

# 방사성 폐기물의 생물정화를 위한 극한세균 데이노코쿠스 라디오두란스의 연구적 고찰

정선욱 · 최용준<sup>†</sup>

서울시립대학교 환경공학부  
(2017년 1월 10일 접수, 2017년 1월 18일 심사, 2017년 1월 31일 채택)

## Research Perspective of an Extremophilic Bacterium, *Deinococcus radiodurans* on Bioremediation of Radioactive Wastes

Sun-Wook Jeong and Yong Jun Choi<sup>†</sup>

School of Environmental Engineering, University of Seoul, 163, Seoulsiripdae-ro, Dongdaemun-gu, Seoul 02504, Republic of Korea  
(Received January 10, 2017; Revised January 18, 2017; Accepted January 31, 2017)

### 초 록

방사성 폐기물에 대한 우려가 증대됨에 따라 생물정화 기술에 대한 관심이 고조되고 있다. 병원과 원자력발전 등에서 발생하는 많은 양의 방사성 폐기물이 환경에 직접 노출됨에 따라, 이를 정화하기 위한 다양한 물리화학적 기술이 보고되고 있다. 하지만, 이러한 방법은 고비용 및 고위험성 과정이 수반되기 때문에 미생물을 이용한 친환경적 생물정화 기술이 요구되고 있다. 최근, 고방사선 노출 등과 같은 극한환경에서 서식할 수 있는 방사선저항성 미생물에 대한 연구가 많이 보고되고 있으며, 이를 이용한 방사성 폐기물 정화에 대한 연구적 관심이 높아지고 있다. 데이노코쿠스 라디오두란스는 대표적인 방사선저항성 미생물로서 높은 방사선에 저항성을 갖는 특성으로 인해 방사성 폐기물 등의 유해물질 정화에 이용될 수 있다. 본 총설에서는 데이노코쿠스 라디오두란스의 방사선내성과 관련한 일반적 기작에 대해 소개하고, 방사성 폐기물의 생물정화 활용 가능성에 대해 논의한다.

### Abstract

Increasing concerns on radioactive wastes have drawn much attention on the development of remediation technologies. Massive amounts of radioactive wastes generated from hospital and nuclear power plants were exposed to our environment. Although physicochemical removal methods were developed, an eco-friendly remediation method has not yet been demonstrated. Recently, an extremophilic bacterium has received much attention due to their extraordinary characteristics. Among them, *Deinococcus radiodurans* (*D. radiodurans*) strain was regarded as the best host organism for the removal of radioactive heavy metals and radionuclides, because of their superb characteristics like tolerance against the high level of radioactivity. In this article, we briefly introduced the extraordinary nature of *D. radiodurans* and also discussed the potential use of *D. radiodurans* strain for the removal of radioactive wastes.

**Keywords:** *Deinococcus radiodurans*, radioactive waste, bioremediation, antioxidation, DNA repair

## 1. Introduction

Over the past few years, radiation and radioactive materials are regarded as an indispensable source to human beings on daily life such as medical application, academic research, and energy generation. The X-ray cinefluography and radiation therapy are commonly applied to patients to diagnose medical treatment condition. And also, huge amount of electricity is generated by nuclear power plant by using ra-

dioactive materials such as uranium as an energy source. In spite of those of advantages, concerns on the radioactive substance and waste has been gradually increased due to the threat of radioactivity to public and environment as appears by serious accidental events. The huge amount of radioactive materials is leaked to environment after the catastrophic nuclear accidents such as the Chernobyl disaster and the Fukushima Daiichi nuclear disaster[1,2]. Not all radioactivity comes from disastrous accidents. The tremendous amount of radioactive waste which is believed to trigger development of cancer and chronic disease also has occurred from biomedical and industrial applications. However, despite the risk of radioactivity, a definite answer for remediation method of radioactive polluted environment has not yet been addressed.

<sup>†</sup> Corresponding Author: University of Seoul,  
School of Environmental Engineering, 163, Seoulsiripdae-ro, Dongdaemun-gu,  
Seoul 02504, Republic of Korea  
Tel: +82-2-6490-2873 e-mail: yongjun2165@uos.ac.kr

Table 1. The Microbial Sources for Bioremediation of Radioactive Substances

Radionuclides	Organism	Mechanism	Reference
Uranium	<i>Deinococcus radiodurans</i>	Bioprecipitation	[73]
		Bioaccumulation	[74]
	<i>Desulfovibrio desulfuricans</i> G20	Bioprecipitation	[59]
		Bioreduction	[75]
		Bioreduction	[76]
		Bioprecipitation	[77]
		Bioreduction	[78]
		Bioreduction	[79]
<i>Citrobacter</i> sp.	Biominalisation	[80]	
Cobalt	<i>Rhodopseudomonas palustris</i> CGA0009	Bioreduction	[9]
	<i>Novosphingobium aromaticivorans</i> F-199		[62]
Neptunium(V)	<i>Shewanella putrefaciens</i>	Bioreduction	[82]
	<i>Citrobacter</i> sp.		
Technetium	<i>Desulfovibrio desulfuricans</i>	Bioreduction	[83]
	<i>Thiobacillus</i> spp	Bioreduction	[84]
	<i>Anaeromyxobacter dehalogenans</i> 2CP-C	Bioreduction	[85]
Plutonium	<i>Geobacter metallireducens</i> GS15	Bioreduction	[86]
	<i>Shewanella oneidensis</i>		[87]
	<i>Bacillus mycoides</i>		
Americium	<i>Serratia</i> sp	Biominalisation	[88]
Iodine	<i>Desulfovibrio desulfuricans</i>	Bioreduction	[89]
	<i>Pseudomonas fluorescens</i>		[90]
Strontium	<i>Halomonas</i> sp.	biominalisation	[91]
	<i>Sporosarcina pasteurii</i>		[92]

