23 The Family *Moritellaceae*

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Abstract
Moritellaceae is a family that belongs to the order *Alteromonadales* within the class *Gammaproteobacteria*. It embraces the genera *Moritella* and *Paramoritella*. Currently seven species and one species are known in the genera *Moritella* and *Paramoritella*, respectively. All species were phenotypically characterized as halophilic facultative anaerobes and isolated from marine environments. The genus *Moritella* has been known to consist solely of psychrophilic species, while *Paramoritella* species is mesophilic. The difference of temperature adaptation between two genera within the same family is quite similar to the evolutionally pattern observed in the two genera, *Colwellia* and *Thalassomonas*, within the family *Colwelliaceae*. The 16S rRNA gene sequences indicate that both genera are related with 93 % similarity level. The entire family is phylogenetically closely related to the family *Shewanellaceae*. *Moritella* species have been isolated from seawater, sediment, and fish samples, which were collected only from cold marine environments. *Moritella* species have been studied as model microorganisms of low-temperature-adapted enzymes, piezophilic adaptation of marine bacteria to the deep sea, and an economically severe fish pathogen. *Moritella* species are also known as producers of polyunsaturated fatty acids (PUFAs) such as docosahexanoic acid (DHA). The genus *Paramoritella* is now comprised of a single species *Paramoritella alkaliphila* isolated from hard coral and marine sand from tropical marine environments. These two genera are clearly differentiated by their habitats, growth temperature properties, G + C mol%, and lower levels of 16S rRNA gene sequence similarity (<93 %).

Taxonomy, Historical, and Current

Short Description of the Family and Its Genera

History of the Family and Its Genera

Until the establishment of genus *Moritella*, the type strain of this genus *Moritella marina* was classified as *Vibrio marinus*, one of the most well-studied psychrophilic microorganisms isolated from cold marine environments (Morita and Haight 1964; Morita and Albright 1965; Albright 1969; Felter et al. 1969).

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V. marinus was originally described by Russell (1891), but the strain was subsequently lost (Colwell and Morita 1964). Later this species was reisolated from seawater off the coast of Oregon at a depth of 1,200 m (Colwell and Morita 1964). A comparative 5S rRNA sequencing study indicated that *V. marinus* was significantly different from previously known *Vibrio* species (MacDonell and Colwell 1984). However, a new taxon was not proposed because only single strain was available at that time (MacDonell and Colwell 1985). *V. marinus* was later proposed to be the type species of a new genus *Moritella* based on DNA homology studies, but was awaiting further validation (Steven 1990). Subsequent comparative 16S rRNA sequencing studies demonstrated that *V. marinus* is more closely related to the genera *Shewanella* and *Pseudoalteromonas* than to the genus *Vibrio* (Kita-Tsukamoto et al. 1993; Gauthier et al. 1995). Additional *Moritella* strains were isolated and used for phylogenetic analysis (Urakawa et al. 1998). The phylogenetic data clearly demonstrated the independency of *V. marinus* from the genus *Vibrio* and the justification of the proposal of new genus. *V. marinus* was transferred to a new genus *Moritella* gen. nov. as *Moritella marina* comb. nov. The genus was proposed by Urakawa et al. (1998) as an effective publication and officially validated in the validation list no. 69 (1999). The genus *Moritella* presently comprises seven species: the type species *M. marina*, which is psychrophilic and non-piezophilic; *Moritella viscosa*, originally described as *Vibrio viscosus*, a marine fish pathogen that causes skin ulceration; *Moritella yayanosii*, an obligate piezophilic species; *Moritella japonica*, a piezophilic bacterium isolated from the Japan Trench; *Moritella profunda*, a piezophilic species isolated from the deep Atlantic sediment; *Moritella abyssi*, a piezophilic bacterium isolated from the deep-sea sediment with *M. profunda*; *Moritella dasanensis*, a psychrophilic and ice-active substance-forming species isolated from the Korean Arctic Dasan station.

In 2004, the genus *Moritella* was officially embraced in the family *Moritellaceae* (Ivanova et al. 2004). The original description of the family was given by Ivanova et al. (2004). Later the description was amended by Hosoya et al. (2009) as a consequence of the discovery and proposal of a new genus *Paramoritella* within the family *Moritellaceae*. The amended description of the family includes the change of 16S rRNA gene signature nucleotides consisting of G/A at position 399, C/T at position 858, G at position 1311, and C at position 1326. The family comprises the type genus *Moritella* Urakawa et al. (1999 [validation list no. 69]) and the genus *Paramoritella* Hosoya et al. (2009).

Short Description of the Family

Original description of *Moritellaceae* (Ivanova et al. 2004) was made before the discovery of *Paramoritella alkaliphila*. Hosoya et al. (2009) emended the description of the family *Moritellaceae* with the minor modification of 16S rRNA gene signature nucleotides. However, since various phenotypic and genotypic features are different between two genera *Moritella* and *Paramoritella*, additional emendation of the family description is needed.

***Moritellaceae* fam. nov.** (modified from Ivanova et al. 2004 emend. Hosoya et al. 2009).

Moritellaceae (Mo.ri.tel.la'ce.ae. N.L. fem. n. *Moritella* type genus of the family, -aceae ending to denote a family, N.L. fem. pl. n. *Moritellaceae* the *Moritella* family). Cells are chemoorganotrophic, halophilic, facultatively anaerobic Gram-negative curved or straight rods motile by a single polar flagellum. Do not form endospores or microcysts. Usually do not denitrify. Arginine dihydrolase is absent. The major isoprenoid quinone is Q-8. The major fatty acids are 14:0, 16:0, and 16:1. As additional major fatty acids, *Moritella* species produce 22:6 and *Paramoritella* species produce 18:1. Members of the family have been isolated solely from marine environments. The family is a member of the order *Alteromonadales* in the class *Gammaproteobacteria* with the following 16S rRNA gene signature nucleotides consisting of G/A at position 399, C/T at position 858, G at position 1311, and C at position 1326. The family comprises the type genus *Moritella* Urakawa et al. (1999) (validation list no. 69) and the genus *Paramoritella* Hosoya et al. (2009).

Moritella Urakawa et al. (1999) (validation list no. 69), gen. nov. (Type genus of the family *Moritellaceae* Ivanova et al. 2004).

Type species: *Moritella marina* (Baumann et al. 1984) Urakawa et al. (1999) (validation list no. 69).

Etymology: N.L. fem. dim. n. *Moritella*, named after Richard Y. Morita to honor his work in marine microbiology.

References: validation list no. 69 (1999) and Urakawa et al. (1998) as an effective publication.

The changes have been made for the descriptions of major quinone and fatty acid components. Habitats were expanded. The order information was added. The reference of type genus was amended from the effective publication to the validation list.

Short Description of the Genera

Description of *Moritella* gen. nov. (Modified from Urakawa et al. 1998).

