in Fig. 2). This trait further confirms the identification of these strains as members of the APB. All strains show similar carotenoid peaks at approximately 408 and 484 nm.

**Biochemical and physiological data**

A variety of physiological characteristics are presented in Table 1. All of the isolates produce both catalase and cytochrome c oxidase.

The group of strains represented by ML6\(^T\) shows an absolute requirement for saline conditions, being unable to grow at concentrations of NaCl or Na\(_2\)SO\(_4\) (or presumably another compatible solute) below 0-5 %. The upper salinity limits for all of the strains are similar. All strains grow at Na\(_2\)SO\(_4\) concentrations up to 10 %, while the upper limit for NaCl is between 6 and 10 % (differing between strains).

All strains tolerate a wide range of pH values and grow between pH 6-0 and 11-0, the latter being the highest value tested.

In a previous study, 33 Mahoney Lake isolates were categorized into three groups based on their ability to utilize organic substrates as sole sources of carbon and energy (Yurkova et al., 2002). The largest group was made up of strains that were able to utilize a wide range of substrates. A second group contained strains with very restricted metabolic abilities and which could utilize only a limited number of organic substrates. A third and final group was made up of strains that did not grow in any media containing only single organic compounds because they require a complex organic source such as yeast extract (Yurkova et al., 2002). The strains described herein fall into all three previously described groups, as shown in Table 1, indicating that the ability to utilize organic substrates is not an adequate taxonomic marker for the APB isolated from Mahoney Lake, where even highly similar and highly related strains show great differences in organic carbon preference.

The isolates described in this paper cannot be repeatedly transferred and cultivated on minimal media in the absence of yeast extract. This indicates that they require an unknown growth factor present in yeast extract. Other strains from Mahoney Lake have been shown to be dependent on vitamin B\(_{12}\) and/or biotin (Yurkova et al., 2002); however, the addition of these vitamins to minimal media was not sufficient to allow the successive cultivation of these isolates.

As is common for the APB, there was variable sensitivity to antibiotics (Table 1). Again, this trait does not appear to be a useful taxonomic marker, as highly similar, highly related strains show markedly different responses to the antibiotics tested.

**DNA composition and phylogenetic analysis**

On the basis of the analysis of almost-complete 16S rRNA gene sequences (>1430 nucleotides), strain ML6\(^T\) is a member of the z-3 group of the Proteobacteria, within the Roseobacter clade (Fig. 3). On the basis of the analysis of the algorithm of De Soete (1983), neighbour-joining and maximum-likelihood, strain ML6\(^T\), along with the purple non-sulfur strain ML42 (Yurkova et al., 2002), define a novel lineage. As bootstrap values are at this level very low, the branching point may change when novel sequences are included. The phylogenetic distance between ML6\(^T\) and ML42 (96-9 %) is like that which is generally found for well-separated species. However, physiological differences clearly place them in different genera (Yurkova et al., 2002). Strain ML6\(^T\) shares less than 93-0 % 16S rRNA gene sequence similarity with its phylogenetically closest taxonomically characterized relatives, i.e. members of the non-phototrophic genera Octadecabacter (92-0–92-9 %) and Ketogulonicigenium (92-2–92-6 %) and the APB.

---

**Fig. 3.** Neighbour-joining dendrogram of 16S rRNA gene sequence relatedness, showing the position of *Roseicyclus mahoneyensis* strain ML6\(^T\) and its phylogenetic neighbours, i.e. the purple non-sulfur strain ML42, members of the genera Ketogulonicigenium and other members of the Roseobacter clade, z-3 cluster of the Proteobacteria. Bootstrap values (500 resamplings) that support branching points above 90 % confidence are indicated. The tree was rooted with the 16S rRNA gene sequences of other members of the ’Alphaproteobacteria’. The asterisk indicates a sequence deposited in the Ribosomal Database Project (http://rdp.cme.msu.edu/index.jsp) rather than EMBL. Bar, 6 substitutions per 100 sequence positions.

---

http://ijs.sgmjournals.org

Downloaded from www.microbiologyresearch.org by

IP: 54.70.40.11

On: Sat, 12 Jan 2019 11:50:29

---

*Roseicyclus mahoneyensis* gen. nov., sp. nov.
species *Roseivivax halodurans* (92·2–92·9 %) and *Roseovarius tolerans* (91·7–92·4 %).