There are several techniques to remove toxic materials from environment such as chemical precipitation, oxidation or reduction, and electrochemical treatments[3]. However, most of these techniques entails expensive physicochemical process as well as secondary contamination. To overcome these shortcomings, there has been attracting increasing interest in bio-based treatment, called "Bioremediation"[4]. Aside from the other physicochemical processes, bioremediation is also commonly used in clean-up contaminated water and soil as it has several advantages over physicochemical processes in terms of less side effect, cost-effectiveness and complete degradation of contaminants through natural processes such as biosorption, bioaccumulation, bio-transformation, and biomineralization, which can be exploited for either *ex situ* or *in situ* (Table 1)[5,6]. For examples, *Desulfovibrio desulfuricans* can couple the oxidation of a range of electron donors to reduction of Tc(VII) so that it was precipitated as an insoluble oxide at cell peripheries[7]. The *Pseudomonas aeruginosa* and *Pseudomonas putida* strains can remove Cd<sup>2+</sup>, Zn<sup>2+</sup>, Cu<sup>2+</sup>, Fe<sup>2+</sup>, Co<sup>2+</sup>, and Ni<sup>2+</sup> from solution by incorporation of inorganic phosphate as a precipitant[8]. Genetically engineered *Escherichia coli* strain expressing Ni/Co transporter (NiCoT) genes from *Rhodopseudomonas palustris* and

*Novosphingobium aromaticivorans* was able to remove trace cobalt from aqueous solutions[9]. However, such radiosensitive organisms cannot be effectively used for remediation of radioactive heavy metals and radionuclide. From this point of view, the extremophile, micro-organisms possess extraordinary characteristics originated from various genetic diversity evolved over a long period time, has been receiving much attentions as best candidate organism for bioremediation of toxic contaminants[10,11].

Among them, *Deinococcus* is well-known microorganism for highly resistance to environmental hazards[12]. *Deinococcus radiodurans* has been extensively studied to elucidate its extraordinary capacity to survive against various environmental stresses such as high level of gamma-irradiation, UV irradiation, and oxidative stresses[13-16]. This extreme resistance is mainly originated from a powerful DNA repair and efficient antioxidation mechanism[16]. Thus, the superior properties of *D. radiodurans* make it an ideal candidate for bioremediation of radioactive heavy metals and radionuclides. In this article, we reviewed remarkable characteristics of *D. radiodurans* and demonstrated the potential use of *D. radiodurans* for remediation of radioactive polluted environments throughout the previous observations.

**Table 2. The Microbial Sources for Bioremediation of Non-radioactive Substances**

Heavy metals	Organism	Mechanism	Reference
Mercury	<i>Deinococcus geothermalis</i>	Bioreduction	[11]
Fe(III)	<i>Geobacter sulfurreducens</i>	Bioreduction	[81]
Cadmium	<i>Pseudomonas veronii</i>	Biosorption	[93]
Lead	<i>Bacillus</i> sp. L14	Biosorption	[94]
Copper	<i>Kocuria flava</i>	Bioprecipitation	[95]
Zinc	<i>Bacillus cereus</i> , <i>Pseudomonas veronii</i>	Biosorption	[93,96]
Arsenic	<i>Sporosarcina ginsengisoli</i>	Biominalisation	[97]
Chromium	<i>Bacillus cereus</i>	Bioreduction	[98]

## 2. Common Features of *D. radiodurans*

In this section, we introduce the unique properties of an extremophilic bacterium *Deinococcus radiodurans* to survive under the acute exposure of irradiation[17]. *D. radiodurans* is first discovered in gamma irradiated canned meat. This bacterium initially named *Micrococcus radiodurans* because of morphological similarity to members of the genus *Micrococcus*. After that, this bacterium was reclassified to *Deinococcus-Thermus* phylum and renamed as *Deinococcus radiodurans*[15,18]. Since its discovery, *Deinococcus* spp. was also found in diverse environments, such as air sample[19], activated sludge[20], soil[21,22], water[23], hot spring[24], Antarctica[25], and surface on paper machine[26] etc. Up to now, 47 species of *Deinococcus* spp. were reported and the genetic information and genome sequence of some strains such as *D. radiodurans*[27,28], *D. geothermalis*[29], *D. deserti*[30], *D. marcopensis*[31], *D. gobiensis*[32], *D. proteolyticus*[33], *D. wulumuqiensis*[34], *D. xibeiensis*[35], *D. phoenixis*[36], and *D. grandis*[37] had completely been revealed in public. It is aerobic, non-motile, non-spore forming, and red pigmented tetrad forming bacterium and well known for its supreme resistance to ionizing radiation.

### 2.1. DNA damage responses in *D. radiodurans*

The acute DNA damage is usually occurred by hydroxyl radical ( $\cdot\text{OH}$ ) and the quintessential reactive oxygen species (ROSs) from ionizing radiation. As the DNA damage appears to be lethal to living organisms, cells possess various mechanisms to repair damaged DNA to survive[38]. The extreme radiation resistance of *D. radiodurans* is mainly originated from a powerful DNA repair system that accomplishes precise and an efficient reassembly of shattered chromosomal DNA by ionizing radiation through excision, mismatch, and recombination process[16,39]. Although DNA repair system of *D. radiodurans* relatively simple compare to those of reported other radiosensitive bacteria such as *E. coli* and *Shewanella oneidensis*, they have remarkable DNA repair capacity[40]. Among the various DNA repair mechanisms in *D. radiodurans*, double strand break (DSB) repair is mainly accomplished by extended synthesis-dependent strand annealing (ESDSA) and some DNA repair proteins such as RecFOR, UvrD, RecJ, RecA, PolI, and PolIII are involved in ESDSA DNA repair mechanism[16,41]. In addition,

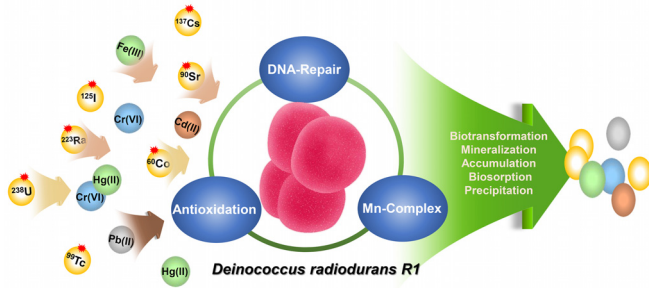
a large number of radiation induced DNA repair related proteins such as DdrBCDO and PprA are identified in *Deinococcaceae*[42].