Moritella (Mo.ri.tel'la. M.L. dim. ending -ella. M.L. fem. n. *Moritella*, named after Richard Y. Morita to honor his work in marine microbiology). Cells are chemoorganotrophic, halophilic, facultatively anaerobic Gram-negative curved or straight rods motile by a single polar flagellum. Colonies are circular, convex, opaque, and nonpigmented. Cells are isolated from cold marine habitats and grow at 4 °C. The optimum growth temperature is below 20 °C. Cells are oxidase and catalase positive, mostly negative for Voges-Proskauer and H_2S production. Do not produce arginine dihydrolase. Utilize *N*-acetyl glucosamine. Acid but no gas is produced from D-glucose. G + C mol% is 40–45. The major isoprenoid quinone is Q-8. The major fatty acids are 14:0, 16:0, 16:1, and 22:6 (docosahexanoic acid [DHA]). In the 16S rRNA gene primary structure, two-base

insertion of thymine presents (between bases 206 and 207 *Escherichia coli* numbering position). The genus *Moritella* is a member of the order *Alteromonadales* in the class *Gammaproteobacteria*. The type species is *Moritella marina* (formerly *Vibrio marinus*).

This modification was made by the critical reviews of original description and expanded knowledge mainly added by the descriptions of six new species and the proposal of the order *Alteromonadales* (Nogi et al. 1998; Nogi and Kato 1999; Benediktsdóttir et al. 2000; Xu et al. 2003; Ivanova et al. 2004; Kim et al. 2008).

Description of *Paramoritella* gen. nov. (Hosoya et al. 2009).

Paramoritella (Pa.ra.mo.ri.tel'la. Gr. prep. *para* beside; N.L. fem. n. *Moritella* a bacterial genus name; N.L. fem. n. *Paramoritella* beside *Moritella*). Cells are Gram-negative, chemoorganotrophic, facultatively anaerobic, require seawater for growth, motile by means of subpolar flagella, and positive for oxidase and catalase. The predominant fatty acids are 14:0, 16:0, 16:1v7c, and 18:1v7c, and the respiratory quinone is Q-8. This genus belongs to the class *Gammaproteobacteria*, and the type species is *Paramoritella alkaliphila*.

Table 23.1
Families within the order *Alteromonadales*

Family	Genus
Moritellaceae	*Moritella, Paramoritella*
Colwelliaceae	*Colwellia, Thalassomonas*
Psychromonadaceae	*Psychromonas*
Ferrimonadaceae	*Ferrimonas, Paraferrimonas*
Shewanellaceae	*Shewanella*
Idiomarinaceae	*Idiomarina, Aliidiomarina*
Pseudoalteromonadaceae	*Algicola, Pseudoalteromonas, Psychrosphaera*
Alteromonadaceae	*Aestuariibacter, Agarivorans, Aliagarivorans, Alishewanella, Alteromonas, Bowmanella, Catenovulum, Glaciecola, Haliea, Marinimicrobium, Marinobacter, Marinobacterium, Melitea, Microbulbifer, Saccharophagus, Salinimonas*

Phylogenetic Structure of the Family and Its Genera

Groups of bacteria belonging to the order *Alteromonadales* are commonly isolated from marine environments (Bowman et al. 1997). Their abundance and importance are also confirmed on the basis of culture-independent molecular techniques (Bowman and McCuaig 2003). Currently eight families are included in this order (Table 23.1). Comparative 16S rRNA gene sequence analysis clearly demonstrates that *Moritella* species are tightly related to each other (>97.8 % sequence similarity) and distinguishable from other members among the order *Alteromonadales* (Fig. 23.1). The phylogenetic position of *Paramoritella* is solitary; it forms an independent genus separated from other genera among the order *Alteromonadales*.

The difference of temperature adaptation between two genera, *Moritella* and *Paramoritella*, within the same family

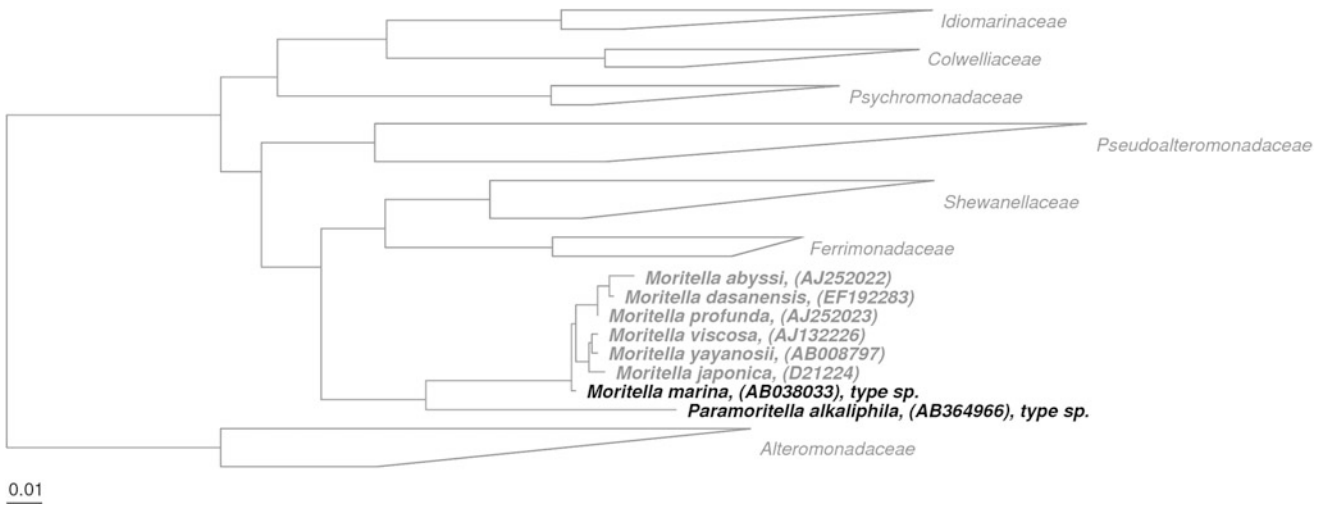

Fig. 23.1
Maximum likelihood phylogenetic tree, based on 16S rRNA gene sequences, showing the family *Moritellaceae* and related members within the order *Alteromonadales*. Scale bar indicates estimated sequence divergence

Moritellaceae is quite similar to the evolutionally pattern observed in two genera, *Colwellia* and *Thalassomonas*, within the family *Colwelliaceae* (Macian et al. 2001). The 16S rRNA gene sequences indicate that the two genera *Moritella* and *Paramoritella* are related with 93 % similarity level. The entire family is phylogenetically closely related to the family *Shewanellaceae* and *Ferrimonaceae* (Fig. 23.1; Ivanova et al. 2004; Hosoya et al. 2009).

