ISSN 0026-2617, Microbiology, 2018, Vol. 87, No. 3, pp. 363–371. © Pleiades Publishing, Ltd., 2018.

EXPERIMENTAL ARTICLES

Isolation of Two Radiation Resistant and Desiccation Tolerant Bacteria, *Modestobacter* sp. A2 and *Maritalea* sp. B9, from Gandom Beryan Hill in the Lut Desert of Iran[1]

M. S. Shirsalimian[a], *, A. Akhavan Sepahy[a], M. A. Amoozegar[b], S. M. Kalantar[c], and R. Dabbagh[d]

[a] *Department of Microbiology, Faculty of Biological Sciences, Islamic Azad University North Tehran Branch, Tehran, Iran*

[b] *Extremophiles Laboratory, Department of Microbiology, School of Biology and Center of Excellence in Phylogeny of Living Organisms, College of Science, University of Tehran, Tehran, Iran*

[c] *Genetics Department, Shahid Sadoughi University of Medical Sciences, Yazd, Iran*

[d] *Nuclear Sciences and Technology Research Institute (NSTRI), Materials and Nuclear Fuel Research School, Tehran, Iran*

**e-mail: m.s.shirsalimian@gmail.com*

Received August 5, 2017

Abstract—Although dryland ecosystems are the most abundant terrestrial biomes on the Earth, relatively little is known about their microbial diversity and potential metabolic activities. Therefore, the bacterial diversity of the Lut Desert in Iran has been remained largely obscure. In this study, ionizing radiation resistant bacteria from arid Gandom Beryan region was investigated by a culture-dependent method. After exposing the soil and surface sand samples to different periods of dehydration in a desiccator containing silica gel, two non-endospore-forming bacterial isolates were recovered by plating on R2A and TSA agar media and then subjected to a desiccation and ionizing radiation resistance assay. The isolates A2 and B9 were still recovered after 8 weeks in a desiccator containing silica gel and were moderately resistant to gamma radiation with a D_{10} value between 2 and 4 kGy. Strains A2 and B9 were affiliated with *Modestobacter muralis* MDVD1^T (99.7% similarity) and *Maritalea mobilis* E6^T (97.3% similarity) respectively, using 16S rRNA gene sequence analysis. This is the first report of radiation resistant bacteria which belongs to the genus *Maritalea*.

Keywords: radiation resistance, desiccation tolerance, Gandom Beryan hill, Lut Desert

DOI: 10.1134/S0026261718030104

Hot arid deserts are characterized by some harsh environmental conditions of life. However, unique extremophiles such as radiation resistant and desiccation tolerant bacteria have been evolved there (Bull and Asenjo, 2013). Beside the low water availability, microorganisms in hot deserts are faced with a combination of extreme environmental stresses including temperature fluctuations, intense solar fluxes, oligotrophic conditions and frequently high salinity levels (Chanal et al., 2006). Resistance to ionizing radiation which is correlated with the production of free radicals, known as reactive oxygen species (ROS), has also been correlated with tolerance to desiccation. Inducing diverse damages to cellular macromolecules such as DNA, proteins and lipids, oxidative stress results from ROSs. Different cellular defense mechanisms e.g. efficient DNA repair systems, pigments such as carotenoids, ROS scavenging enzymes (e.g., catalases, superoxide dismutases, and peroxidases) and antioxidant complexes containing Mn^{2+} were described to overcome oxidative stress in both desiccation tolerant and radioresistant microorganisms (Slade and Radman, 2011). The bacterial genera *Deinococcus* (Slade and Radman, 2011) and *Rubrobacter* (Terato et al., 2011) show the highest radioresistance level among all microbial species.

Correlation between desiccation tolerance and radiation resistance phenotypes has been demonstrated for more than four decades (Mattimore and Battista, 1996; Tanaka et al., 2004). According to the "desiccation adaptation hypothesis," on the one side, environmental background gamma radiation doses on the Earth is very low (175 mGy year^{-1} is the highest measured dose rate), and on the other side drylands compared to environments with high gamma radiation flux were more common on the Earth's surface. As a result, desiccation has been proposed as a key selective pressure to evolve unusual radiation resistance phenotype in radioresistant bacteria (Fredrickson et al., 2008; Mattimore and Battista, 1996; Slade and Radman, 2011). For instance, the evolution of resistant structures with a low water content and undetectable metabolic activity such as endospore in bacteria and akinete in cyanobacteria has been a suitable strategy

[1] The article is published in the original.

for the distribution of primitive cells. However, resistance against desiccation in bacteria is not considered in dormant forms and this extreme feature is taken into consideration in vegetative cells (Slade and Radman, 2011). Continuous isolation of different bacterial radioresistant species in the genera *Deinococcus*, *Hymenobacter*, *Kocuria*, *Kineococcus* (Rainey et al., 2005), *Geodermatophilaceae* (Busarakam et al., 2016; Rainey et al., 2005; Sun et al., 2015) and cyanobacterium *Chroococcidiopsis* (Billi et al., 2000) from desert soils and arid environments around the world can proved the above hypothesis.