PprI, novel regulatory protein, plays an important role in DNA damage response as well as various cellular metabolisms such as stress response, transcription, translation, cell cycle control, and signal transduction. Under the exposure to radiation, the expression of *recA* and *pprA* gene were positively controlled by PprI to enhance DNA repair capacity[43-45]. In addition, DdrO is another essential protein able to bind specific consensus nucleotide sequence called Radiation/Desiccation Response Motif (RDRM) of genes[46]. Thus, the expression of genes containing RDRM sequence genes involved in DNA repair mechanism is tightly repressed by DdrO under the normal condition[46]. Recently, Devigne et al. and Ludanyi et al. suggested that PprI-DdrO pathway has critical roles in repairing mechanism for damaged DNA in *D. radiodurans* and *D. deserti*[47,48]. Moreover, it has been reported that DrRRA[49], RadS/RadR[50], and several small non-coding RNAs (sRNAs)[51] found in *D. radiodurans* may play an important role for withstanding high dose of radiation.

### 2.2. Antioxidation mechanism in *D. radiodurans*

Various reactive oxygen species (ROSs) including hydroxyl radical, superoxide anion radical, and hydrogen peroxide are generated by the ionizing radiation from radioactive wastes[10]. During the treatment of radioactive waste, the organism was suggested to be exposed to the ROSs which trigger DNA breaks and protein oxidation resulting in lethal damage to the cell. Therefore, the organism used for bioremediation of radioactive polluted environment should have cellular mechanisms to protect and repair cells from cellular damages induced by ROSs[38].

There are mainly two types of scavenger mechanisms, enzymatic and non-enzymatic mechanisms in *D. radiodurans*. First, enzymatic ROS scavenging is mediated by three catalases, four SODs, two peroxidases, and two DNA protection (Dps) proteins during starvation[16]. Superoxide dismutase (SOD) alternatively removes or adds electrons from superoxide to make the molecules encounter subsequently stable species such as  $\text{O}_2$  and hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). Dps proteins protect DNA from oxidative stress by chelating  $\text{Fe}^{2+}$  and reducing  $\text{H}_2\text{O}_2$ [52]. Second, divalent manganese complexes and carotenoids are also responsible for non-enzymatic scavenging mechanisms. Previous studies reported that high ratio of  $\text{Mn}^{2+}/\text{Fe}^{2+}$  was observed in radio-tolerant mi-



**Figure 1.** The scheme of bioremediation process for the removal of radioactive wastes using *D. radiodurans* R1 strain. The various radioactive wastes represented in the colored small circles are managed by *D. radiodurans* R1 strain through bioremediation process.

croorganisms exposed to high dose of ionizing radiation[53,54]. It is interesting to note that intracellular level of  $Mn^{2+}$  is higher than that of radiosensitive bacteria such as *E. coli*, *Enterococcus faecium*, *P. putida*, and *S. oneidensis*, whereas relatively lower in ferrous ion[54]. The complex of free amino acids or peptides with  $Mn^{2+}$  and orthophosphate (or bicarbonate) catalytically decompose  $H_2O_2$  and scavenge superoxide radicals[55]. It has been reported that *D. radiodurans* was inherently able to produce large amount of new carotenoid-like pigment, named as deinoxanthin, acts as a hydroxyl radical scavenger[56]. The deletion study of *crtB* and *crtI* which are involved in deinoxanthin biosynthetic pathway revealed that deinoxanthin plays important roles in scavenging ROSs induced by ionizing radiation, UV, and  $H_2O_2$ [57]. *In vitro* test of scavenging activity of deinoxanthin have also shown that it showed decomposing activity of  $H_2O_2$  as well as singlet oxygen, and the scavenging activity is much higher than those of carotenes (lycopene and  $\beta$ -carotene) and xanthophylls (zeaxanthin and lutein)[58].

### 3. Potential Application of *D. radiodurans* on Bioremediation of Radioactive Polluted Environment

Due to the unique DNA repair system and strong anti-oxidation mechanism described above, *D. radiodurans* can survive against acute exposure to more than 10-20 kGy which is lethal to living organisms without any genotypic and phenotypic changes[16]. Therefore, *D. radiodurans* has been attempted to clean-up radioactive contaminated toxic compounds. Genetically engineered *D. radiodurans* harboring *phoN* from *Salmonella enterica* and *phoK* from *Sphingomonas* sp. which encodes the nonspecific acid phosphatase and ribose-phosphate pyrophosphokinase, respectively, was able to efficiently precipitate uranium from diluted nuclear waste[59]. The genetically engineered *D. radiodurans* expressing the *merA* gene encoding mercuric ion reductase from *E. coli* strain BL308 was able to efficiently reduce toxic  $Hg^{2+}$ , which is main component of radioactive waste sites, to monoatomic volatile  $Hg(0)$ [60]. There was also previous report on recombinant *D. radiodurans* expressing toluene dioxygenase (*tod*) from *P. putida* capable of degrading indole, toluene, chlorobenzene, and 3, 4-dichloro-1-butene under high level of chronic ionizing radiation (60 Gy/h)[61]. The recombinant *D. radiodurans* overexpressed with the

*nxiA* and *nvoA* genes from *Rhodopseudomonas palustris* CGA009 and *Novosphingobium aromaticivorans* F-199, respectively, showed efficient removal efficacy of  $^{60}Co$  (> 60%) from spent decontamination solution[62].

Recently, the new possibility of nanotechnology on environmental remediation for increasing number of toxic compounds has been addressed. Nanoparticles have been used to cover the treatment of industrial wastewater contaminated by toxic metals, radionuclides, organic, and inorganic solutes[63,64]. Recently, Choi *et al* reported that radioactive iodine ( $^{125}I$ ) was efficiently absorbed by chemically synthesized gold nanoparticles (AuNPs) embedded desalting column under the various aqueous media[65]. There are also several studies on the microbial synthesis of various nanoparticles[66-72]. Microbial synthesis of gold and silver nanoparticles using *D. radiodurans* has been reported and considered it as an antimicrobial reagent[71,72]. Although there had been a few reports on microbial synthesis of nanoparticles, direct use of biogenic nanoparticles on bioremediation has not yet been reported. Therefore, development of genetically engineered *D. radiodurans* strain capable of synthesizing nanoparticles and its application on removal of radioactive wastes is worth investigating for the advances on bioremediation technology.