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                    200                     220
                     .....|....  |....|....  |
E.coli               GGGGGAC--C  TTCGGGCCTC  T
M.marina             GGGCCTCTTC  TTGAAAGCTC  T
M.viscosus           GGGCCTCTTC  TTGAAAGCTC  T
M.japonica           GGGCCTCTTC  TTGAAAGCTC  T
M.yayanosii          GGGCCTCTTC  TTGAAAGCTC  T
M.profunda           GGGCCTCTTC  TTGAAAGCTC  T
M.abyssi             GGGCCTCTTC  TTGAAAGCTC  T
M.dasanensis         GGGCCTCTTC  TTGAAAGCTC  C
P.alkaliphila        GGGGGAC--C  TTCGGGCCTC  G
S.putrefaciens       AGGGGAC--C  TTCGGGCCTT  C
F.balearica          AGGGGCT--C  TTCGGACCTT  G
C.psychroerythraea   GGGGGAT--T  TTCGGACCTC  T
I.abyssalis          GGGGGAC--C  TTCGGGCCTC  A
A.macleodii          GGG------C  TTCGGCTCCG  G
P.espejiana          GGG------C  TTCGGCTCCG  G
P.antarctica         TGGCCTCTAT  TTATAAGCTA  T
P.aquimarina         TGGCCTCTAT  TTATATGCTA  T
P.leiognathi         GGGGGAC--C  TTCGGGCCTC  T
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Fig. 23.2
16S rRNA gene alignment of *Moritella* species and related taxa. Nucleotide numbering corresponds to the 16S rRNA gene of *Escherichia coli*. Unique T-T insertions at position between 206 and 207 among *Moritella* species are colored as red. The bacteria used in comparison with seven *Moritella* species are as follows: *Escherichia coli*, *Paramoritella alkaliphila*, *Shewanella putrefaciens*, *Ferrimonas balearica*, *Colwellia psychroerythraea*, *Idiomarina abyssalis*, *Alteromonas macleodii*, *Pseudoalteromonas espejiana*, *Psychromonas antarctica*, *Psychromonas aquimarina*, *Photobacterium leiognathi*

Molecular Analyses

The 16S rRNA Gene Signature Nucleotides

The signature nucleotides of the genus *Moritella* are A, T, G, and C at positions 399, 858, 1311, and 1326. Thymine-thymine insertion is found between bases 206 and 207 (*Escherichia coli* numbering). It was originally proposed by Urakawa et al. (1998) with the comparison of *M. marina* and 11 marine isolates. The robustness of these signature nucleotides has not been changing even after six new species have been reported. Although majorities of related taxa in the class *Gammaproteobacteria* do not have these insertions, *Psychromonas* species have AT insertion between bases 206 and 207 (Fig. 23.2).

In the family level, 16S rRNA gene signature nucleotides were amended: G/A at position 399, C/T at position 858, G at position 1311, and C at position 1326 (Hosoya et al. 2009).

DNA-DNA Hybridization

Comparative 16S rRNA analysis revealed that all *Moritella* species are tightly related to each other (>97.8 % sequence similarity). Since the similarity level among the genus is more than >97 %, DNA-DNA hybridization is essential for the discrimination of species (Wayne et al. 1987). The DNA-DNA relatedness among the genus *Moritella* is listed (Table 23.2). No obvious DNA-DNA hybridization groups were found, and the values ranged between 30 % and 60 %.

Table 23.2
DNA-DNA relatedness among members in the genus *Moritella*

		1	2	3	4	5	6	7
1	*M. marina*	–						
2	*M. japonica*	39[a]	–					
3	*M. yayanosii*	40[b]/30[c]		–				
4	*M. viscosa*	43[d]		57.5[b]	–			
5	*M. profunda*	41.5[b]				–		
6	*M. abyssi*			60[b]		55[b]	–	
7	*M. dasanensis*	43.5[e]					45.7[e]	–

Data adopted from:
[a]Nogi et al. (1998)
[b]Xu et al. (2003)
[c]Kato et al. (1998)
[d]Lunder et al. (2000)
[e]Kim et al. (2008)

Genome Analyses

Whole Genome Analysis

Whole genome sequence analyses have been done for *Moritella* sp. PE36 and *M. dasanensis* ArB 0140^T. *Moritella* sp. PE36 was selected because of its piezophilic nature. *M. dasanensis* was analyzed because of an interest of ice-pitting and hexagonal ice crystal formation activities. Currently, *M. viscosa* is also sequenced at Trust Sanger Institute because of its pathogenicity against marine fish.

Genome Analysis of PE36

Moritella sp. PE36 was isolated from 288 km offshore of San Diego in the Pacific Ocean at a depth of 3,584 m. This strain was characterized as deep-sea piezophile heterotroph, adapted to high pressure, and grows in a minimal medium with single carbon sources. Its optimum growth pressure was approximately 41.4 MPa, close to the pressure of its isolation depth (DeLong et al. 1997). The closest neighbor of this strain is *M. abyssi* based on the 16S rRNA gene sequence similarity (99.3 %). As well as other *Moritella* species, this strain contains polyunsaturated fatty acids (PUFAs) (DeLong and Yayanos 1985, 1986). The genome is 5,236,340 bp long, contains a plasmid (49,993 bp) and approximately 4,726 protein-encoding genes, 127 tRNA and 10 *rrn* operons, and the mol % G + C of DNA is 41.03 % (Kerman 2008). The value of mol% G + C is quite similar to the report of *M. abyssi* (41.6 %) (Xu et al. 2003).

Genome Analysis of *Moritella dasanensis*

The draft genome sequence of *M. dasanensis* ArB 0140^T was reported (Lee et al. 2012). The draft genome is 4,889,582 bp long, contains 4,293 protein-encoding genes, 91 tRNA genes and 10 rRNA operons, and the mol% G + C of DNA is 40.82 %. *Moritella* sp. strain PE36 and *Shewanella violacea* strain DSS12^T are the closest neighbors of strain ArB 0140^T. Further analysis of the *M. dasanensis* genome will be conducted to identify the genes involved in the cold adaptation mechanism and the ecological roles of this organism in the Arctic Ocean.

Phenotypic Analyses

Physiology and Identification Keys

Moritella and *Paramoritella* species are Gram-negative, chemoorganotrophic, halophilic, and facultative anaerobic motile rods. In a conventional phenotypic identification, strains belonging to the family *Moritellaceae* were classified into the members of the family *Vibrionaceae*. Thus, there is no wonder why many strains previously reported as *Vibrio* species were later deemed or reclassified as *Moritella* species (Benediktsdóttir et al. 2000; Colwell and Morita 1964; Morita 1975; DeLong et al. 1997; Hamamoto et al. 1995; Rüger and Tan 1992). Phenotypic comparison of *Moritella* and *Paramoritella* species is listed in *Table 23.3*.

The species of the genus *Moritella* are characterized as their low optimum and maximum growth temperatures. Three strains are facultative piezophiles and one strain, *M. yayanosii* is known as an obligate piezophile. Phenotypic differentiation can be achieved based on the acid production from sugars and the utilization patterns of carbon sources (*Table 23.3*). All strains are catalase and oxidase positive. Major isoprenoid quinone is Q-8. All strains reduce nitrate to nitrite without producing gas. None of the strains form pigmented colonies.