The study of arid and hyperarid desert ecosystems has become increasingly common and the majority of to date studies have been conducted on the Atacama Desert in northern Chile as the driest and oldest desert on the Earth by NASA (Azua-Bustos et al., 2012). The Lut Desert (the word Lut means bare; little or no vegetation) with an area of 199000 km^2 between 28° N and 32° N latitude, as the 25th largest desert in the world is located in eastern part of Iran. The Lut Desert with a surface temperature more than 70°C between 2003 and 2010 is considered as the one of hottest places on the Earth. A black hill with an area of about 200 km^2 which covered by volcanic lava, locally called Gandom Beryan (translated as Toasted Wheat), is located in 80 km of north of Shahdad in Kerman province, Iran. It is the existence of background black rocks together with surrounding yellowish color soil that greatly differentiates this area. Due to its black appearance, the hill absorbs considerable amount of sun's energy, leading to extraordinary high temperature. In addition, a saline river, locally called Shoor River, as the only permanent river flowing at the heart of the Lut Desert. The physicochemical properties of this river and its microbial diversity was presented elsewhere (Shirsalimian et al., 2017). The Lut Desert has attracted enormous attention recently and was inscribed as the Iran's first natural site in UNESCO's World Heritage List in 2016.

So far, little has been written about microbiological features of the Lut Desert: two strains of *Deinococcus* spp., resistant to >15 kGy of gamma radiation and >600 J/m^2 of UV radiation, were isolated from a soil sample collected from the Lut Desert (Mohseni et al., 2014). Also, three radioresistant haloarchaeal strains belonging to the family *Halobacteriaceae*, *Natrialba aegyptia*, *Natrinema pallidum* and *Haloterrigena jeotgali*, with a D_{10} value between 2 and 3 kGy were isolated from Shoor River (Shirsalimian et al., 2017).

In this study, 16S rRNA gene analyses with cultivation were used to characterize the diversity of desiccation tolerant bacteria in soil and surface sand samples from Gandom Beryan hill. Then, we investigated whether they could also be tolerant to ionizing radiation. Two isolates belonging to the genera *Modestobacter* and *Maritalea* showed resistance to gamma radiation and desiccation.

MATERIALS AND METHODS

Site description and sample collection. A mixed sample of soil (upper 5 cm) and surface sands were collected in sterile glass containers from Gandom Beryan hill (31°01′00″ N, 57°40′20″ E) in July 2015, in the Lut Desert of Iran (Fig. 1). The samples were kept at ambient temperature until processed. Analysis of physicochemical parameters of the soil sample also was carried out (Kavir Jonoob, Yazd). Flame photometry was used to measure the concentration of sodium and potassium ions. Determination of the ferrous and manganese contents was performed by atomic absorption spectroscopy. Concentration of other ions was calculated by methods based on titration. Total nitrogen and absorbable phosphorous contents were measured by Kjeldahl and Olsen methods, respectively. Organic carbon was determined by a potassium dichromate titration (Carter and Gregorich, 2007). The pH was determined with a pH meter.

Isolation and culture conditions. A sterile glass petri dish was filled with 5 grams of each sample in 4 replicates and incubated in a desiccator containing silica gel at 30°C (Chen and Alexander, 1972). After 1, 2, 4, and 8 weeks, a petri dish was removed from desiccator and then samples were diluted in sterile 0.85% NaCl solution (w/v) and finally plated onto R2A and TSA agar media. Single colonies were purified on the same agar plates by successive cultivation after 14 days incubation at 30°C. Isolates which were found by microscopic examination (Light microscope Olympus CH40, 100× magnification) to be endospore-forming species were discarded because their possible resistance against stresses found in deserts including prolonged desiccation, solar irradiance and starvation is due to their endospore form.

Desiccation resistance assay. To assess the desiccation tolerance, isolates were grown in a liquid medium at 30°C for 24 h. In all experiments, strain A2 was grown in the complex Luedemann medium (Luedemann, 1968) containing 0.5% (w/v) yeast extract, 1.5% (w/v) malt extract, 0.01% (w/v) glucose, 1% (w/v) soluble starch and 0.2% (w/v) $CaCO_3$. Agar (1.5% w/v) was used to solidify medium. Also, strain B9 was grown and plated on TSB and TSA media. Cells were collected by centrifugation, then washed and suspended in 0.85% NaCl solution to achieve an approximate concentration of 10^7–10^8 cfu mL^{-1}. 25 μL aliquots, in triplicate, were pipetted into the each well of a standard 96-well microplate. A single microplate was considered for each desiccation time and then microplates were placed inside a desiccator containing silica gel at 30°C. After 1, 2, 4 and 8 weeks after desiccation, a microplate was removed and the percentages of survival were determined in the following steps: the desiccated cells were revived by adding 250 μL of sterile 0.85% NaCl solution to each well, cells 10-fold serially diluted, plated and the CFUs counted after a 7 days incubation at 30°C (Fredrickson et al.,

Fig. 1. (a) The Lut Desert is located in eastern part of Iran; (b) location of the Gandom Beryan hill; (c) sampling site used in this study; (d and e) hillside and surface of Gandom Beryan hill; (f) Kalut-neighboring Gandom Beryan from south side.

2008). The percentages of survival were evaluated using viable cells present in the original inocula. Tolerance to desiccation were compared to *Deinococcus radiodurans* R1 (ATCC 13939) and *Escherichia coli* (ATCC 10799) as desiccation resistant and sensitive strains, respectively. *D. radiodurans* R1 was grown in TGY broth (1% tryptone, 0.1% glucose, 0.5% yeast extract) at 30°C and *E. coli* grown in Luria-Bertani medium at 37°C.