## 4. Conclusion

During the last few decades, concerns on the treatment of radioactive waste has been gradually increased as the radioactive materials are significant part of our life and the management of radioactive waste is critical for sustainability of public and environment health. Recent advances in biotechnology, especially focus on extremophilic bacterium, allow us to develop bioremediation processes which has advantages over the currently used physicochemical processes in terms of 1) cost-effectiveness, 2) natural process without less side effects, 3) sufficiently applicable to inaccessible contaminated areas. Therefore, *D. radiodurans* has potential to be used as promising host microorganism for removal of radioactive waste (Figure 1). Furthermore, advances in bioremediation will be achieved by engineering of microorganisms to have novel abilities worth investigating for industrial applications.

## Acknowledgement

This work has been performed with the financial support in Seoul Green Environment Center (SGEC), KOREA.

The authors declare no financial and commercial conflict of interest.

## References

1. N. Yoshida and J. Kanda, Tracking the Fukushima radionuclides, *Science*, **336**, 1115-1116 (2012).
2. K. O. Buesseler, S. R. Jayne, N. S. Fisher, I. I. Rypina, H. Baumann, Z. Baumann, C. F. Breier, E. M. Douglass, J. George, A. M. Macdonald, H. Miyamoto, J. Nishikawa, S. M. Pike, and S. Yoshida, Fukushima-derived radionuclides in the ocean and biota

- off Japan, *Proc. Natl. Acad. Sci., U. S. A.*, **109**, 5984-5988 (2012).
3. F. F. Evans, S. Rosado, G. V. Sebastian, R. Casella, PLOA Machado, C. Holmstrom, S. Kjelleberg, J. D. Van Elsas, and L. Seldin, Impact of oil contamination and biostimulation on the diversity of indigenous bacterial communities in soil microcosms, *FEMS Microbiol. Ecol.*, **49**, 295-305 (2004).
  4. S. K. Brar, M. Verma, R. Y. Surampalli, K. Misra, R. D. Tyagi, N. Meunier, and J. F. Blais, Bioremediation of hazardous wastes: A review, *Pract. Period. Hazard. Toxic Radioact. Waste Manag.*, **10**, 59-72 (2006).
  5. D. Prakash, P. Gabani, A. K. Chandel, Z. Ronen, and O. V. Singh, Bioremediation: a genuine technology to remediate radionuclides from the environment, *Microb. Biotechnol.*, **6**, 349-360 (2013).
  6. G. M. Gadd, Bioremedial potential of microbial mechanisms of metal mobilization and immobilization, *Curr. Opin. Biotechnol.*, **11**, 271-279 (2000).
  7. J. R. Lloyd, J. Ridley, T. Khizniak, N. N. Lyalikova, and L. E. Macaskie, Reduction of technetium by *Desulfovibrio desulfuricans*: biocatalyst characterization and use in a flow-through bioreactor, *Appl. Environ. Microbiol.*, **65**, 2691-2696 (1999).
  8. R. AP. Thomas, A. J. Beswick, G. Basnakova, R. Moller, and L. E. Macaskie, Growth of naturally occurring microbial isolates in metal-citrate medium and bioremediation of metal-citrate wastes, *J. Chem. Technol. Biotechnol.*, **75**, 187-195 (2000).
  9. G. Raghu, V. Balaji, G. Venkateswaran, A. Rodrigue, and P. M. Mohan, Bioremediation of trace cobalt from simulated spent decontamination solutions of nuclear power reactors using *E. coli* expressing NiCoT genes, *Appl. Microbiol. Biotechnol.*, **81**, 571-578 (2008).
  10. M. Daly, Engineering radiation-resistant bacteria for environmental biotechnology, *Curr. Opin. Biotechnol.*, **11**, 280-285 (2000).
  11. H. Brim, A. Venkateswaran, H. M. Kostandarithes, J. K. Fredrickson, and M. J. Daly, Engineering *Deinococcus geothermali*s for bioremediation of high-temperature radioactive waste environments, *Appl. Environ. Microbiol.*, **69**, 4575-4582 (2003).
  12. E. Gerber, R. Bernard, S. Castang, N. Chabot, F. Coze, A. Dreux-Zighe, E. Hauser, P. Hivin, P. Joseph, C. Lazarelli, G. Letellier, J. Olive, and J.-P. Leonetti, *Deinococcus* as new chassis for industrial biotechnology: biology, physiology and tools, *J. Appl. Microbiol.*, **119**, 1-10 (2015).
  13. D. M. Sweet and B. E. Moseley, The resistance of *Micrococcus radiodurans* to killing and mutation by agents which damage DNA, *Mutat. Res.*, **34**, 175-186 (1976).