Currently *P. alkaliphila* is a solitary species in the genus *Paramoritella*. Since only single species is known, it is unclear whether alkaliphilic nature of *P. alkaliphila* is a common feature among the genus. If it were a common feature among the genus, the members of family *Moritellaceae* would be characterized as their extremophilic natures such as psychrophilly, piezophilly, and alkaliphilly.

Fatty Acid Composition

The high occurrence of the polyunsaturated fatty acid is a common feature among psychrophilic and piezophilic bacteria. The occurrence of 22:6 (docosahexanoic acid [DHA]) in fatty acid profiles is one of the most conspicuous properties of the members of the genera *Moritella* and *Colwellia* (DeLong et al. 1997; Kato et al. 1998). The fatty acid profiles of *Moritella* are different from the deep-sea *Shewanella* species that produce 20:5 (eicosapentaenoic acid [EPA]), but no DHA (Kato and Nogi 2001).

Isoprenoid Quinone Profile

The major isoprenoid quinone of *Moritella* species is Q-8. *Paramoritella alkaliphila* also has Q-8 as a major isoprenoid quinone. Thus, having Q-8 as a major isoprenoid quinone is a common feature among the family *Moritellaceae*. On the other hand, members of the genus *Shewanella* produce Q-7 and Q-8 together as the isoprenoid quinones (Kato and Nogi 2001). Thus, they are distinguishable from the species belonging to the family *Moritellaceae*.

Isolation, Enrichment, and Maintenance Procedures

Isolation and Enrichment

The most common medium used for both isolation and cultivation of *Moritella* species is ZoBell 2216 medium, which contains peptone and yeast extract (ZoBell 1941); now this medium is commercially available as Difco Marine Broth 2216 and Marine Agar 2216 (BD). All *Moritella* species can be cultured with this medium.

All *Moritella* species show psychrophilly and not tolerant for ambient laboratory temperatures. Thus, sample preparation and treatments must be cautioned so that microorganisms are kept

Table 23.3
Phenotypic comparison of *Moritella* and *Paramoritella* species

	M. marina	*M. japonica*	*M. yayanosii*	*M. profunda*	*M. abyssi*	*M. dasanensis*	*M. viscosa*	*P. alkaliphila*
Optimum growth temperature at atmospheric pressure	15	10	NG	2	4–6	9	15	30
Maximum growth temperature	<20	<20	ND	12	14	18	21–24	37–39
Optimum pressure (MPa) at 10 °C	0.1	50	80	22	30	ND	ND	ND
G + C content (mol%)	42.5	45.0	44.6	41.4	41.6	40.8	42.5	57
Growth at 20 °C	–	–	–	–	–	–	+	+
Gelatinase	+	+	+	–	–	+	+	+
Indole production	–	–	–	–	+	–	–	–
Acid production from								
Cellobiose	+	–	–	–	+	–	–	ND
D-Galactose	+	–	–	±	+	–	+	ND
Glycerol	+	+	–	–	–	–	–	–
Maltose	+	–	+	–	+	+	ND	ND
D-Mannitol	–	–	+	–	+	–	–	–
D-Mannose	–	–	+	–	–	–	–	ND
Xylose	–	–	+	–	–	–	–	–
Utilization as carbon source								
D-Arabinose	–	–	–	–	–	+	ND	ND
Cellobiose	+	–	–	–	+	–	ND	+
D-Galactose	+	–	–	+	+	–	ND	+
Glycerol	+	+	–	+	+	+	ND	ND
Maltose	+	–	–	–	+	–	ND	+
Trehalose	–	–	–	–	–	+	ND	+
Xylose	–	–	+	–	–	–	ND	+

Data are from Morita and Haight (1964), Nogi et al. (1998), Nogi and Kato (1999), Lunder et al. (2000), Benediktsdóttir et al. (2000), Xu et al. (2003), and Kim et al. (2008)
NG no growth, *ND* not determined

in cold and never exposed warm temperature for any extended period of time. For example, Rüger and Tan (1992) reported that agar plates and all solutions were chilled to 4 °C on a cold tray during the whole inoculation procedure.

For the selective enrichment of psychrophiles, low-temperature incubation ranged between 2 °C and 4 °C is widely used and recommended (Kato et al. 1998; Kim et al. 2008; Rüger and Tan 1992). Although, psychrophiles grow fast under the low-temperature conditions, incubation periods should be longer than typical mesophiles (Rüger and Tan 1992).

Four currently known *Moritella* species (*M. japonica*, *M. profunda*, *M. abyssi*, *and M. yayanosii*) are piezophilic and grow better under the pressure than atmospheric pressure. Thus, the use of a pressure vessel may require obtaining piezophilic strains from the deep sea (*Fig. 23.3*). Especially, obligate piezophiles such as *M. yayanosii* are only attained by using a pressure vessel (Kato et al. 1998). A sterilized plastic pouch is used for the isolation and cultivation of piezophilic bacterium. After inoculating the strain, the pouch is sealed without bubbles and stored in water filled and pressurized in the vessel.

Maintenance

To store bacterial cultures, low-temperature preservation is often used. That is because typical mesophilic bacteria only grow slowly or halt growing under the low-temperature condition. However, this rule cannot be applied in the case of *Moritella* species due to their psychrophilic nature. Since these psychrophilic bacteria grow well at low temperature, the transfer of cultures should be more frequent than mesophilic cultures. For example, *M. viscosa* is maintained on marine agar at 4 °C and reinoculated every 1 or 2 months (Benediktsdóttir et al. 2000). For short-term preservation, stab cultures in semisolid

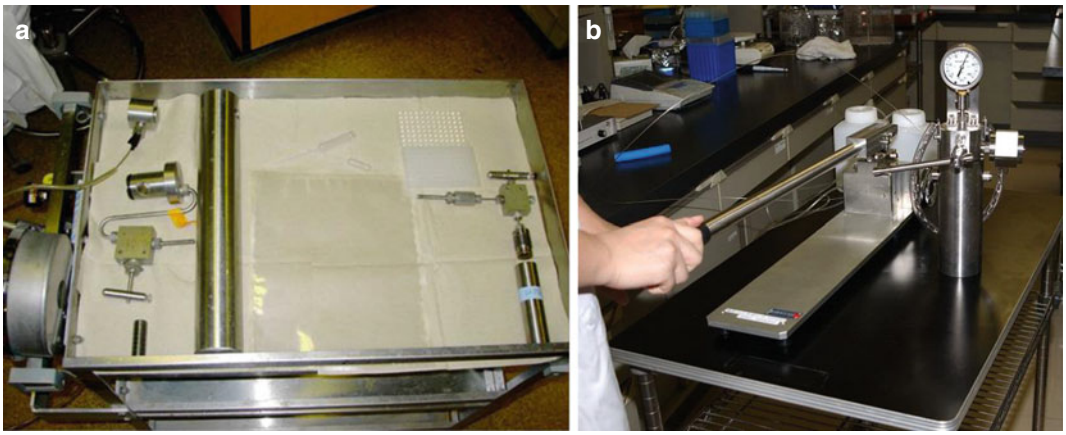

Fig. 23.3
High-pressure cultivation system consisted of a pressure-resistant container (a) and a hand pump with a coupler to inject water into the container (b). Various plastic cultivation units are also shown in a panel (a). This type of culture apparatus is essential to grow *Moritella yayanosii* (Courtesies of D. Bartlett, Scripps Institution of Oceanography, University of California and Y. Oshida, Japan Collection of Microorganisms, RIKEN BioResource Center)

