Note

Moritella profunda sp. nov. and *Moritella abyssi* sp. nov., two psychropiezophilic organisms isolated from deep Atlantic sediments

Ying Xu,[1] Yuichi Nogi,[2] Chiaki Kato,[2] Ziyuan Liang,[1] Hans-Jürgen Rüger,[3] Daniel De Kegel[1] and Nicolas Glansdorff[1]

Correspondence
Ying Xu
xuying@vub.ac.be

[1]J. M. Wiame Research Institute for Microbiology, Free University of Brussels (VUB), and Flanders Inter-University Institute for Biotechnology, 1, ave E. Gryson, B-1070 Brussels, Belgium

[2]The DEEP STAR Group, Japan Marine Science and Technology Center, 2-15 Natsushima-cho, Yokosuka 237-0061, Japan

[3]Alfred Wegener Institut für Polar-und Meeresforschung, Am Handelshafen 12, D-27570 Bremerhaven, Germany

Strains 2674^T (=LMG 21259^T =JCM 11435^T) and 2693^T (=LMG 21258^T =JCM 11436^T) were isolated from Atlantic sediments at a temperature of 2 °C and a depth of 2815 m off the West African coast. Polyphasic evidence indicates that the two strains belong to the genus *Moritella* and represent distinct species, for which the names *Moritella profunda* sp. nov. (for strain 2674^T) and *Moritella abyssi* sp. nov. (for strain 2693^T) are proposed. The moderate piezophily of the two organisms is intermediate between that of the type species, *Moritella marina*, which is not piezophilic, and *Moritella yayanosii*, an obligate piezophile. Both are strict psychrophiles with slightly different cardinal temperatures: at 0·1 MPa, maximal growth rates are observed at 2 °C (*M. profunda*) and 4 °C (*M. abyssi*) with maximum temperatures of 12 °C (*M. profunda*) or 14 °C (*M. abyssi*). The optimal pressure is lower than that at the site of isolation, and raising the temperature to 10 °C makes the organisms more piezophilic.

Below 2000 m depth, the temperature of the ocean usually does not rise above 2–3 °C (Yayanos, 1995). The deep sea is thus a habitat favourable to psychrophilic micro-organisms (highest growth temperature below 20 °C; Morita, 1975). From the analysis of sediments collected from the tropical Atlantic off West Africa between 1500 and 4500 m depth, Rüger & Tan (1992) concluded that psychrophiles with maximum growth temperatures below 12 °C were predominant among cultivable bacteria. Since the hydrostatic pressure increases by 0·1 MPa every 10 m down the water column, deep-sea resident organisms are expected to display various levels of piezophily or piezotolerance (Yayanos, 1995). Since the isolation of the first pure culture of a true piezophilic bacterium, collected at a depth of 5700 m (Yayanos *et al.*, 1979), several psychropiezophilic species have been described (Kato *et al.*, 1995, 1996; Nogi *et al.*, 1998). Obligate piezophiles, i.e. unable to grow at atmospheric pressure, have been isolated from the deepest Pacific trenches (Yayanos, 1995; Kato *et al.*, 2000; Bartlett, 2000). Most cultivable psychropiezophiles have been found to belong to a few genera of the *γ-Proteobacteria*, *Colwellia*, *Moritella*, *Photobacterium* and *Shewanella* (DeLong *et al.*, 1997), and more recently, *Psychromonas*, a genus that also includes non-piezophilic organisms (Nogi *et al.*, 2002, Xu *et al.*, 2003).

Moritella is a recently described genus that presently comprises four species: the type, *Moritella marina* (formerly *Vibrio marinus*; Steven, 1990; Urakawa *et al.*, 1998), which is non-piezophilic and psychrotolerant; *Moritella japonica* (Nogi *et al.*, 1998), a moderate piezophile isolated from the Japan Trench at a depth of 6356 m; *Moritella yayanosii*, an obligate piezophile collected from the Challenger Deep in the Mariana Trench at a depth of 10 898 m (Nogi & Kato, 1999); and *Moritella viscosa* (Benediktsdóttir *et al.*, 2000), originally described as *Vibrio viscosus* (Lunder *et al.*, 2000), a psychrotolerant marine pathogen of salmonids isolated from North Atlantic fish farms. From Atlantic sediments, we have isolated two novel psychrophilic isolates (strains 2674^T and 2693^T) that represent novel species of *Moritella*.