**Concluding remarks**

The presence of Bchl a incorporated into the reaction centre, the LH1 and LH2 complexes, the inability to grow photoheterotrophically under anaerobic conditions, the strong inhibition of Bchl synthesis by light and the absence of an intracytoplasmic membrane system prompt us to conclude that all of the novel strains described in this work are indeed members of the APB.

The phylogenetic analysis revealed that these strains have identical rRNA gene sequences and constitute a distinct branch closely related to the chemotrophic genera *Octadecabacter* and *Ketogulonicigenium*, as well as to phototrophs of the genera *Roseivivax* and *Roseovarius*.

Morphological, physiological and biochemical properties allow us to differentiate the novel strains easily from their close phylogenetic neighbours in the genera *Octadecabacter* and *Ketogulonicigenium*. Members of the genus *Octadecabacter* are obligate psychrophiles and form rod-shaped cells containing gas vacuoles (Gosink et al., 1997), whereas *Ketogulonicigenium* species are facultatively anaerobic, ovoid rods that exhibit relatively narrow pH, temperature and salinity ranges (Urbance et al., 2001). Neither *Octadecabacter* nor *Ketogulonicigenium* species form the vibrioid or cyscical cells characteristic of our Mahoney Lake isolates, and neither contain Bchl a or carotenoid pigments, although all species of *Ketogulonicigenium* produce an unidentified, water-soluble, brown pigment.

Additionally, the strains represented by ML6T differ significantly from their closest phototrophic relatives, members of the genera *Roseivivax* and *Roseovarius*, in terms of their cellular morphology and photosynthetic LH apparatus. Although both *Roseivivax* and *Roseovarius* were isolated from a similar habitat (i.e. a saline lake) and exhibit broad tolerance to saline conditions similar to that found in the Mahoney Lake isolates, they do not produce a peripheral LH2 complex and form normal motile rods (Suzuki et al., 1999; Labrenz et al., 1999).

On the basis of these important taxonomic markers and the low 16S rRNA gene sequence similarity (<93·0 %) between the novel isolates and their closest phylogenetic relatives, we propose the novel genus *Roseicyclus*, with *Roseicyclus mahoneyensis* as the type species.

**Description of Roseicyclus mahoneyensis sp. nov.**

Roseicyclus mahoneyensis (ma.ho.ne.y'en'sis, N.L. masc. adj. mahoneyensis from Mahoney Lake, where the species was originally isolated).

Shows the following properties in addition to those given for the genus. Cells are elongated rods (0·6 × 2·6 μm) or vibrioid cells (0·6–0·7 × 2·7–3·0 μm). Bchl gives *in vivo* absorption spectrum peaks at 805–806 and 870–871 nm. Aerobic organoheterotrophic and facultative phototroph. Best substrate for growth is yeast extract; growth also occurs on acetate, pyruvate, glutamate, butyrate, citrate, malate, succinate, lactate, fructose and glucose, depending on the strain. Strains differ in their ability to hydrolyse starch and Tween 60; all strains hydrolyse gelatin. Optimum temperature for growth is 30 °C, with growth occurring at temperatures as low as 4 °C and as high as 37 °C, depending on the strain. Absolute requirement for saline conditions, with growth occurring over a wide range of NaCl and Na2SO4 concentrations, from 0·5 to 10 %. Growth occurs over a wide range of pH values, from pH 6·0 to 11·0. May or may not be resistant to a variety of antibiotics including penicillin G, streptomycin, tetracycline, ampicillin, kanamycin and nalidixic acid, depending on the strain. Requires an unidentified growth factor present in yeast extract. The DNA G+C content is 66·2 mol%.

The habitat of the first isolated strains is the meromictic saline Mahoney Lake in south-central British Columbia, Canada. The type strain is ML6T (= DSM 16097T = VKM B-2346T).

**ACKNOWLEDGEMENTS**

This research was funded by grants from the NSERC (Canada) to V. Y. and J. T. B. We thank K. J. Hall and T. G. Northcote for collection of samples from Mahoney Lake and H. G. Trüper for assistance with the nomenclature.