medium are available for quarter to half year at low temperature (<4 °C). For long-term storage, preparation of glycerol stocks in an appropriate medium (10–20 % glycerol [v/v]) is the best preservation method. In a laboratory, a deep freezer is commonly used at −80 °C to preserve glycerol cultures. For more stable long-term storage, glycerol stocks in liquid nitrogen or lyophilization can be used. Culture collections maintain *Moritella* species as glycerol stocks or freeze-dried samples. Availability of lyophilization is confirmed in the case of *M. marina* strain ATCC 15381^T at American Type Culture Collection. *M. yayanosii* is an obligate piezophilic bacterium; this species cannot grow at atmospheric pressure. Thus, the maintenance of this culture requires a unique pressure vessel (*Fig. 23.3*). This strain is cultured in marine broth at 10 °C and 70 MPa. *M. yayanosii* is capable to survive under atmospheric pressure for a few hours. Thus, one can inoculate and collect the cells under atmospheric pressure. *M. yayanosii* JCM 10263^T is preserved as a glycerol stock (10 % glycerol in marine broth [v/v]) in a liquid nitrogen tank (vapor phase) at Japan Collection of Microorganisms, RIKEN BioResource Center.

Ecology

Habitats

Although two genera *Moritella* and *Paramoritella* form the family *Moritellaceae*, their growth temperature properties are quite different; members of *Moritella* genus are characterized as psychrophiles, but *P. alkaliphila* is a mesophilic bacterium. Judging by their growth temperature properties, their habitats do not likely overlap each other; one is isolated from a tropical ocean, while others are isolated from permanently cold marine environments. Thus, habitats will be separately discussed in the following sections.

Habitats for *Moritella* Species

Approximately 71 % of the surface area in our planet is covered by the oceans. As oceans present an average depth of 3,800 m and more than 97 % of the ocean water locates below epipelagic zone, cold-temperature environments (<4 °C) represent the most common marine habitats for millions of creatures. One of the hypotheses of microbial evolution is that thermophiles were the first to evolve, followed by the mesophiles and then the psychrophiles (Morita 1975). Thus, ancestors of *Moritella* species have set out to adapt this vast last frontier. Now they successfully inhabit throughout the depth of the oceans (Kato et al. 1998). Though quantitative study of distribution pattern of *Moritella* species is quite limited, members of *Moritella* species occupy large portion of culturable facultative anaerobic isolates below the thermocline. Approximately 62 % (19/29 strains) of facultative anaerobic isolates from the deep Pacific Ocean were identified as *Moritella* species (Urakawa et al. 1999). *Moritella* species have been found only from deeper than 500 m depth, in contrast with the distribution of *Photobacterium* isolates, which were isolated from both deep and shallow (<500 m) waters (Urakawa et al. 1999). Bowman and colleagues (1997) isolated many psychrophilic bacteria from the Antarctic sea ice. Interestingly majority isolates were identified as members of *Alteromonadaceae* such as *Colwellia*, *Shewanella*, and *Marinobacter*; however, no *Moritella* strains were isolated. Since majority of species have been isolated from the deep sea, the major habitats for *Moritella* species are likely marine environments below the thermocline, where it is permanently maintained cold. Although quantitative measurements have not been done, at least two species, *M. viscosa* and *M. dasanensis*, were isolated from cold shallow waters. Thus, some *Moritella* species likely inhabit cold shallow waters.

Moritella species have been isolated from seawater, seafloor, and marine fish (Colwell and Morita 1964; Urakawa et al. 1998, 1999).

One of the best-studied marine bacteria *Vibrio* are known as one of the major components of surface microbial flora of marine life forms (Thompson et al. 2006). They are also frequently found in intestines of marine fish. Since *Moritella* species are also facultatively anaerobes, there is no wonder *Moritella* strains have been isolated from the intestines of deep-sea fish (Nakayama et al. 2005). *Moritella* species may share similar ecological niche characterized as hypoxia or anoxia with other facultative anaerobes such as *Vibrio*, *Photobacterium*, *Colwellia*, and *Shewanella* species in various cold marine environments, such as ocean floor (Bowman and McCuaig 2003; Bowman et al. 2003), digestive tracts of marine organisms (Nakayama et al. 2005), and microscale anaerobic environments (i.e., marine snow) (Alonso and Pernthaler 2005).

Although majority of *Moritella* species likely establish mutualistic relationships with marine organisms, one of the members of *Moritella* species, *M. viscosa*, is known as a fish pathogen, which causes winter ulcer for sea-farmed Atlantic salmon (Fig. 23.4). The mortality is limited, but the disease has economic significance due to lowered quality of the fish (Lunder et al. 2000).

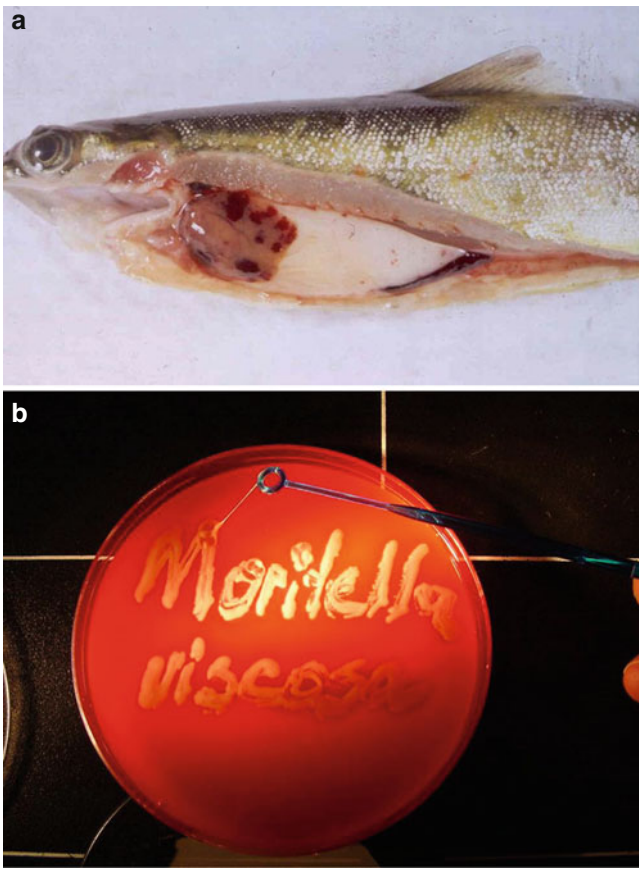

Fig. 23.4
***Moritella viscosa*. (a) Atlantic salmon with skin ulcer disease caused by *Moritella viscosa*. Internal symptoms include petechial hemorrhages on the liver. (b) Colonies of *Moritella viscosa*. The name of this species was originated from this viscous colony formation (Courtesy of B. Guðmundsdóttir, University of Iceland)**

Habitats for *Paramoritella* Species

Two strains (A3F-7^T and ssthio04PA2-7c) of marine heterotrophic alkaliphilic bacterium *P. alkaliphila* were isolated from hard coral (*Favites complanata*) and marine sand collected from the Republic of Palau, respectively. It suggests that *P. alkaliphila* may distribute widely in tropical marine environments.