Gamma radiation resistance assay. A washed cell suspension was prepared as described above. 1 mL aliquots of final cell suspension from each strain, in triplicate, was irradiated in a sterile 1.5 mL Eppendorf tube with a gamma cell ^{60}Co source (Gamma Beam-

Table 1. Physicochemical composition of the soil of Gandom Beryan

Parameters	Value
pH	7.62
Organic carbon (% O.C)	0.143
Total nitrogen (% N)	0.013
Absorbable phosphorous, ppm	13.02
Absorbable potassium, ppm	110.4
Ferrous, g/L	0.006
Manganese, g/L	0.002
Sodium, g/L	15.6
Chloride, g/L	17.7
Sulfate, g/L	11.3
Magnesium, g/L	0.07
Calcium, g/L	1.5
Bicarbonate, g/L	0.7
Carbonate, g/L	0.0

150 Type B, Canada) at different doses (up to 6 kGy in steps of 1 kGy) of gamma radiation at room temperature. An unexposed tube served as a non-irradiated control. After irradiation, the cell suspensions were serially diluted in sterile 0.85% NaCl solution. Colony counting on the agar plates after incubation at 30°C for 7 days was carried out. The percentages of survival were calculated by dividing the surviving cells after irradiation to viable cells in the non-irradiated control (Gtari et al., 2012). *D. radiodurans* R1 and *E. coli* were used as positive and negative controls, respectively.

16S rRNA gene sequencing. Bacterial genomic DNA was extracted using a DNP™ Kit (CinnaGen, Iran) according to the manufacturer's protocol. The 16S rRNA genes were amplified with bacterial universal primers 8F (5'-AGA-0GTTTGATCCTG-GCTCA-3') as forward and 1492R (5'-GGT-TACCTTGTTACGACTT-3') as reverse (Spencer and Ragout de Spencer, 2004). PCR reaction was performed in a Reddy 2× PCR MasterMix (Ampliqon, Denmark) using by a Thermocycler (Veriti 96-well Thermal Cycler, Applied Biosystems) at conditions as follow: 95°C for 5 min, followed by 30 cycles each of 94°C for 1 min, 57°C for 1 min, 72°C for 75 s, with a final extension step at 72°C for 7 min. The quality of PCR products were checked by electrophoresis on 1% agarose gel and then purified and sequenced by Macrogen services (Seoul, South Korea).

Phylogenetic analysis. The identities of the 16S rRNA gene sequences were determined using BLASTn program in the GenBank database (http://www.ncbi.nlm.nih.gov) and through EzTaxon server (http://www.ezbiocloud.net), and then aligned with the sequences of the closely related strains retrieved from EzTaxon using ClustalX software (Thompson et al., 1997). A phylogenetic tree was constructed by the neighbor-joining method (Saitou and Nei, 1987) with bootstrap values based on 1000 replicates (Felsenstein, 1985) contained in the MEGA software package, version 6 (Tamura et al., 2013).

RESULTS

Sample characteristic analysis. Black Gandom Beryan hill is only one of the unique phenomena found in the Lut Desert. Some physicochemical characteristics and ion concentrations of the soil sample were presented in Table 1. Chloride, sodium and sulfate are the main ions in the soil. Low levels of organic carbon and total nitrogen in the tested soil indicated the oligotrophic conditions in the soil of Gandom Beryan region. The pH was about neutral.

Identification of microorganisms. In a study of the culturable diversity of radioresistant bacteria in the soil and surface sands of arid Gandom Beryan hill locating in the Lut Desert of Iran, two non-endospore-forming pigmented colonies were obtained on R2A and TSA agar plates after different desiccation periods in a desiccator. A pale-pink colored colony with gram-positive cocci occurring in diads and tetrads, designated A2, was isolated from a mixture of surface sand sample of Gandom Beryan hill on R2A agar medium. An orange pigmented colony on TSA medium, designated B9, was also isolated from a mixture of soil sample of Gandom Beryan hill. Cells of isolate B9 were gram-positive with a diplococcic or tetrad shaped. The 16S rRNA gene sequence similarities of these isolates to relevant sequences were evaluated. A search on the EzTaxon database showed that the strain A2 was affiliated with *Modestobacter muralis* MDVD1^T (99.7% similarity) in the family *Geodermatophilaceae*. The strain B9 exhibited closest similarity to the *Maritalea mobilis* E6^T (97.3% similarity) in the class *Alphaproteobacteria*. Phylogenetic analysis was performed by construction of a dendrogram (Figs. 2, 3). The GenBank/DDBJ accession numbers for the 16S rRNA gene sequences of strains A2 and B9 are LC331307 and LC331308, respectively.