Strains 2674^T and 2693^T were collected from the same station during the GEOTROPEX '83 marine expedition at a depth of 2815 m in the Sierra Leone Rise region of the eastern tropical Atlantic (latitude 5°37·0′N, longitude

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of *M. profunda* 2674^T and *M. abyssi* 2693^T are AJ252023 and AJ252022.

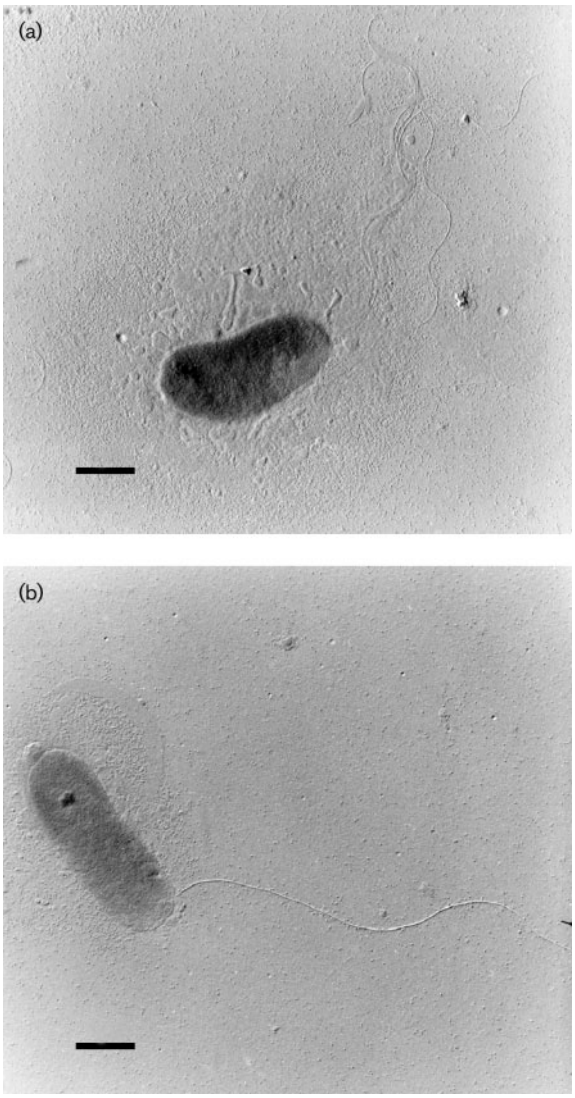

Fig. 1. Electron micrographs of stained, shadow-cast cells of strains 2674^T (a) and 2693^T (b). Micrographs were obtained as described by Xu *et al.* (2003). Bars, 1 μm.

19°58·9′W). Samples were taken by means of a box-grab sampler and cultured on chilled sea-water agar plates as described by Xu *et al.* (2003). The temperature was 2 °C. Details of the sampling and isolation procedure have been described by Rüger & Tan (1992).

Of the reference *Moritella* strains used in this study, *M. marina* ATCC 15381^T, *M. japonica* JCM 10249^T (Nogi *et al.*, 1998) and *M. yayanosii* JCM 10263^T (Nogi & Kato, 1999) were grown as described in the latter reference and *M. viscosa* NCIMB 13584^T was grown according to Benediktsdóttir *et al.* (2000). Sources of other reference strains, their maintenance and growth conditions were as described in Nogi *et al.* (1998) and Nogi & Kato (1999).

High-pressure cultivation and characterization of the novel isolates was carried out as described by Xu *et al.* (2003), with

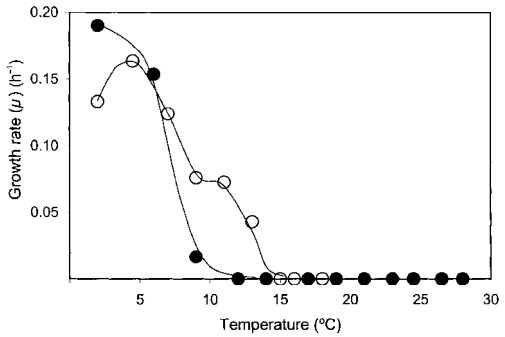

Fig. 2. Effect of temperature on growth rates of strains 2674^T (●) and 2693^T (○) under atmospheric pressure. Growth rates, μ, were calculated as $1/t_d$ [t_d is doubling time (h)].

the exception that DNA–DNA hybridization was performed at 40 °C for 3 h.