  14. J. R. Battista, Against all odds: the survival strategies of *Deinococcus radiodurans*, *Annu. Rev. Microbiol.*, **51**, 203-224 (1997).
  15. M. M. Cox and J. R. Battista, *Deinococcus radiodurans*-the consummate survivor, *Nat. Rev. Microbiol.*, **3**, 882-892 (2005).
  16. D. Slade and M. Radman, Oxidative stress resistance in *Deinococcus radiodurans*, *Microbiol. Mol. Biol. Rev.*, **75**, 133-191 (2011).
  17. C. C. Lange, L. P. Wackett, K. W. Minton, and M. J. Daly, Engineering a recombinant *Deinococcus radiodurans* for organo-pollutant degradation in radioactive mixed waste environments, *Nat. Biotechnol.*, **16**, 929-933 (1998).
  18. B. W. Brooks and R. G. E. Murray, Nomenclature for *Micrococcus radiodurans* and other radiation resistant cocci: *Deinococcaceae* fam. nov. and *Deinococcus* gen. nov., including five species, *Int. J. Syst. Bacteriol.*, **31**, 353-360 (1981).
  19. S. H. Yoo, H. Y. Weon, S. J. Kim, Y. S. Kim, B. Y. Kim, and S. W. Kwon, *Deinococcus aerolatus* sp. nov. and *Deinococcus aerophilus* sp. nov., isolated from air samples, *Int. J. Syst. Evol. Microbiol.*, **60**, 1191-1195 (2010).
  20. W. T. Im, H. M. Jung, L. N. Ten, M. K. Kim, N. Bora M. Goodfellow, S. Y. Lim, J. W. Jung, and S. T. Lee, *Deinococcus aquaticus* sp. nov., isolated from fresh water, and *Deinococcus caeni* sp. nov., isolated from activated sludge, *Int. J. Syst. Evol. Microbiol.*, **58**, 2348-2353 (2008).
  21. A. D. Groot, V. Chapon, P. Servant, R. Christen, M. F. Saux, S. Sommer, and T. Heulin, *Deinococcus deserti* sp. nov., a gamma-radiation-tolerant bacterium isolated from the Sahara Desert, *Int. J. Syst. Evol. Microbiol.*, **55**, 2441-2446 (2005).
  22. F. A. Rainey, K. Ray, M. Ferreira, B. Z. Gatz, M. F. Nobre, D. Bagaley, B. A. Rash, M. J. Park, A. M. Earl, N. C. Shank, A. M. Small, M. C. Henk, J. R. Battista, P. Kämpfer, and M. S. da Costa, 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.*, **71**, 5225-5235 (2005).
  23. K. Suresh, G. S. Reddy, S. Sengupta, and S. Shivaji, *Deinococcus indicus* sp. nov., an arsenic resistant bacterium from aquifer in West Bengal, India, *Int. J. Syst. Evol. Microbiol.*, **54**, 457-461 (2004).
  24. A. C. Ferreira, M. F. Nobre, F. A. Rainey, M. T. Silva, R. Wait, J. Burghardt, A. P. Chung, and M. S. da Costa, *Deinococcus geothermali*s sp. nov. and *Deinococcus murrayi* sp. nov., two extremely radiation-resistant and slightly thermophilic species from hot springs, *Int. J. Syst. Bacteriol.*, **47**, 939-947 (1997).
  25. P. Hirsch, C. A. Gallikowski, J. Siebert, K. Peissl, R. Kroppenstedt, P. Schumann, E. Stackebrandt, and R. Anderson, *Deinococcus frigens* sp. nov., *Deinococcus saxicola* sp. nov., and *Deinococcus marmoris* sp. nov., low temperature and draught-tolerating, UV resistant bacteria from continental Antarctica, *Syst. Appl. Microbiol.*, **27**, 636-645 (2004).
  26. M. Kolari, U. Schmidt, E. Kuismanen, and M. S. Salkinoja-Salonen, Firm but slippery attachment of *Deinococcus geothermali*s, *J. Bacteriol.*, **184**, 2473-2480 (2002).
  27. O. White, J. A. Eisen, J. F. Heidelberg, E. K. Hickey, J. D. Peterson, R. J. Dodson, D. H. Haft, M. L. Gwinn et al., Genome sequence of the radioresistant bacterium *Deinococcus radiodurans* R1, *Science*, **286**, 1571-1577 (1999).
  28. X. Hua and Y. Hua, Improved complete genome sequence of the extremely radioresistant bacterium *Deinococcus radiodurans* R1 obtained using PacBio single-molecule sequencing, *Genome Announc.*, **4**, e00886-16 (2016).
  29. K. S. Makarova, M. V. Omelchenko, E. K. Gaidamakova, V. Y. Matrosova, A. Vasilenko, M. Zhai, A. Lapidus, A. Copeland, E. Kim, M. Land, K. Mavromatis, S. Pitluck, P. M. Richardson, and M. J. Daly, *Deinococcus geothermali*s: The pool of extreme radiation resistance genes shrinks, *PLoS One*, **2**, e955 (2007).
  30. A. de Groot, R. Dulermo, P. Ortet, L. Blanchard, P. Guérin, B. Fernandez, B. Vacherie, and C. Dossat, E. Jolivet, P. Siguire, M. Chandler, M. Barakat, A. Dedieu, and J. Armengaud, Alliance of proteomics and genomics to unravel the specificities of Sahara bacterium *Deinococcus deserti*, *PLoS Genet.*, **5**, e1000434 (2009).
  31. R. Pukall, A. Zeytun, S. Lucas, A. Lapidus, N. Hammon, S.