Resistance to desiccation. In the following step, desiccation tolerance for the strains A2 and B9 after exposure to different periods of dehydration was investigated, as well as *D. radiodurans* R1 and *E. coli* strains were used for comparison. After 8 weeks in a desiccator containing silica gel, strain A2 remained viable and exhibited a 23% survival rate. Whereas, the viability of *D. radiodurans* R1 decreased to about 15% over 8 weeks which was in agreement with previous studies (Fredrickson et al., 2008). The survival percentages for strain A2 at 1st, 2nd, and 4th week were calculated 62, 53, and 50%, respectively. Also, strain B9 could survive after 8 weeks of desiccation and 15×10^4 cfu mL^{-1} which equal to a 0.15% survival percentage were recovered. A rapid decline in viability for strain B9 occurred after initial 7 days and a survival

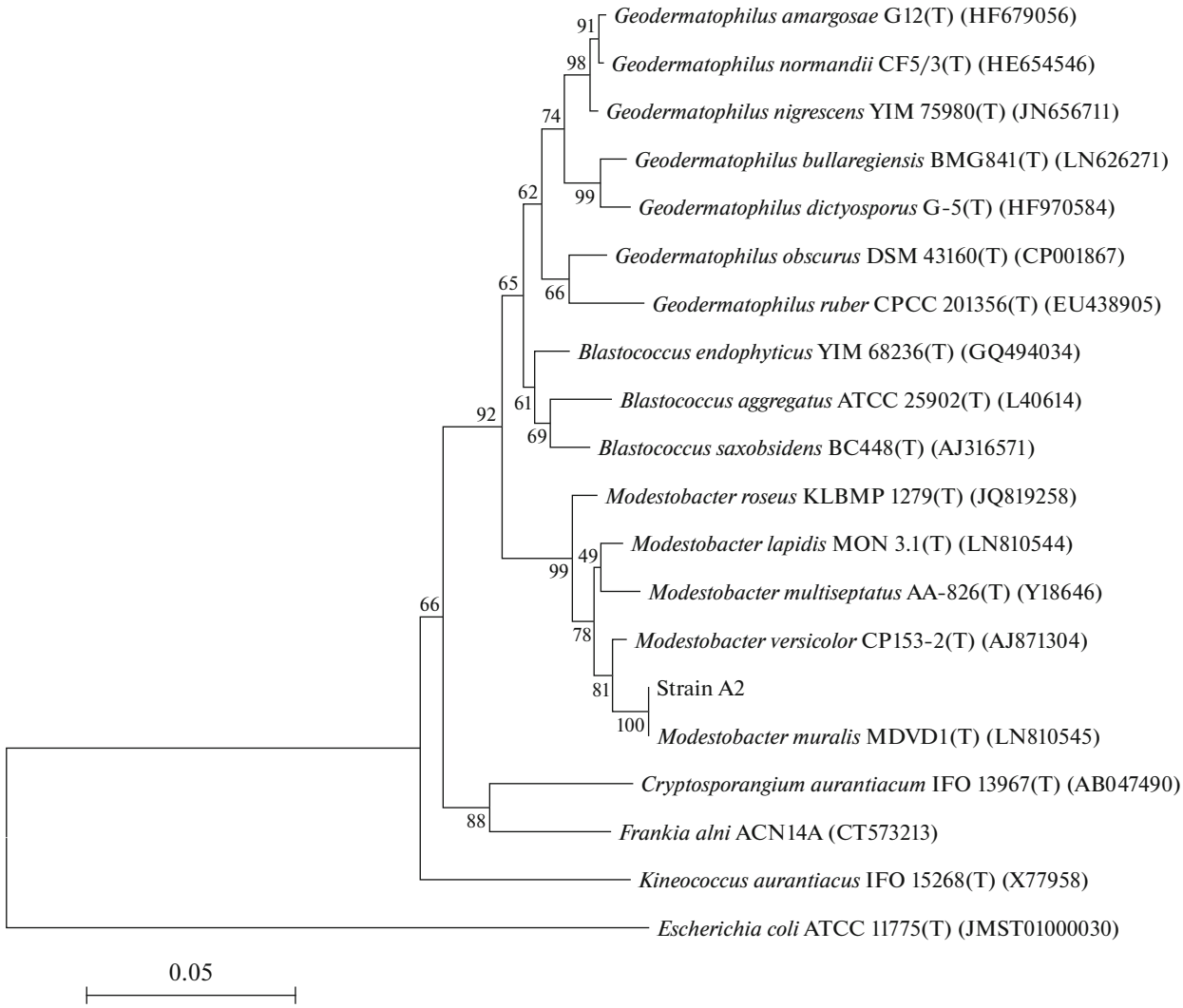

Fig. 2. Phylogenetic neighbor-joining tree based on 16S rRNA gene sequences showing the phylogenetic relationship of the strain A2 to the genera *Modestobacter*, *Geodermatophilus* and *Blastococcus* within the family *Geodermatophilaceae*. *Escherichia coli* (ATCC 11775) was used as outgroup. Bootstrap values (expressed as percentages of 1000 replications) are given at nodes. Bar, 0.05 substitutions per nucleotide position.

percentage of 2.6% was observed, while the survival rate was almost constant during the next 49 days. In addition, the viability of the *E. coli* reduced dramatically upon a week of desiccation and showed very little or no survival after 2 weeks of desiccation. It should be noted that as desiccator was opened at each time, the relative humidity within desiccator increased and upon resealing it decreased again. Therefore, the survival rates of bacteria may be affected by cycles of desiccation and partial rehydration (Mattimore and Battista, 1996).

A survival curve for the strains A2 and B9 as well as *D. radiodurans* R1 was drawn. As shown in Fig. 4, strain A2 like *D. radiodurans* R1 displayed a sigmoid-shaped desiccation survival curve with a shoulder before the exponential part, compared to a linear curve for the survival of B9 strain.