The cells of both strains are Gram-negative, motile, do not form spores and present rather similar dimensions and morphologies (Fig. 1; see species descriptions below).

For strain 2674^T under atmospheric pressure, the highest growth rate in Bacto Marine broth (Fig. 2) was recorded at 2 °C (about 5·5 h doubling time; no lower temperature was tested). Growth was observed up to 10–12 °C on all media but not at higher temperatures. Up to 8 °C, the final optical density (approx. 10^9 cells ml^{-1}) remained the same. Under identical conditions, strain 2693^T showed the highest growth rate at 4–5 °C (Fig. 2); no growth was observed above 14 °C. Neither strain grew in the absence of NaCl.

Pressure affected the two strains differently. For strain 2674^T at 6 °C, the growth-pressure profile peaked at 20–24 MPa, a lower pressure than at the place of isolation (28 MPa); at 10 °C, the optimal pressure was not markedly different but the degree of piezophily of the strain increased considerably (Fig. 3a). For strain 2693^T, the optimum pressure was 19–20 MPa at 6 °C but, at 10 °C, the optimum was around 30 MPa (Fig. 3b). By comparing Figs 2 and 3, it can be noted that, under the more anaerobic conditions of the pressure cell, strain 2674^T grew much better at 10 °C than in full aerobiosis. The oxygen tolerance of this strain thus appears to be lower at the upper end of its temperature range.

Both strains are facultatively anaerobic, oxidase-positive, chemo-organotrophic and prototrophic (except for possible vitamin dependence, not tested). Their patterns of acid production from carbohydrates, tested according to Xu *et al.* (2003), were, however, different (see descriptions). Both are relatively oligotrophic: glucose or galactose at a concentration as low as 0·5 mg ml^{-1} already elicited good growth on minimal medium plates (Rüger, 1988) incubated at 4 °C.

Several carbon sources were used by both strains at a concentration of 1 g carbon l^{-1} under atmospheric pressure in minimal medium (Rüger, 1988), but the range was

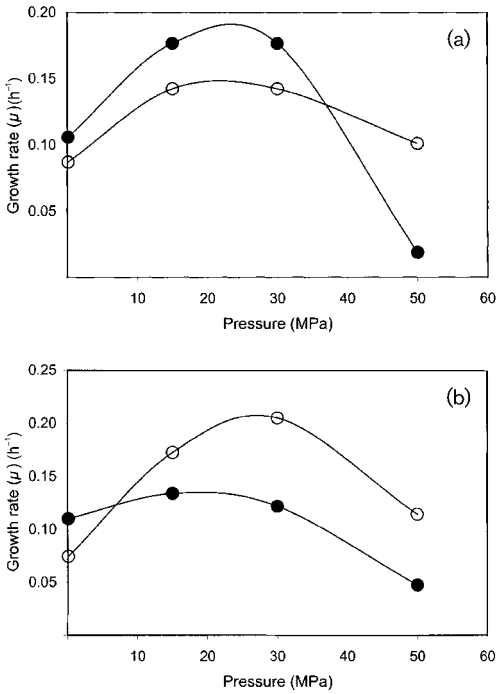

Fig. 3. Growth response of strain 2674^T (a) and strain 2693^T (b) under different pressures at 6 (●) and 10 (○) °C. Growth rates were calculated as described in Fig. 2.

distinctly narrower for strain 2674^T (see descriptions). No gas was produced from nitrate, but both reduced nitrate to nitrite. Both strains proved to be sensitive to several antibiotics (as tested with Oxoid disks placed on sea-water agar plates) including the vibriostatic agent O/129. Salient properties of strains 2674^T and 2693^T and reference species are listed in Table 1 and in the descriptions below.

The G+C contents of both strains were similar to those of other *Moritella* species (Table 1). Moreover, comparative analysis of their complete 16S rRNA sequences with cognate sequences from various *γ-Proteobacteria* placed them in the *Moritella* cluster within a branch with a high bootstrap value (see Fig. 3 of Xu *et al.*, 2003). Between the two strains, there was 98·5 % identity. With respect to *M. marina*, *M. yayanosii*, *M. japonica* and *M. viscosa*, strain 2674^T exhibited 99·1, 98·9, 98·8 and 98·6 % identity, whereas strain 2693^T gave 98·6, 98·3, 98·7 and 98·5 % identity. In terms of similarity to other genera, the highest values were to species of *Shewanella* (93 % or less).