- Deshpande, M. Nolan, J. F. Cheng, S. Pitluck, K. Liolios, L. Pagani, N. Mikhailova, N. Ivanova, K. Mavromatis, A. Pati, R. Tapia, C. Han, L. Goodwin, A. Chen, K. Palaniappan, M. Land, L. Hauser, Y. J. Chang, C. D. Jeffries, E. M. Brambilla, M. Rohde, M. Goker, J. C. Detter, T. Woyke, J. Bristow, J. A. Eisen, V. Markowitz, P. Hugenholtz, N. C. Kyrpides, and H. P. Klenk, Complete genome sequence of *Deinococcus maricopensis* type strain (LB-34T), *Stand. Genomic Sci.*, **4**, 163-172 (2011).
32. M. Yuan, M. Chen, W. Zhang, W. Lu, J. Wang, M. Yang, P. Zhao, R. Tang, X. Li, Y. Hao, Z. Zhou, Y. Zhan, H. Yu, and M. Lin, Genome sequence and transcriptome analysis of the radio-resistant bacterium *Deinococcus gobiensis*: Insights into the extreme environmental adaptations, *PLoS One*, **7**, e34458 (2012).
33. A. Copeland, A. Zeytun, M. Yassawong, M. Nolan, S. Lucas, N. Hammon, S. Deshpande, J. F. Cheng, C. Han, R. Tapia, L. A. Goodwin, S. Pitluck, K. Mavromatis, K. Liolios, I. Pagani, N. Ivanova, A. Pati, A. Chen, K. Palaniappan, M. Land, L. Hauser, C. D. Jeffries, E. M. Brambilla, M. Rohde, J. Sikorski, R. Pukall, M. Goker, J. C. Detter, T. Woyke, J. Bristow, J. A. Eisen, V. Markowitz, N. C. Kyrpides, H. P. Klenk, and A. Lapidus, Complete genome sequence of the orange-red pigmented, radio-resistant *Deinococcus proteolyticus* type strain (MRP<sup>T</sup>), *Stand. Genomic Sci.*, **6**, 240-250 (2012).
34. X. Xu, L. Jiang, Z. Zhang, Y. Shi, and H. Huang, Genome sequence of a gamma- and UV-ray-resistant Strain, *Deinococcus wulumuqiensis* R12, *Genome Announc.*, **1**, e00206-13 (2013).
35. Y. Hu, X. Xu, P. Song, L. Jiang, Z. Zhang, and H. Huang, Draft genome sequence of *Deinococcus xibeiensis* R13, a new carotenoid-producing strain, *Genome Announc.*, **1**, e00987-13 (2013).
36. V. G. Stepanov, P. Vaishampayan, K. Venkateswaran, and G. E. Fox, Draft genome sequence of *Deinococcus phoenicis*, a novel strain isolated during the phoenix lander spacecraft assembly, *Genome Announc.*, **2**, e00301-14 (2014).
37. K. Satoh, T. Onodera, K. Omoso, K. T. Yano, T. Katayama, Y. Oono, and I. Narumi, Draft genome sequence of the radioresistant bacterium *Deinococcus grandis*, isolated from freshwater fish in Japan, *Genome Announc.*, **4**, e01631-15 (2016).
38. J. A. Imlay, Cellular defenses against superoxide and hydrogen peroxide, *Annu. Rev. Biochem.*, **77**, 755-776 (2008).
39. M. M. Cox, J. L. Keck, and J. R. Battista, Rising from the Ashes: DNA Repair in *Deinococcus radiodurans*, *PLoS Genet.*, **6**, e1000815 (2010).
40. D. Ghosal, M. V. Omelchenko, E. K. Gaidamakova, V. Y. Matrosova, A. Vasilenko, A. Venkateswaran, M. Zhai, H. M. Kostandarithes, H. Brim, K. S. Makarova, L. P. Wackett, J. K. Fredrickson, and M. J. Daly, How radiation kills cells: survival of *Deinococcus radiodurans* and *Shewanella oneidensis* under oxidative stress, *FEMS Microbiol. Rev.*, **29**, 361-375 (2005).
41. K. Zahradka, D. Slade, A. Bailone, S. Sommer, D. Averbeck, M. Petranovic, A. B. Lindner, and M. Radman, Reassembly of shattered chromosomes in *Deinococcus radiodurans*, *Nature*, **443**, 569-573 (2006).
42. E. Griffiths and R. S. Gupta, Identification of signature proteins that are distinctive of the *Deinococcus-Thermus* phylum, *Int. Microbiol.*, **10**, 201-208 (2007).
43. A. M. Earl, M. M. Mohundro, I. S. Mian, and J. R. Battista, The IrrE protein of *Deinococcus radiodurans* R1 is a novel regulator of *recA* expression, *J. Bacteriol.*, **184**, 6216-6224 (2002).
44. Y. Hua, I. Narumi, G. Gao, B. Tian, K. Satoh, S. Kitayama, and B. Shen, PprI: a general switch responsible for extreme radio-resistance of *Deinococcus radiodurans*, *Biochem. Biophys. Res. Commun.*, **306**, 354-360 (2003).
45. H. Lu, G. Gao, G. Xu, L. Fan, L. Yin, B. Shen, and Y. Hua, *Deinococcus radiodurans* PprI switches on DNA damage-response and cellular survival networks after radiation damage, *Mol. Cell. Proteom.*, **8**, 481-494 (2009).
46. Y. Wang, Q. Xu, H. Lu, L. Lin, L. Wang, H. Xu, X. Cui, H. Zhang, T. Li, and Y. Hua, Protease activity of PprI facilitates DNA damage response: Mn<sup>(2+)</sup>-dependence and substrate sequence-specificity of the proteolytic reaction, *PLoS One*, **10**, e0122071 (2015).
47. M. Ludanyi, L. Blanchard, R. Dulermo, G. Brandelet, L. Bellanger, D. Pignol, D. Lemaire, and A. de Groot, Radiation response in *Deinococcus deserti*: IrrE is a metalloprotease that cleaves repressor protein DdrO, *Mol. Microbiol.*, **94**, 434-449 (2014).
48. A. Devigne, S. Ithurbide, T. C. Bouthier, F. Passot, M. Mathieu, S. Sommer, and P. Servant, DdrO is an essential protein that regulates the radiation desiccation response and the apoptotic-like cell death in the radioresistant *Deinococcus radiodurans* bacterium, *Mol. Microbiol.*, **96**, 1069-1084 (2015).
49. L. Wang, X. Guangzhi, H. Chen, Y. Zhao, N. Xu, B. Tian, and Y. Hua, DrRRA: a novel response regulator essential for the extreme radioresistance of *Deinococcus radiodurans*, *Mol. Microbiol.*, **67**, 1211-1222 (2008).
50. S. S. Desai, Y. S. Rajpurohit, H. S. Misra, and D. N. Deobagkar, Characterization of the role of the RadS/RadR two-component system in the radiation resistance of *Deinococcus radiodurans*, *Microbiology*, **157**, 2974-2982 (2011).
51. C. H. Tsai, R. Liao, B. Chou, and L. M. Contreras, Transcriptional analysis of *Deinococcus radiodurans* reveals novel small RNAs that are differentially expressed under ionizing radiation, *Appl. Environ. Microbiol.*, **81**, 1754-1764 (2015).
52. A. Martinez and R. Kolter, Protection of DNA during oxidative stress by the nonspecific DNA-binding protein Dps, *J. Bacteriol.*, **179**, 5188-5194 (1997).
53. J. K. Fredrickson, S. M. Li, E. K. Gaidamakova, V. Y. Matrosova, M. Zhai, H. M. Sulloway, J. C. Scholten, M. G. Brown, D. L. Balkwill, and M. J. Daly, Protein oxidation: key to bacterial desiccation resistance?, *ISME J.*, **2**, 393-403 (2008).
54. M. J. Daly, E. K. Gaidamakova, V. Y. Matrosova, A. Vasilenko, M. Zhai, A. Venkateswaran, M. Hess, M. V. Omelchenko, H. M. Kostandarithes, K. S. Makarova, L. P. Wackett, J. K. Fredrickson, and D. Ghosal, Accumulation of Mn(II) in *Deinococcus radiodurans* facilitates gamma-radiation resistance, *Science*, **306**, 1025-1028 (2004).
55. M. J. Daly, E. K. Gaidamakova, V. Y. Matrosova, J. G. Kiang, R. Fukumoto, D. Y. Lee, N. B. Wehr, G. A. Viteri, B. S. Berlett, and R. L. Levine, Small-molecule antioxidant proteome-shields in *Deinococcus radiodurans*, *PLoS One*, **5**, e12570 (2010).
56. L. Lemee, E. Peuchant, M. Clerc, M. Brunner, and H. Pfander, Deinoxanthin: a new carotenoid isolated from *Deinococcus radiodurans*, *Tetrahedron*, **53**, 919-926 (1997).
57. L. Zhang, Q. Yang, X. Luo, C. Fang, Q. Zhang, and Y. Tang, Knockout of *crtB* or *crtI* gene blocks the carotenoid biosynthetic pathway in *Deinococcus radiodurans* R1 and influences its resistance to oxidative DNA-damaging agents due to change of free rad-