Resistance to gamma radiation. There is a close relation between desiccation tolerance and ionizing radiation resistance mechanisms (Mattimore and Battista, 1996). The isolates A2 and B9, *D. radiodurans* R1 and *E.coli* were tested for their resistance to different doses of gamma radiation. The D_{10} value, the radiation dose necessary to provide a 90% reduction in viability, was 3–4 kGy for *Modestobacter* sp. A2, whereas the D_{10} value of *Maritalea* sp. B9 for gamma rays was about 2–3 kGy (Fig. 5). Strains A2 and B9 showed no loss of viability at 1 kGy dose of gamma radiation. Strain A2 could survive up to 5 kGy and 0.2×10^4 cfu mL^{-1} were recovered at this dose, whereas strain B9 showed no viability following exposure to 5 kGy of gamma radiation. A 6 kGy dose of gamma rays kills all cells in the original cultures of the strains A2 and B9. *D. radiodurans* R1 culture showed highly radioresis-

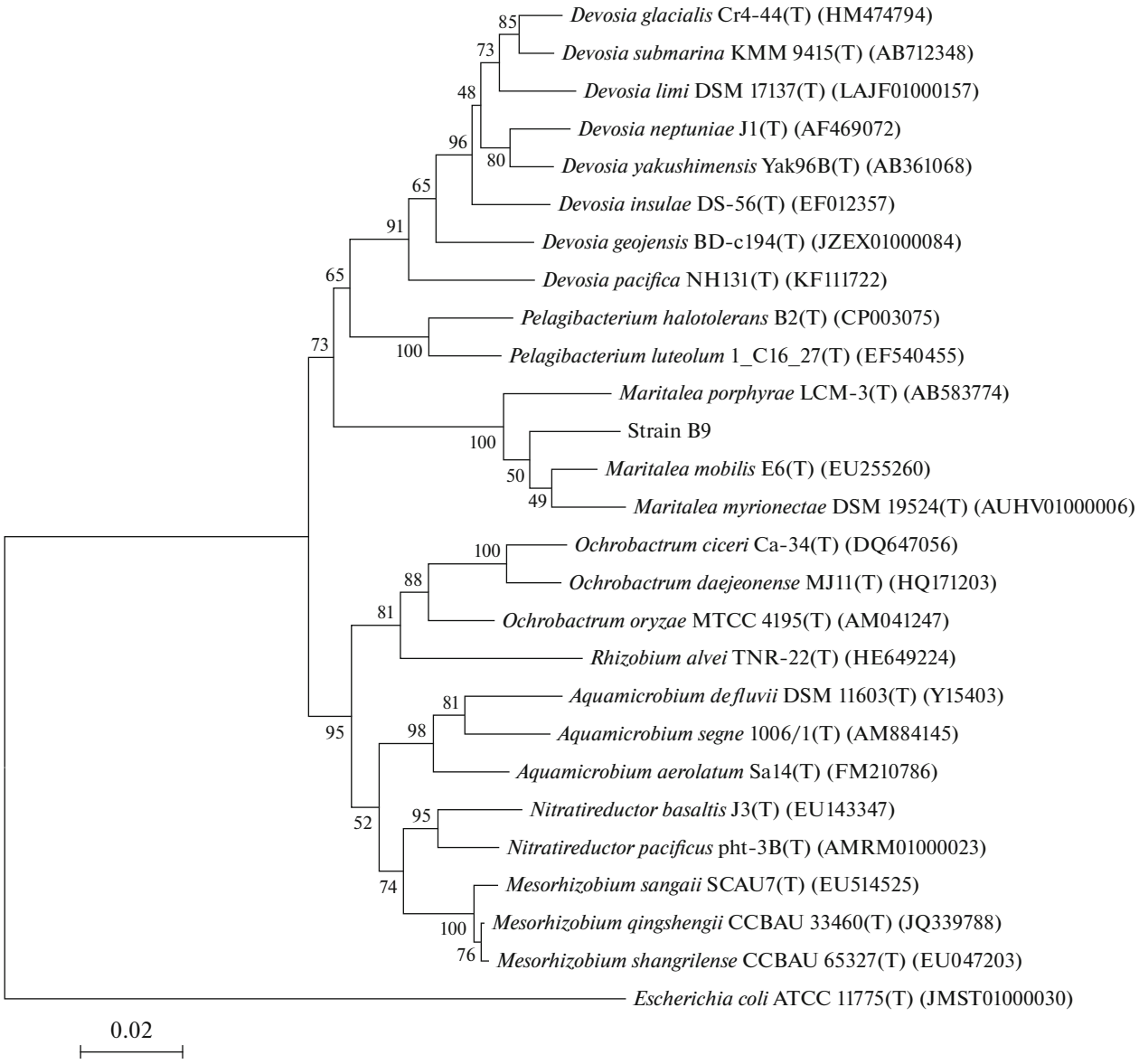

Fig. 3. A phylogenetic dendrogram which was generated by the neighbor-joining method demonstrated the phylogenetic relationship of the strain B9 to the genera *Maritalea* and *Devosia* within the family *Hyphomicrobiaceae* and other related species in the class *Actinobacteria*. *Escherichia coli* (ATCC 11775) was used as outgroup. Bootstrap values (expressed as percentages of 1000 replications) are given at nodes. Bar, 0.02 substitutions per nucleotide position.

tance up to 6 kGy gamma rays dose without loss of survival. The cell numbers in *E. coli* culture was reduced dramatically after receiving a 1 kGy dose of gamma radiation.