Reciprocal DNA–DNA hybridizations distinguished the two strains both from each other (55 % similarity) and from already described *Moritella* species; values were between 41·5 % for the pair 2674^T/*M. marina* and 60 % for the pair 2693^T/*M. yayanosii*. Other pairs gave values between 40 (*M. marina*/*M yayanosii*) and 57·5 % (*M. viscosa*/*M. yayanosii*).

Table 1. Phenotypic comparison of *Moritella* species

Strains: 1, *M. marina* ATCC 15381^T; 2, *M. japonica* JCM 10249^T; 3, *M. yayanosii* JCM 10263^T; 4, *M. profunda* sp. nov. JCM 11435^T; 5, *M. abyssi* sp. nov. JCM 11436^T. NG, No growth; ±, weak response after 2 weeks. All strains are positive for catalase and oxidase; the major isoprenoid quinone is Q-8. All reduce nitrate to nitrite but not to gas. None produces acid from arabinose, inositol, D-lactose, D-raffinose, sucrose, D-sorbitol or D-trehalose. None grows on arabinose, sucrose, D-sorbitol or D-trehalose as sole carbon sources.

Characteristic	1	2	3	4	5
Conditions for maximum growth rate:					
Temperature (°C) at 0·1 MPa	18	10	NG	2	4–6
Pressure (MPa) at 10 °C	0·1	50	80	22	30
DNA G+C content (mol%)	42·5	45·0	44·6	41·4	41·6
Gelatinase	+	+	+	−	−
Amylase	±	−	−	−	+
Indole produced	−	−	−	−	+
Acid produced from:					
Cellobiose	+	−	−	−	+
D-Galactose	+	−	−	±	+
Glycerol	+	+	−	−	−
Maltose	+	−	+	−	+
D-Mannitol	−	−	+	−	+
D-Mannose	−	−	+	−	−
Xylose	−	−	+	−	−
Utilization as carbon source:					
Cellobiose	+	−	−	−	+
D-Galactose	+	−	−	+	+
Glycerol	+	+	−	+	+
Maltose	+	−	−	−	+
Xylose	−	−	+	−	−

The observed percentages thus remain below the value currently accepted to differentiate species within a particular genus (<70 % binding; Wayne *et al.*, 1987).

As in other *Moritella* species, major fatty acids of cells of both strains grown in Bacto Marine broth 2216 (see Nogi *et al.*, 1998 for sample analysis) were C14 : 0, C16 : 0, C16 : 1 and C22 : 6 (docosahexaenoic acid; DHA). The occurrence of DHA is characteristic of the genus *Moritella* (DeLong *et al.*, 1997; Kato *et al.*, 1998). Similarly, the major isoprenoid quinone (Komagata & Suzuki, 1987; Nogi *et al.*, 1998) was Q-8, as in other *Moritella* species (Nogi & Kato, 1999).

On the basis of the polyphasic analysis reported in this study, we propose to name strains 2674^T and 2693^T as *Moritella profunda* sp. nov. and *Moritella abyssi* sp. nov. on the basis of their origin (bottom sediments at a depth of 2800 m). As for other members of the *Vibrionaceae*, they are both facultatively anaerobic, capable of fermentative metabolism and oxidase-positive.

Considering their depth of isolation, it is no surprise that both are piezophilic and strictly psychrophilic; the term piezophilic appears more adequate than piezotolerant, since growth can actually be enhanced by increasing the hydrostatic pressure. *M. profunda* is more psychrophilic than *M. abyssi* (maximal growth rate at 2 °C or possibly less compared with 4 °C); both exhibit a relationship between the effects of temperature and pressure which has already been described for other psychropiezophilic species (see Kato *et al.*, 1995; Yayanos, 1995) but also for thermopiezophiles (Marteinsson *et al.*, 1997): the optimal pressure is lower than at the place of isolation and increasing the temperature makes the strains more piezophilic. The shift of optimal pressure accompanying an increase in temperature from 6 to 10 °C is particularly pronounced for *M. abyssi* (strain 2693^T) whereas, for *M. profunda* (strain 2674^T), for which 10 °C is already close to the maximum temperature at 0·1 MPa (12 °C), it is the range of pressures compatible with good growth that is extended considerably by such an increase. Partial compensation of the 'gelling' effect of high pressure on membrane lipids could result from the increase in molecular mobility brought about by a rise in temperature (Marteinsson *et al.*, 1997). Alternatively, an increase in temperature could compensate for inhibition of enzyme activity due to pressure-induced compression. In a recent review on microbial adaptation to the psychropiezosphere (Glansdorff & Xu, 2002) and in the accompanying paper (Xu *et al.*, 2003), we have stressed that psychropiezophilic enzymes are molecular compromises between two conflicting requirements: efficient catalysis at low temperature requires enzyme flexibility (Gerday *et al.*, 1997), whereas reduced compressibility and enhanced rigidity are necessary at high pressure (Gross & Jaenicke, 1994). The characterization of two novel psychrophilic species of *Moritella*, which appear intermediate between surface dwellers and obligate piezophiles, is therefore of interest.