Short Description of the Species

Moritella marina (Baumann, Furniss and Lee 1984) Urakawa, Kita-Tsukamoto, Steven, Ohwada, and Colwell 1999, comb. nov. (Type species of the genus)

Type strain: strain MP-1 = ATCC 15381 = CIP 102861 = NCCB 79030 = NCIMB 1144.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: AB038033.
Basonym: *Vibrio marinus* (Russell 1891) Baumann et al. 1984.
Other synonym: *Vibrio marinus* (Russell 1891) Ford 1927.
Etymology: L. fem. adj. *marina*, of or belonging to the sea, marine.
References: validation list no. 69 (1999); effective publication (Urakawa et al. 1998).

V. marinus was first isolated from the Gulf of Naples and described as *Spirillum marinus* by Russell (1891). Later 16 of *Vibrio marinus*-like strains were reisolated (Colwell and Morita 1964). However, only one strain, *V. marinus* MP-1 ^{T}, which was isolated from seawater 125 miles off the Oregon coast at a depth of 1,200 m, is still available as ATCC 15381^T (Morita and Haight 1964). The description and detailed characteristics of *Moritella marina* comb. nov. (ma.ri'na. L. adj. *marina*, of the sea, marine) are based on the data from Colwell and Morita (1964) and Colwell (1965). It should be noted that one of the strains, *V. marinus* strain PS 207, which was isolated from the skin of a Pacific cod and can grow at 30 °C, was later reclassified as *Vibrio logei* (= ATCC 15382) (Colwell and Morita 1964; Colwell 1965; Margaret et al. 1971).

Moritella japonica Nogi, Kato, and Horikoshi 1999, sp. nov.

Type strain: strain DSK1 = CIP 106291 = DSM 14879 = JCM 10249.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: D21224.

Etymology: N.L. fem. adj. *japonica*, pertaining to the Japan Trench, where this strain originated.
References: validation list no. 69 (1999); effective publication (Nogi et al. 1998).

M. japonica was isolated from the Japan Trench at a depth of 6,356 m. It was reported as a first barophilic species among *Moritella* genus (Fig. 23.5). This strain is able to grow in pressure vessels under hydrostatic pressures in a range of 0.1–70 MPa and at temperatures in a range of 4–15 °C. This species is not able to grow at temperatures above 20 °C. The optimum temperature and pressure conditions for growth are 15 °C and 50 MPa, respectively.

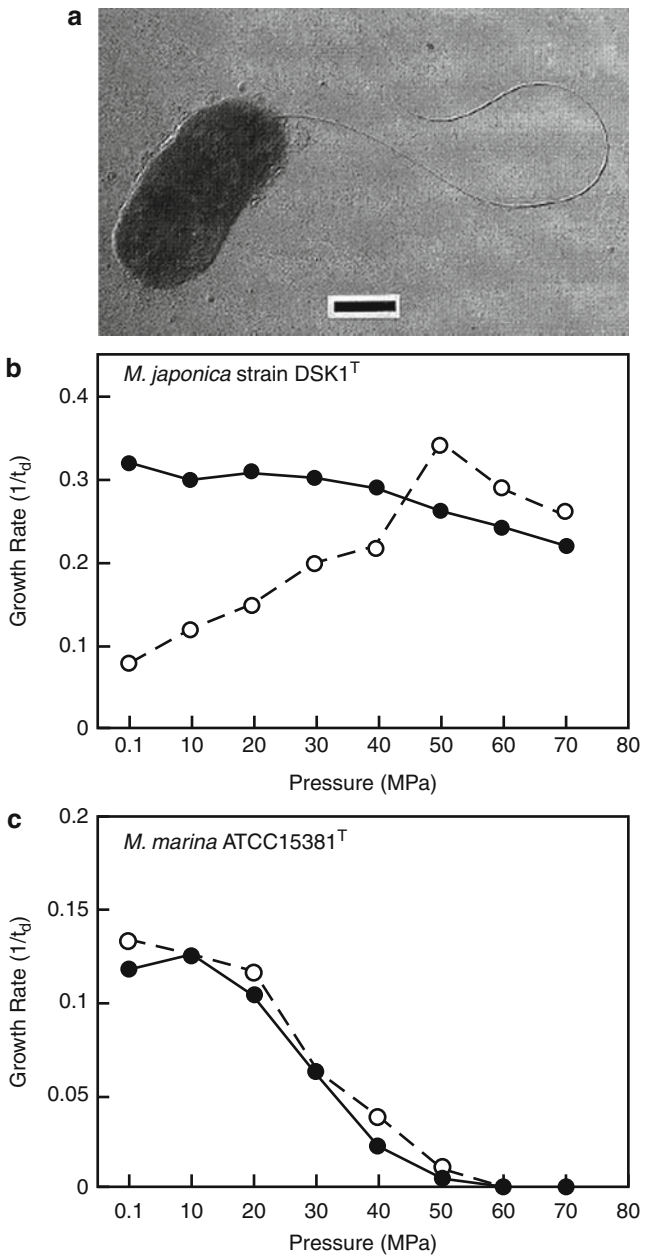

Fig. 23.5
***Moritella japonica*. Electron micrograph of stained, shadow-cast cell of strain DSK1^T (a). Growth rate comparison between *M. japonica* (b) and *Moritella marina* (c) under the pressure conditions at 10 °C (*closed circles with solid line*) and 15 °C (*open circles with dashed line*). Bar, 500 nm. t_d indicates doubling time (Data from Nogi et al. (1998))**

Moritella yayanosii Nogi and Kato 1999, sp. nov.

Type strain: strain DB21MT-5 = JCM 10263.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: AB008797.
Etymology: N.L. gen. masc. n. *yayanosii*, of Yayanos, named in honor of American deep-sea biologist Aristides Yayanos.
References: validation list no. 71 (1999); effective publication (Nogi and Kato 1999).