DISCUSSION

The genus *Modestobacter* as well as the genera *Geodermatophilus* and *Blastococcus* constitutes the family *Geodermatophilaceae* which belongs to the order *Geodermatophilale*. Members of this family are known for their unusual resistance against a number of extreme environmental stresses and can colonize different harsh environmental niches such as Antarctic or hot desert soils, high altitude soils and rocks and historic monument surfaces. *Modestobacter* strains are gram-positive rods and cocci actinobacteria, occurring singly or in pairs which do not form endospore. Cells often form short multiseptate filaments. Colonies appear pink, dark brown or black pigmented (Busarakam et al., 2016; Gtari et al., 2012). At the time of writing, the genus *Modestobacter* consists of 6 species (http://www.bacterio.net/Modestobacter.html).

Strain A2 isolated from the present study was affiliated with *Modestobacter muralis* MDVD1^T (99.7% similarity) based on 16S rRNA gene sequence analy-

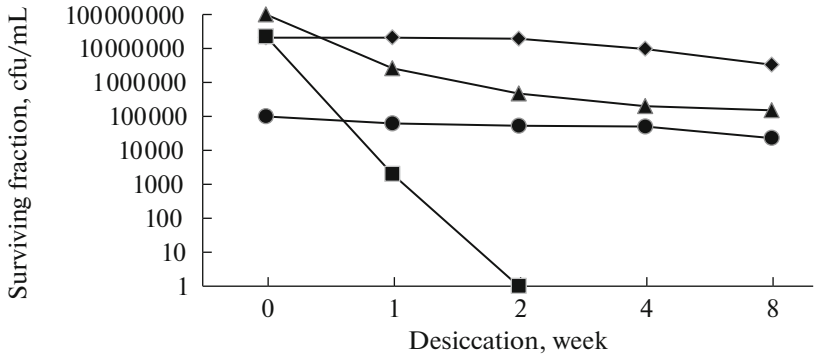

Fig. 4. Survival curves of *Deinococcus radiodurans* R1 (◆), A2 isolate (●), B9 isolate (▲) and *E. coli* (■) following exposure to desiccation.

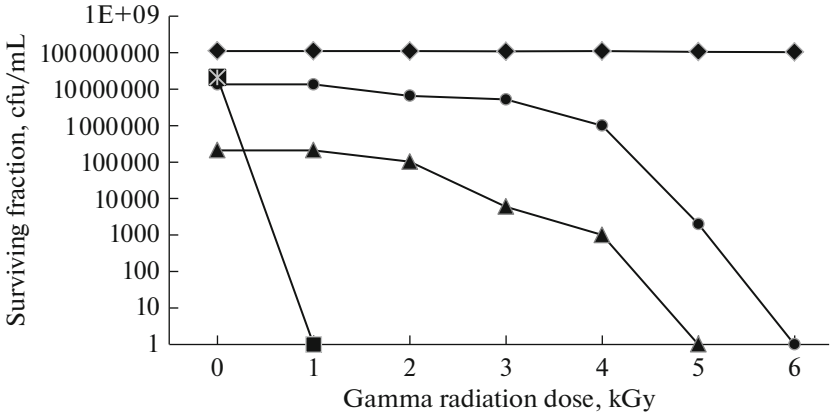

Fig. 5. Survival curves of *Deinococcus radiodurans* R1 (◆), A2 isolate (●), B9 isolate (▲) and *E. coli* (■) following exposure to gamma radiation.

sis. Resistance level to 56 days of desiccation in a desiccator containing silica gel for *Modestobacter* sp. A2 (23%) was even more than the classic desiccation tolerant *D. radiodurans* bacterium (15%). *Modestobacter* sp. A2 was found to be moderately resistant against gamma radiation with a D_{10} value between 3 and 4 kGy.

Gtari et al (2012) investigated the resistance profiles of a strain of *Modestobacter multiseptatus*, named as BC501, which was isolated from Carrara marble cave in Italy to different environmental stresses. 10% of original cells from strain BC501 were recovered after 60 days of desiccation period in a desiccator containing silica gel and 6 kGy of gamma rays. Strain BC501 was significantly less resistant to desiccation than the *Modestobacter* sp. A2, whilst radioresistance level of strain BC501 was about 2 times higher than that of *Modestobacter* sp. A2. The same radioresistance and desiccation tolerance profiles between strain A2 obtained from arid Gandom Beryan hill and strain BC501 isolated from rock surfaces confirms environmental niches that were occupied by members of the family *Geodermatophilaceae*. Gtari et al. suggested that the *Geodermatophilus-Modestobacter-Blastococcus* and the *Deinococcus-Thermus* clades are similar in terms of the presence of the resistant/sensitive traits to ionizing radiation because unlike *Geodermatophilus* and *Modestobacter*, the genus *Blastococcus* is sensitive against effects of different oxidative stress-producing agents.