Description of *Moritella profunda* sp. nov.

Moritella profunda (pro.fun′da. L. fem. adj. *profunda* from the deep).

Cells are Gram-negative, curved, relatively short to coccoid, non-sporulating rods, single or in pairs, 0·9–1·2 μm wide by 1·5–5·0 μm long, with rounded ends. Motile by means of a single, unsheathed, polar flagellum. On peptone/yeast extract/sea-water agar, colonies are smooth, colourless, flat and entire with an irregular margin. They become creamy-pink and pink on King's media A and B, respectively. Moderately halophilic: no growth is observed in the absence of NaCl but normal growth occurs with half-strength sea water. Strictly psychrophilic, with a temperature range from 2 (or lower, not tested) to 12 °C under atmospheric pressure in Bacto Marine broth. The maximum growth rate is obtained at 2 °C (possibly lower). The organism is piezophilic: growth in Bacto Marine broth is stimulated markedly by hydrostatic pressure, 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. At both extremes of the pressure domain, but mainly under high pressure, elongated forms may be observed. Facultatively anaerobic, prototrophic (possible vitamin dependency, not tested) chemo-organotroph capable of both fermentative and respiratory metabolism. Catalase, cytochrome oxidase, DNase and lipase tests are positive. Indole is not produced and arginine dihydrolase, lysine decarboxylase and ornithine decarboxylase tests are negative. Nitrate is reduced to nitrite but no gas is produced. Acid is formed oxidatively and fermentatively from glucose (but no gas), D-fructose and D-galactose (weakly). No acid is produced from, adonitol, L-arabinose, cellobiose, dulcitol, glycerol, inositol, lactose, maltose, mannitol, D-mannose, D-raffinose, L-rhamnose, sorbitol, sucrose, D-trehalose and xylose. Utilization of the following carbon sources is positive within 4 weeks at 4 °C: D-galactose, gluconate, α-D-glucose, ribose, citrate, pyruvate, glycerol, L-alanine, L-arginine and L-glutamate. Acetate is utilized after prolonged incubation for up to 6 weeks. The following carbon sources give negative results: L-arabinose, cellobiose, maltose, D-mannose, salicin, sucrose, D-trehalose, xylose, propionate, adipate, fumarate, succinate, β-hydroxybutyrate, lactate, mannitol, sorbitol, L-aspartate, L-histidine, L-ornithine, putrescine, *p*-hydroxybenzoate and quinate. Susceptible to disks (Oxoid) containing 10 μg O/129, 2 U penicillin G, 10 μg tetracycline, 10 μg chloramphenicol, 50 μg furazolidone and 300 U polymyxin B. The G+C content of the type strain is 41·4 mol%. The major isoprenoid quinone is Q-8. Predominant cellular fatty acids are C14 : 0, C14 : 1, C16 : 0, C16 : 1 and C22 : 6.

The type strain, strain 2674^T (=LMG 21259^T =JCM 11435^T), was collected from the upper layer of deep Atlantic sediments at a depth of 2815 m off the West African coast.

Description of *Moritella abyssi* sp. nov.

Moritella abyssi (a.bys′si. L. gen. n. *abyssi* from the abyss).