- icals scavenging ability, *Arch. Microbiol.*, **188**, 411-419 (2007).
58. B. Tian, Z. Xu, Z. Sun, J. Lin, and Y. Hua, Evaluation of the antioxidant effects of carotenoids from *Deinococcus radiodurans* through targeted mutagenesis, chemiluminescence, and DNA damage analyses, *Biochim. Biophys. Acta*, **1770**, 902-911 (2007).
  59. D. Appukuttan, A. S. Rao, and S. K. Apte, Engineering of *Deinococcus radiodurans* R1 for bioprecipitation of uranium from dilute nuclear waste, *Appl. Environ. Microbiol.*, **72**, 7873-7878 (2006).
  60. H. Brim, S. C. McFarlan, J. K. Fredrickson, K. W. Minton, M. Zhai, L. P. Wackett, and M. J. Daly, Engineering *Deinococcus radiodurans* for metal remediation in radioactive mixed waste environments, *Nat. Biotechnol.*, **18**, 85-90 (2000).
  61. C. C. Lange, L. P. Wackett, K. W. Minton, and M. J. Daly, Engineering a recombinant *Deinococcus radiodurans* for organo-pollutant degradation in radioactive mixed waste environments, *Nat. Biotechnol.*, **16**, 929-933 (1998).
  62. G. Raghu, S. S. Singh, S. K. Lunavat, M. M. Pamarthi, A. Rodrigue, B. Vadivelu, P. B. Phanithi, V. Gopala, and S. K. Apte, Engineered *Deinococcus radiodurans* R1 with NiCoT genes for bioremoval of trace cobalt from spent decontamination solutions of nuclear power reactors, *Appl. Microbiol. Biotechnol.*, **99**, 9203-9213 (2015).
  63. L. Newsome, K. Morris, and J. R. Lloyd, The biogeochemistry and bioremediation of uranium and other priority radionuclides, *Chem. Geol.*, **363**, 164-184 (2014).
  64. L. Xiangqian, X. Huizhong, Z. S. Chen, and G. Chen, Biosynthesis of Nanoparticles by Microorganisms and Their Applications, *J. Nanomater.*, **2011**, 1-16 (2011).
  65. M. H. Choi, H. E. Shim, S. J. Yun, S. H. Park, D. S. Choi, B. S. Jang, Y. J. Choi, and J. J. Jeon, Gold-nanoparticle-immobilized Desalting columns for highly efficient and specific removal of radioactive iodine in aqueous media, *ACS Appl. Mater. Interfaces*, **8**, 29227-29231 (2016).
  66. L. Du, H. Jiang, X. Liu, and E. Wang, Biosynthesis of gold nanoparticles assisted by *Escherichia coli* DH5 $\alpha$  and its application on direct electrochemistry of hemoglobin, *Electrochem. Commun.*, **9**, 1165-1170 (2007).
  67. M. I. Husseiny, M. A. El-Aziz, Y. Badr, and M. A. Mahmoud, Biosynthesis of gold nanoparticles using *Pseudomonas aeruginosa*, *Spectrochim. Acta A*, **67**, 1003-1006 (2007).
  68. S. Bose, M. F. Hochella, Y. A. Gorby, D. W. Kennedy, D. E. McCready, A. S. Madden, and B. H. Lower, Bioreduction of hematite nanoparticles by the dissimilatory iron reducing bacterium *Shewanella oneidensis* MR-1, *Geochim. Cosmochim. Acta*, **73**, 962-976 (2009).
  69. M. M. G. Babu and P. Gunasekaran, Production and structural characterization of crystalline silver nanoparticles from *Bacillus cereus* isolate, *Colloids Surf. B*, **74**, 191-195 (2009).
  70. S. He, Z. Guo, Y. Zhang, S. Zhang, J. Wang, and N. Gu, Biosynthesis of gold nanoparticles using the bacteria *Rhodospseudomonas capsulate*, *Mater. Lett.*, **61**, 3984-3987 (2007).
  71. R. R. Kulkarni, N. S. Shaiwale, D. N. Deobagkar, and D. D. Deobagkar, Synthesis and extracellular accumulation of silver nanoparticles by employing radiation-resistant *Deinococcus radiodurans*, their characterization, and determination of bioactivity, *Int. J. Nanomed.*, **10**, 963-974 (2015).
  72. J. Li, Q. Li, X. Ma, B. Tian, T. Li, J. Yu, S. Dai, Y. Weng, and Y. Hua, Biosynthesis of gold nanoparticles by the extreme bacterium *Deinococcus radiodurans* and an evaluation of their antibacterial properties, *Int. J. Nanomed.*, **11**, 5931-5944 (2016).
  73. C. S. Misra, D. Appukuttan, V. S. Kantamreddi, A. S. Rao, and S. K. Apte, Recombinant *D. radiodurans* cells for bioremediation of heavy metals from acidic/neutral aqueous wastes, *Bioeng. Bugs*, **3**, 44-48 (2012).
  74. J. K. Fredrickson, H. M. Kostandarithes, S. W. Li, A. E. Plymale, and M. J. Daly, Reduction of Fe(III), Cr(VI), U(VI), and Tc(VII) by *Deinococcus radiodurans* R1, *Appl. Environ. Microbiol.*, **66**, 2006-2011 (2000).
  75. R. B. Payne, D. M. Gentry, B. J. Rapp-Giles, L. Casalot, and J. D. Wall, Uranium reduction by *Desulfovibrio desulfuricans* strain G20 and a cytochrome c3 mutant, *Appl. Environ. Microbiol.*, **68**, 3129-3132 (2002).
  76. D. R. Lovley and E. J. Phillips, Reduction of uranium by *Desulfovibrio desulfuricans*, *Appl. Environ. Microbiol.*, **58**, 850-856 (1992).
  77. K. S. Nilgiriwala, A. Alahari, A. S. Rao, and S. K. Apte, Cloning and overexpression of alkaline phosphatase PhoK from *Sphingomonas* sp. strain BSAR-1 for bioprecipitation of uranium from alkaline solutions, *Appl. Environ. Microbiol.*, **74**, 5516-5523 (2008).
  78. A. S. Madden, A. I. Swindle, M. J. Beazley, J. W. Moon, B. Ravel, and T. J. Phelps, Longterm solid-phase fate of co-precipitated U(VI)-Fe(III) following biological iron reduction by *Thermoanaerobacter*, *Am. Mineral.*, **97**, 1641-1652 (2012).
  79. T. V. Khijniak, A. I. Slobodkin, V. Coker, J. C. Renshaw, F. R. Livens, E. A. Bonch-Osmolovskaya, N. K. Birkeland, N. N. Medvedeva-Lyalikova, and J. R. Lloyd, Reduction of uranium(VI) phosphate during growth of the thermophilic bacterium *Thermoterrabacterium ferrireducens*, *Appl. Environ. Microbiol.*, **71**, 6423-6426 (2005).
  80. L. E. Macaskie, R. M. Empson, A. K. Cheetham, C. P. Grey, and A. J. Skarnulis, Uranium bioaccumulation by a *Citrobacter* sp. as a result of enzymically mediated growth of polycrystalline H<sub>2</sub>UO<sub>4</sub>, *Science*, **257**, 782-784 (1992).
  81. J. R. Lloyd, C. Leang, C., A. L. Hodges Myerson, M. V. Coppi, S. Cuifo, B. Methe, S. J. Sandler, and D. R. Lovley, Biochemical and genetic characterization of PpcA, a periplasmic c-type cytochrome in *Geobacter sulfurreducens*, *Biochem. J.*, **369**, 153-161 (2003).
  82. J. R. Lloyd, P. Yong, and L. E. Macaskie, Biological reduction and removal of Np(V) by two microorganisms, *Environ. Sci. Technol.*, **34**, 1297-1301 (2000).
  83. J. R. Lloyd, J. Ridley, T. Khizniak, N. N. Lyalikova, and L. E. Macaskie, Reduction of technetium by *Desulfovibrio desulfuricans*: biocatalyst characterization and use in a flowthrough bioreactor, *Appl. Environ. Microbiol.*, **65**, 2691-2696 (1999).
  84. N. N. Lyalikova and T. V. Khizhnyak, Reduction of heptavalent technetium by acidophilic bacteria of the genus *Thiobacillus*, *Microbiology*, **65**, 468-473 (1996).
  85. M. J. Marshall, A. C. Dohnalkova, D. W. Kennedy, A. E. Plymale, S. H. Thomas, F. E. Löffler, R. A. Sanford, J. M. Zachara, J. K. Fredrickson, and A. S. Beliaev, Electron donordependent radionuclide reduction and nanoparticle formation by *Anaeromyxobacter dehalogenans* strain 2CP-C, *Environ. Microbiol.*, **11**, 534-543 (2009).