Xu et al. (2009) isolated a pale-yellow colony on LOSWM medium from coastal seawater collected from Tianjin, China and presented it as a novel genus and species, *Zhangella mobilis*, in the family *Hyphomicrobiaceae*. Further phylogenetic analysis transferred the *Zhangella mobilis* from the genus *Zhangella* to the genus *Maritalea*, with the name *Maritalea mobilis* (Fukui et al., 2012). Three species in this genus have been defined until today (http://www.bacterio.net/Maritalea.html).

In the present study, strain B9 showed the highest 16S rRNA gene sequence similarity to *Maritalea mobilis* $E6^T$ (97.3%) and less than 96% similarity to other relatives. Due to low similarity level in 16S rRNA gene sequence, strain B9 can be proposed as a new taxon and needs more investigations using polyphasic taxon-

omy. Radioresistance has not been reported in the family *Hyphomicrobiaceae* and this study is the first showing that the genus *Maritalea* belonging to this family is resistant to gamma radiation and desiccation. In contrast to *D. radiodurans* R1, resistance level of strain B9 experienced a sharp fall after 7 days of desiccation, while the level fell slightly over the next following days. Like haloarchaeal strains isolated from Shoor River in the Lut Desert, resistance to desiccation in B9 strain did not follow the sigmoid survival curve pattern of *D. radiodurans* and showed a more resistance to desiccation in more long-term periods of time (Shirsalimian et al., 2017). *Maritalea* sp. B9 remained viable after desiccation for 8 weeks (a survival percentage of 0.15%) and was moderately resistant to gamma radiation with a D_{10} value between 2 and 3 kGy.

There has been an upward trend toward in the study of microbial diversity in arid and hyperarid desert ecosystems. Research into understanding of these habitats and their diverse microbial life such as radiation resistant, desiccation tolerant, extremely halophiles and lithobiontic microorganisms was begun only a few decades ago, mainly in the Atacama Desert by NASA (Azua-Bustos et al., 2012). Two main strategies were used in desert-dwelling microorganisms to achieve high resistances against ionizing radiation and desiccation: protection-based mechanisms by ROS-scavenging capacity such as Mn^{2+} complexes, carotenoids and antioxidant enzymes; and well-developed DNA repair systems. These strategies to combat oxidative stress could provide new promising approaches for bioremediation of radioactive waste sites, delaying aging and preventing cancers (Slade and Radman, 2011). Microbiology of the Lut Desert and Gandom Beryan hill located there has not been subjected to study until today. The study of the microbial biodiversity of this desert through both culture-dependent and -independent methods can open various biotechnological applications in the future.

In this study, isolation of desiccation tolerant and radiation resistant bacteria from arid Gandom Beryan region located in the Lut Desert was investigated. In all, the results which obtained from the present study can confirm the desiccation adaptation hypothesis. A new strain of *Modestobacter* was isolated from surface sands collected from Gandom Beryan hill as was isolated in other deserts in the world. Conversely, there has not been any report on desiccation tolerance and radioresistance properties in the bacterial genus *Maritalea* belonging to the family *Hyphomicrobiaceae*, making the present study unique with respect to the strain B9 isolation. However, a polyphasic description of the strain B9 is required according to low16S rRNA gene sequence similarity. *Modestobacter* sp. A2 and *Maritalea* sp. B9 were resistant against gamma radiation with a D_{10} value between 2 and 4 kGy and maintained their viability over the period of 8 weeks of desiccation.

ACKNOWLEDGMENTS

The authors would like to thank all the members of the Owj-e-Kavir climbing team for sample collection.

REFERENCES

Azua-Bustos, A., Urrejola, C., and Vicuna, R., Life at the dry edge: microorganisms of the Atacama Desert, *FEBS Lett.*, 2012, vol. 586, no. 18, pp. 2939–2945.

Billi, D., Friedmann, E.I., Hofer, K.G., Caiola, M.G., and Ocampo-Friedmann, R., Ionizing-radiation resistance in the desiccation-tolerant cyanobacterium *Chroococcidiopsis, Appl. Environ. Microbiol.*, 2000, vol. 66, no. 4, pp. 1489–1492.

Bull, A.T. and Asenjo, J.A., Microbiology of hyper-arid environments: recent insights from the Atacama Desert, Chile, *Antonie van Leeuwenhoek*, 2013, vol. 103, pp. 1173–1179.

Busarakam, K., Bull, A.T., Trujillo, M.E., Riesco, R., Sangal, V., Van Wezel, G.P., and Goodfellow, M., *Modestobacter caceresii* sp. nov., novel actinobacteria with an insight into their adaptive mechanisms for survival in extreme hyper-arid Atacama Desert soils, *Syst. Appl. Microbiol.*, 2016, vol. 39, pp. 243–251.

Carter, M.R., and Gregorich, E.G., *Soil Sampling and Methods of Analysis*, 2007, CRC.

Chanal, A., Chapon, V., Benzerara, K., Barakat, M., Christen, R., Achouak, W., Barras, F., and Heulin, T., The desert of Tataouine: an extreme environment that hosts a wide diversity of microorganisms and radiotolerant bacteria, *Environ. Microbiol.*, 2006, vol. 8, pp. 514–525.

Chen, M., and Alexander, M., Survival of soil bacteria during prolonged desiccation, *Soil. Biol. Biochem.*, 1973, vol. 5, no. 2, pp. 213–221.