M. yayanosii was isolated from a sediment sample collected from the Mariana Trench, Challenger Deep at a depth of 10,898 m. The sediment was pressurized at approximately 100 MPa in a pressure vessel placed in a refrigerator (2–4 °C). For single-colony isolation, cultures were incubated under a pressure of 100 MPa in plastic bags (Fig. 23.3). Growth of cells under conditions of 0.1–100 MPa at 10 °C in pressure vessels was tested in marine broth (Kato et al. 1998). *M. yayanosii* is an obligate piezophilic bacterium that can grow at 100 MPa. The optimal pressure condition for growth is 80 MPa, and no growth is detected at pressures of less than 50 MPa. All physiological tests were performed in pressure vessels at 70 MPa at 10 °C (Nogi and Kato 1999). Acid is produced from D-mannose and xylose, which are effective characteristics to distinguish this species from other *Moritella* species (Table 23.3).

Moritella viscosa (Lunder, Sørum, Holstad, Steigerwalt, Mowinckel and Brenner 2000) Benediktsdóttir, Verdonck, Sproer, Helgasön, and Swings 2000, comb. nov.

Type strain: strain NVI 88/478 = ATCC BAA-105 = NCIMB 13584.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: AJ132226.
Basonym: *Vibrio viscosus* Lunder et al. (2000).
Etymology: L. fem. adj. *viscosa*, viscous, sticky, because of its thread-forming, adherent colonies.
Reference: Benediktsdóttir et al. (2000).

The type strain of *Moritella viscosa* NVI 88/478^T was originally isolated in 1988 in Norway from an Atlantic salmon with winter ulcer and proposed as *V. viscosus* (Lunder et al. 2000). This species has been reported as a pathogen that causes winter ulcer of Atlantic salmon and other marine fish from Norway, Iceland, and Scotland (Benediktsdóttir et al. 2000). Colonies are viscous and can form long threads when removed from the agar surface (Fig. 23.4). The maximum growth temperature of *M. viscosa* is

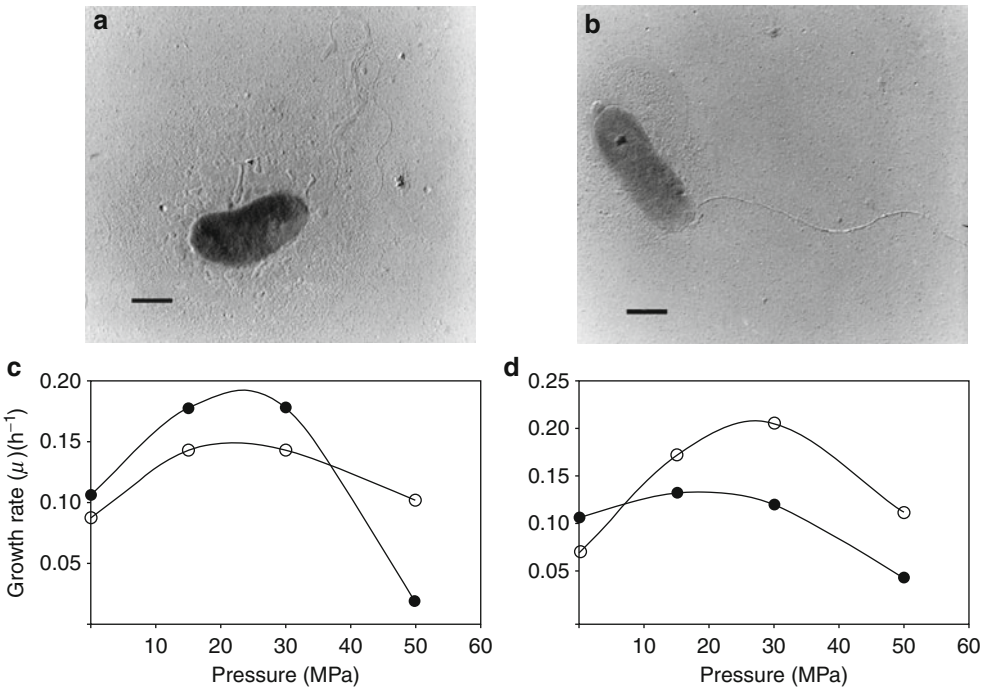

Fig. 23.6

Electron micrographs of stained, shadow-cast cells of *Moritella profunda* 2674^T (a) and *Moritella abyssi* 2693^T (b) and growth response of *M. profunda* (c) and *M. abyssi* (d) under different pressures at 6 °C (*closed circles*) and 10 °C (*open circles*). Bars, 1 μm. Growth rates were calculated as 1/td [t_d is doubling time (h)] (Data from Xu et al. (2003))

likely the highest among currently known *Moritella* species but different according to the literature. Lunder et al. (2000) reported that the growth occurred at 4–25 °C, but not at 30 °C. However, Benediktsdóttir et al. (2000) refuted that no strain was able to grow at 25 °C, but all grew at 21 °C and 4 °C after careful inspection.

Moritella profunda Xu, Nogi, Kato, Liang, Rüger, De Kegel, and Glansdoff 2003, sp. nov.

Type strain: strain 2674 = JCM 11435 = LMG 21259.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: AJ252023.
Etymology: L. fem. adj. *profunda*, from the deep.
Reference: Xu et al. (2003).

Moritella profunda is a psychropiezophilic bacterium isolated from a deep-sea sediment collected at a depth of 2,815 m in the Sierra Leone Rise region of the eastern tropical Atlantic (Fig. 23.6). The sample was cultured at 2 °C on a chilled seawater agar plate prepared with a medium containing 1.5 g peptone, 0.5 g yeast extract, 0.01 g $FePO_4 \cdot 4H_2O$, 750 mL sea water, and 250 ml distilled water. The maximum growth rate is given at 2 °C or possibly lower temperature; thus, this species has the lowest optimum temperature among the family *Moritellaceae*. Cells can grow at atmospheric pressure, but the piezophilic growth is stimulated with a maximum of 20–24 MPa at 6 °C and slightly higher at 10 °C. At 6 °C, the maximum pressure is between 50 and 60 MPa; it is increased considerably by raising the temperature to 10 °C. Elongated cells are occasionally found in the high-pressure incubated cultures.

Moritella abyssi Xu, Nogi, Kato, Liang, Rüger, De Kegel, and Glansdoff 2003, sp. nov.

Type strain: strain 2693 = JCM 11436 = LMG 21258.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: AJ252022.
Etymology: L. gen. n. *abyssi*, of/from the abyss.
Reference: Xu et al. (2003).

The type strain, strain 2693^T, was collected from the upper layer of deep Atlantic sediments (2,815 m) off the West African coast in 1983 (Fig. 23.6). *M. abyssi* is a piezophilic bacterium; cells can grow at atmospheric pressure, but the optimum pressures are 19–20 MPa at 6 °C and 30 MPa at 10 °C. The strain was isolated by the same manner with *M. profunda*. Cells are often elongated and show irregular forms under atmospheric pressure. Positive for indole test.

Moritella dasanensis Kim, Park, Lee, Park, Jung, Kang, Joo, Seo, and Kang 2008, sp. nov.