Cells are Gram-negative, slightly curved, non-sporulating rods, single or in pairs, 0·8–1·2 μm wide by 2·0–7·0 μm long, with rounded ends. Motile by means of a single, unsheathed flagellum. On peptone/yeast extract/sea-water agar, colonies are smooth, punctiform, translucent, colourless, flat and entire with an irregular margin. On King's medium A, colonies appear creamy. Moderately halophilic, no growth being observed in the absence of NaCl but normal growth in half-strength sea water. Strictly psychrophilic, with a temperature range from 2 (or lower) to 14 °C under atmospheric pressure in Bacto Marine broth. The maximum growth rate is obtained at 4–5 °C. Piezophilic: growth in Bacto Marine broth is stimulated by hydrostatic pressure, with a maximum at 19–20 MPa at 6 °C and 29–30 MPa at 10 °C. Elongated and irregular forms are often observed under atmospheric pressure. Facultatively anaerobic, prototrophic (possible vitamin dependency, not tested) chemo-organotroph capable of both fermentative and respiratory metabolism. Catalase, cytochrome oxidase, DNase, lipase and indole tests are positive. Arginine dihydrolase, lysine decarboxylase and ornithine decarboxylase tests are negative. Nitrate is reduced to nitrite but no gas is produced. Acid is formed oxidatively and fermentatively from glucose (but no gas), from cellobiose, D-galactose, D-fructose, maltose and mannitol. No acid is produced from adonitol, L-arabinose, dulcitol, glycerol, inositol, lactose, mannose, melibiose, D-raffinose, L-rhamnose, salicin, sucrose, sorbitol, D-trehalose or xylose. Utilization of the following carbon sources is positive within 4 weeks at 4 °C: cellobiose, D-galactose, gluconate, α-D-glucose, maltose, ribose, salicin, fumarate, succinate, citrate, lactate, pyruvate, glycerol, mannitol, L-alanine, L-arginine, L-aspartate and L-glutamate. Positive after prolonged incubation for 6 weeks: acetate and β-hydroxybutyrate (weakly). Negative: L-arabinose, D-mannose, sucrose, D-trehalose, xylose, propionate, adipate, sorbitol, L-histidine, L-ornithine, putrescine, *p*-hydroxybenzoate and quinate. Susceptible to disks (Oxoid) containing 10 μg O/129, 2 U penicillin G, 10 μg tetracycline, 10 μg chloramphenicol, 50 μg furazolidone and 300 U polymyxin B. The G+C content is 41·6 mol%. The major isoprenoid is Q-8. Predominant cellular fatty acids are C14 : 0, C14 : 1, C16 : 0, C16 : 1 and C22 : 6.

The type strain, strain 2693^T (=LMG 21258^T =JCM 11436^T), was collected from the upper layer of deep Atlantic sediments (2815 m) off the West African coast.

Acknowledgements

This work was supported by the Flanders Foundation for Joint Fundamental Research. We thank Mr Kurino and his co-workers for operating the DEEPBATH high-pressure microbial cultivation system and Mr J.-P. ten Have for artwork.

References

Bartlett, D. H. (2000). Microbial adaptations to the psychrosphere/piezosphere. In *Molecular Marine Microbiology*, pp. 185–201. Edited by D. H. Bartlett. Wymondham, UK: Horizon Scientific.

Benediktsdóttir, E., Verdonck, L., Spröer, C., Helgason, S. & Swings, J. (2000). Characterization of *Vibrio viscosus* and *Vibrio wodanis* isolated at different geographical locations: a proposal for reclassification of *Vibrio viscosus* as *Moritella viscosa* comb. nov. *Int J Syst Evol Microbiol* **50**, 479–488.

DeLong, E. F., Franks, D. G. & Yayanos, A. A. (1997). Evolutionary relationships of cultivated psychrophilic and barophilic deep-sea bacteria. *Appl Environ Microbiol* **63**, 2105–2108.

Gerday, C., Aittaleb, M., Arpigny, J. L., Baise, E., Chessa, J. P., Garsoux, G., Petrescu, I. & Feller, G. (1997). Psychrophilic enzymes: a thermodynamic challenge. *Biochim Biophys Acta* **1342**, 119–131.

Glansdorff, N. & Xu, Y. (2002). Microbial life at low temperatures: mechanisms of adaptation and extreme biotopes. Implications for exobiology and the origin of life. *Recent Res Devel Microbiol* **6**, 1–21.

Gross, M. & Jaenicke, R. (1994). Proteins under pressure. The influence of high hydrostatic pressure on structure, function and assembly of proteins and protein complexes. *Eur J Biochem* **221**, 617–630.

Kato, C., Sato, T. & Horikoshi, K. (1995). Isolation and properties of barophilic and barotolerant bacteria from deep-sea mud samples. *Biodivers Conserv* **4**, 1–9.