**REFERENCES**


nonpigmented, psychrophilic gas vacuolated bacteria from polar sea
Hall, K. J. & Northcote, T. G. (1986). Conductivity-temperature
standardization and dissolved solids estimation in a meromictic
Aquatic Bacteriology, pp. 207–240. Edited by B. Austin. New York:
Wiley.
Prokaryotes: an Evolving Electronic Resource for the Micro-
biological Community, 3rd edn, release 3.6, 22 June 2001. Edited by
link/service/books/10125/
Kellenberger, E., Ryter, A. & Sechaud, J. (1958). Electron micro-
scope study of DNA-containing plasms. II. Vegetative and mature
plague DNA as compared with normal bacterial nucleoids in different
Labrenz, M., Collins, M. D., Lawson, P. A., Tindall, B. J., Schumann,
budding bacterium with variable bacteriochlorophyll a production
Maidak, B. L., Olsen, G. J., Larsen, N., Overbeek, R., McCaughey,
osine/thymidine ratios in complex mixtures by high-performance
liquid chromatography for determination of the mole percentage
guanine + cytosine of DNA. J Chromatogr 479, 297–306.
Northcote, T. G. & Halsey, T. G. (1969). Seasonal changes in the
limnology of some meromictic lakes in southern British Columbia.
J Fish Res Board Can 26, 1763–1787.
Overman, J., Beatty, J. T., Hall, K. J., Pfennig, N. & Northcote, T. G.
and population dynamics of Anoebobacter purpureus in a mero-
control the growth of aerobic heterotrophic bacterioplankton in a
Pfennig, N. (1969). Rhodospirillum tenue sp. n., a new species of the
Pfennig, N. (1978). Rhodocyclus purpureus gen. nov. and sp. nov., a
ring-shaped vitamin B12-requiring member of the family Rhodo-
Rainey, F. A., Ward-Rainey, N., Kroppenstedt, R. M. & Stackebrandt,
E. (1996). The genus Nocardiopsis represents a phylogenetically
coherent taxon and a distinct actinomycete lineage: proposal of
phototrophic bacteria: new evidence for the diversity, ecological
importance and applied potential of this previously overlooked
Shiba, T. (1991). Roseobacter litoralis gen. nov., sp. nov. and
Roseobacter denitrificans sp. nov., aerobic pink-pigmented bacteria
which contain bacteriochlorophyll a. Syst Appl Microbiol 14, 140–145.
nov., an aerobic bacterium which contains bacteriochlorophyll a. Int
bacteria which contain bacteriochlorophyll a. Appl Environ Microbiol
38, 43–45.
Roseivivax halodurans gen. nov., sp. nov. and Roseivivax halotolerans
sp. nov., aerobic bacteriochlorophyll-containing bacteria isolated
composition by reversed-phase high-performance liquid chromato-
Urbance, J. W., Bratina, B. J., Stoddard, S. F. & Schmidt, T. M.
(2001). Taxonomic characterization of Ketogulonigenium vulgare
gen. nov., sp. nov., and Ketogulonigenium robustum sp. nov., which
51, 1059–1070.
tolerance of obligately aerobic, phototrophic bacteria in a microbial
Yorkov, V., Stackebrandt, E., Holmes, A. & 7 other authors (1994).
Phylogenetic positions of novel aerobic, bacteriochlorophyll a-
containing bacteria and description of Roseococcus thiisulfatophilus
gen. nov., sp. nov., Erythromicrobium ramosum gen. nov., sp. nov.,
Yorkov, V. V., Krieger, S., Stackebrandt, E. & Beatty, J. T.
(1999). Citromicrobium bathyomarinum, a novel aerobic bacterium
isolated from deep-sea hydrothermal vent plume waters that
contains photosynthetic pigment-protein complexes. J Bacteriol
181, 4517–4525.
Yorkova, N., Rathgeber, C., Swiderski, J., Stackebrandt, E., Beatty,
J. T., Hall, K. J. & Yorkov, V. (2002). Diversity, distribution and
physiology of the aerobic phototrophic bacteria in the mixolimnion
of a meromictic lake. FEMS Microbiol Ecol 40, 191–204.