Type strain: strain ArB 0140 = JCM 14759 = KCCM 42845 = KCTC 10814.

GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: EF192283.
Etymology: N.L. fem. adj. *dasanensis*, pertaining to the Korean Arctic Dasan station where the type strain was isolated.
Reference: Kim et al. (2008).

M. dasanensis KCTC10814^T was isolated from surface seawater off the near shore of Kongsfjorden in the Svalbard Archipelago, Norway. The strain was isolated on a marine agar at 3 °C and maintained at the same temperature. Anaerobic growth of *M. dasanensis* was not tested in the original publication (Kim et al. 2008) but later confirmed (H. -J. Kim, personal communication). Strain ArB 0140^T grows between −3 °C and 18 °C. The optimal growth temperature is 9 °C. Based on the Ratkowsky growth model analysis (Ratkowsky et al. 1983), the notional minimum, optimum, and maximum growth temperatures were estimated as −11.9 °C, 9 °C, and 17.8 °C, respectively (Fig. 23.7). The unique feature of this species is the ability to secrete ice-active substances, which are macromolecular substances that affect the shape of ice crystals by binding to the growing ice crystals (Fig. 23.8). Ice-modifying activity was not observed in *M. marina*, *M. japonica*, and *M. abyssi*. The G + C mol% of this species must be amended. The G + C mol % reported in Kim et al. (2008) was 46.9 %, which was the highest G + C content value in the family. However, the G + C content obtained from the draft genome sequence of this species was 40.82 %, which was the lowest G + C value among the family.

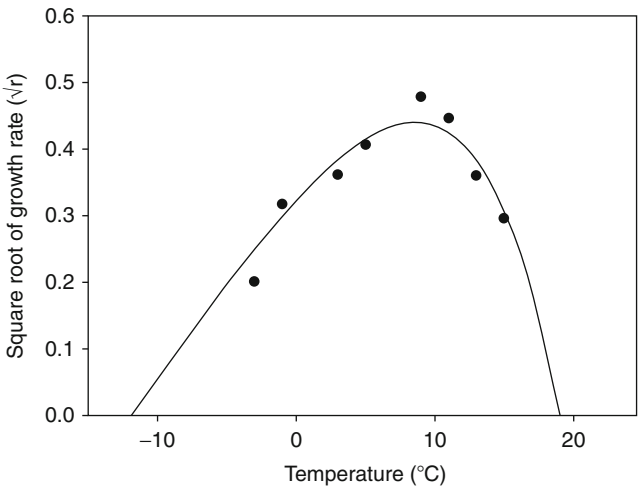

Fig. 23.7
Growth rate of *Moritella dasanensis* ArB 0140^T determined by using a temperature gradient incubator. The growth of culture at −3 °C and −1 °C was determined in a water bath. Fitted line was calculated by the Ratkowsky model (Ratkowsky et al. 1983) (Data from Kim et al. (2008))

***Paramoritella alkaliphila* Hosoya, Suzuki, Adachi, Matsuda, and Kasai 2009, gen. nov.**

Type strain: strain A3F-7 = MBIC 06429 = DSM 19956.
GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain: AB364966.
Etymology: Gr. prep. para, beside; N.L. fem. n. *Moritella*, a bacterial genus name; N.L. fem. n. *Paramoritella*, beside *Moritella*.
Reference: Hosoya et al. (2009).

Two strains of marine, heterotrophic, alkaliphilic bacteria, designated A3F-7^T and ssthio04PA2-7c, were isolated

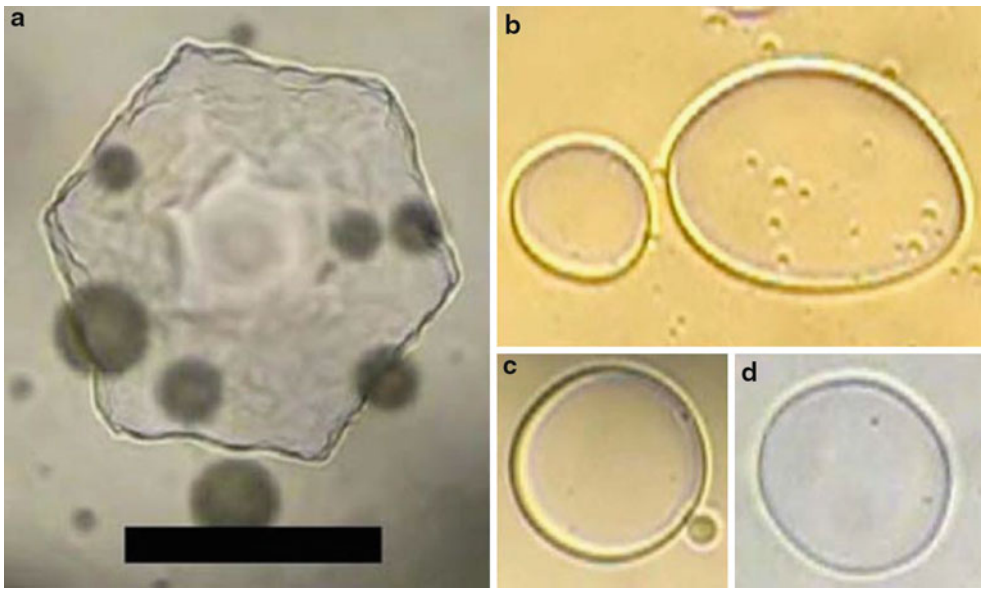

Fig. 23.8
Ice-modifying activity of *Moritella dasanensis* ArB 0140^T and other *Moritella* species. This activity was observed by using a nanolitre osmometer. (a) *M. dasanensis*, (b) *M. marina*, (c) *M. japonica*, and (d) *M. abyssi*. Bar, 100 μm (Data from Kim et al. (2008))

from hard coral (*Favites complanata*) and marine sand collected from the Republic of Palau, respectively. Strain A3F-7^T was isolated by using marine agar adjusted to pH 11 with Na_2CO_3 and $NaHCO_3$. Strain ssthio04PA2-7c was isolated from marine sand collected from the Republic of Palau in 2004. Strain ssthio04PA2-7c was isolated by using thio medium. A high level of DNA-DNA relatedness indicated that these two isolates were the same species. Phenotypic features resemble to other *Moritella* species except for the growth temperature and pH properties. The optimum temperature is 30 °C; growth occurs at 15 °C and 37 °C and growth is not observed at 8 or 40 °C. The pH range for growth is 7.0–11.0, and the optimum pH for growth is 9.0.

Application

Moritella species have been studied as model microorganisms of low-temperature-adapted enzymes (Morita 1975 and references therein; Deming 2002 and references therein), barophilic adaptation of marine bacteria to the deep sea (Lauro and Bartlett 2008 and references therein). *Moritella* species are also known as producers of long-chain fatty acids such as DHA (DeLong and Yayanos 1985, 1986).

Acknowledgments

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