Kato, C., Masui, N. & Horikoshi, K. (1996). Properties of obligately barophilic bacteria isolated from a sample of deep-sea sediment from the Isu-Bonin trench. *J Mar Biotechnol* **4**, 96–99.

Kato, C., Li, L., Nogi, Y., Nakamura, Y., Tamaoka, J. & Horikoshi, K. (1998). Extremely barophilic bacteria isolated from the Mariana Trench, Challenger Deep, at a depth of 11000 meters. *Appl Environ Microbiol* **64**, 1510–1513.

Kato, C., Qureshi, M. & Horikoshi, K. (2000). Pressure response in deep-sea piezophilic bacteria. In *Molecular Marine Microbiology*, pp. 175–184. Edited by D. H. Bartlett. Wymondham, UK: Horizon Scientific.

Komagata, K. & Suzuki K. (1987). Lipid and cell-wall analysis in bacterial systematics. *Methods Microbiol* **19**, 161–207.

Lunder, T., Sørum, H., Holstad, G., Steigerwalt, A. G., Mowinckel, P. & Brenner, D. J. (2000). Phenotypic and genotypic characterization of *Vibrio viscosus* sp. nov. and *Vibrio wodanis* sp. nov. isolated from Atlantic salmon (*Salmo salar*) with 'winter ulcer'. *Int J Syst Evol Microbiol* **50**, 427–450.

Marteinsson, V. T., Moulin, P., Birrien, J. L., Gambacorta, A., Vernet, M. & Prieur, D. (1997). Physiological responses to stress conditions and barophilic behavior of the hyperthermophilic vent archaeon *Pyrococcus abyssi*. *Appl Environ Microbiol* **63**, 1230–1236.

Morita, R. Y. (1975). Psychrophilic bacteria. *Bacteriol Rev* **39**, 144–167.

Nogi, Y. & Kato, C. (1999). Taxonomic studies of extremely barophilic bacteria isolated from the Mariana Trench and description of *Moritella yayanosii* sp. nov., a new barophilic bacterial isolate. *Extremophiles* **3**, 71–77.

Nogi, Y., Kato, C. & Horikoshi, K. (1998). *Moritella japonica* sp. nov., a novel barophilic bacterium isolated from a Japan Trench sediment. *J Gen Appl Microbiol* **44**, 289–295.

Nogi, Y., Kato, C. & Horikoshi, K. (2002). *Psychromonas kaikoae* sp. nov., a novel piezophilic bacterium from the deepest cold-seep sediments in the Japan Trench. *Int J Syst Evol Microbiol* **52**, 1527–1532.

Rüger, H.-J. (1988). Substrate-dependent cold adaptations in some deep-sea sediment bacteria. *Syst Appl Microbiol* **11**, 90–93.

Rüger, H.-J. & Tan, T. L. (1992). Community structures of cold and low-nutrient adapted heterotrophic sediment bacteria from the deep eastern tropical Atlantic. *Mar Ecol Prog Ser* **57**, 45–52.

Steven, S. E. (1990). *Molecular systematics of Vibrio and Photobacterium*. PhD dissertation, University of Maryland, College Park, MD, USA.

Urakawa, H., Kita-Tsukamoto, K., Steven, S. E., Ohwada, K. & Colwell, R. R. (1998). A proposal to transfer *Vibrio marinus* (Russell 1891) to a new genus *Moritella* gen. nov. as *Moritella marina* comb. nov. *FEMS Microbiol Lett* **165**, 373–378.

Wayne, L. G., Brenner, D. J., Colwell, R. R. & 9 other authors (1987). Report of the ad hoc committee on reconciliation of approaches of bacterial systematics. *Int J Syst Bacteriol* **37**, 463–464.

Xu, Y., Nogi, Y., Kato, C., Liang, Z., Rüger, H.-J., De Kegel, D. & Glansdorff, N. (2003). *Psychromonas profunda* sp. nov., a psychropiezophilic bacterium from deep Atlantic sediments. *Int J Syst Evol Microbiol* **53**, 527–532.

Yayanos, A. A. (1995). Microbiology to 10,500 meters in the deep sea. *Annu Rev Microbiol* **49**, 777–805.

Yayanos, A. A., Dietz, A. S. & Van Boxtel, R. V. (1979). Isolation of a deep-sea barophilic bacterium and some of its growth characteristics. *Science* **205**, 808–810.