Felsenstein, J., Confidence limits on phylogenies: an approach using bootstrap, *Evolution.*, 1985, vol. 39, pp. 783–791.

Fredrickson, J.K., Li, S.M., Gaidamakova, E.K., Matrosova, V.Y., Zhai, M., Sulloway, H.M., Scholten, J.C., Brown, M.G., Balkwill, D.L., and Daly, M.J., Protein oxidation: key to bacterial desiccation resistance?, *ISME J.*, 2008, vol. 2, pp. 393–403.

Fukui, Y., Abe, M., Kobayashi, M., Ishihara, K., Oikawa, H., Yano, Y., and Satomi, M., *Maritalea porphyrae* sp. nov., isolated from a red alga (*Porphyra yezoensis*), and transfer of *Zhangella mobilis* to *Maritalea mobilis* comb. nov., *Int. J. Syst. Evol. Microbiol.*, 2012, vol. 62, pp. 43–48.

Gtari, M., Essoussi, I., Maaoui, R., Sghaier, H., Boujmil, R., Gury, J., Pujic, P., Brusetti, L., Chouaia, B., Crotti, E., Daffonchio, D., Boudabous, A., and Normand, P., Contrasted resistance of stone-dwelling *Geodermatophilaceae* species to stresses known to give rise to reactive oxygen species, *FEMS Microbiol. Ecol.*, 2012, vol. 80, pp. 566–577.

Luedemann, G.M., *Geodermatophilus*, a new genus of the *Dermatophilaceae* (*Actinomycetales*), *J. Bacteriol.*, 1968, vol. 96, pp. 1848–1858.

Mattimore, V. and Battista, J.R., Radioresistance of *Deinococcus radiodurans*: functions necessary to survive ionizing radiation are also necessary to survive rolonged desiccation, *J. Bacteriol.*, 1996, vol. 178, pp. 633–637.

Mohseni, M., Abbaszadeh, J, and Nasrollahi Omran, A., Radiation resistant of native *Deinococcus* spp. isolated from the Lout desert of Iran ''the hottest place on Earth'', *Int. J. Environ. Sci. Technol.*, 2014, vol. 11, pp. 1939–1946.

Rainey, F.A., Ray, K., Ferreira, M., Gatz, B.Z., Nobre, M.F., Bagaley, D., Rash, B.A., Park, M.J., Earl, A.M., Shank, N.C., Small, A.M., Henk, M.C., Battista, J.R., Kämpfer, P., and da Costa, M.S., Extensive diversity of ionizing-radiation-resistant bacteria recovered from Sonoran Desert soil and description of nine new species of the genus *Deinococcus* obtained from a single soil sample, *Appl. Environ. Microbiol.*, 2005, vol. 71, pp. 5225–5235.

Saitou, N. and Nei, M., The neighbor-joining method: a new method for reconstructing phylogenetic trees, *Mol. Biol. Evol.*, 1987, vol. 4, pp. 406–425.

Shirsalimian, M.S., Amoozegar, M.A., Akhavan Sepahy, A., Kalantar, S.M., and Dabbagh, R., Isolation of extremely halophilic *Archaea* from a saline river in the Lut Desert of Iran, moderately resistant to desiccation and gamma radiation, *Microbiology* (Moscow), 2017, vol. 86, pp. 403–411.

Slade, D. and Radman, M., Oxidative stress resistance in *Deinococcus radiodurans, Microbiol. Mol. Biol. Rev.*, 2011, vol. 75, pp. 133–191.

Spencer, J.F.T. and Ragout de Spencer, A.L., *Environmental Microbiology: Methods and Protocols*, Humana, 2004.

Sun, H.M., Zhang, T., Yu, L.Y., Sen, K., and Zhang, Y.Q., Ubiquity, diversity and physiological characteristics of *Geodermatophilaceae* in Shapotou National Desert Ecological Reserve, *Front. Microbiol.*, 2015, vol. 6.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., and Kumar, S., MEGA6: molecular evolutionary genetics analysis version 6.0., *Mol. Biol. Evol.*, 2013, vol. 30, pp. 2725–2729.

Tanaka, M., Earl, A.M., Howell, H.A., Park, M.J., Eisen, J.A., Peterson, S.N., and Battista, J.R., Analysis of *Deinococcus radiodurans*'s transcriptional response to ionizing radiation and desiccation reveals novel proteins that contribute to extreme radioresistance, *Genetics.*, 2004, vol. 168, no. 1, pp. 21–33.

Terato, H., Suzuki, K., Nishioka, N., Okamoto, A., Shimazaki-Tokuyama, Y., Inoue, Y., and Saito, T., Characterization and radio-resistant function of manganese superoxide dismutase of *Rubrobacter radiotolerans, J. Radiat. Res.*, 2011, vol. 52, no. 6, pp. 735–742.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., and Higgins, D.J., The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools, *Nucleic. Acids. Res.*, 1997, vol. 25, pp. 4876–4882.

Xu, H.Y., Chen, L.P., Fu, S.Z., Fan, H.X., Zhou, Y.G., Liu, S.J., and Liu, Z.P., *Zhangella mobilis* gen. nov., sp. nov., a new member of the family *Hyphomicrobiaceae* isolated from coastal seawater, *Int. J. Syst. Evol. Microbiol.*, 2009, vol. 59, pp. 2297–2301.