86. H. Boukhalfa, G. A. Icopini, S. D. Reilly, and M. P. Neu, Plutonium (IV) reduction by the metal-reducing bacteria *Geobacter metallireducens* GS15 and *Shewanella oneidensis* MR1, *Appl. Environ. Microbiol.*, **73**, 5897-5903 (2007).
87. B. Luksiene, R. Druteikiene, D. Peciulyte, D. Baltrunas, V. Remeikis, and A. Paskevicius, Effect of microorganisms on the plutonium oxidation states, *Appl. Radiat. Isot.*, **70**, 442-449 (2012).
88. L. E. Macaskie, B. C. Jeong, and M. R. Tolley, Enzymically accelerated biomineralization of heavy metals: Application to the removal of americium and plutonium from aqueous flows, *FEMS Microbiol. Rev.*, **14**, 351-367 (1994).
89. T. Councell, E. Landa, and D. Lovley, Microbial reduction of iodate, *Water Air Soil Pollut.*, **100**, 99-106 (1997).
90. S. Anderson and V. D. Appanna, Microbial formation of crystalline strontium carbonate, *FEMS Microbiol. Lett.*, **116**, 43-48 (1994).
91. V. Achal, X. Pan, and D. Zhang, Bioremediation of strontium (Sr) contaminated aquifer quartz sand based on carbonate precipitation induced by Sr resistant *Halomonas* sp, *Chemosphere*, **89**, 764-768 (2012).
92. F. G. Ferris, C. M. Fratton, J. P. Gerits, S. Schultze Lam, and B. S. Lollar, Microbial precipitation of a strontium calcite phase at a groundwater discharge zone near Rock Creek, British Columbia, Canada, *Geomicrobiol. J.*, **13**, 57-67 (1995).
93. D. L. Vullo, H. M. Ceretti, E. A. Hughes, S. Ramyrez, and A. Zalts, Cadmium, zinc and copper biosorption mediated by *Pseudomonas veronii* 2E, *Bioresour. Technol.*, **99**, 5574-5581 (2008).
94. H. Guo, S. Luo, L. Chen, X. Xiao, Q. Xi, W. Wei, G. Zeng, C. Liu, Y. Wan, J. Chen, and Y. He, Bioremediation of heavy metals by growing hyperaccumulator endophytic bacterium *Bacillus* sp. L14, *Bioresour. Technol.*, **101**, 8599-8605 (2010).
95. V. Achal, X. Pan, and D. Zhang, Remediation of copper-contaminated soil by *Kocuria flava* CR1, based on microbially induced calcite precipitation, *Ecol. Eng.*, **37**, 1601-1605 (2011).
96. K. Hryniewicz, G. Dabrowska, C. Baum, K. Niedojadlo, and P. Leinweber, Interactive and single effects of ectomycorrhiza formation and *Bacillus cereus* on metallothionein MT1 expression and phytoextraction of Cd and Zn by Willows, *Water Air Soil Pollut.*, **223**, 957-968 (2012).
97. V. Achal, X. Pan, Q. Fu, and D. Zhang, Biomineralization based remediation of As (III) contaminated soil by *Sporosarcina ginsengisoli*. *J. Hazard. Mater.*, **201-202**, 178-184 (2012).
98. P. Kanmani, J. Aravind, and D. Preston, Remediation of chromium contaminants using bacteria, *Int. J. Environ. Sci. Technol.*, **9**, 183-193 (2012).