Genomics update

Some bacteria degrade explosives, others prefer boiling methanol

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The list of completely sequenced microbial genomes, released in August and September of 2007 (Table 1), is relatively short. Still, it includes some remarkable environmental microorganisms, such as the sulfur-reducing crenarchaeon *Ignicoccus hospitalis*, host of the smallest archaeon *Nanoarchaeum equitans*, the soil bacterium *Bacillus pumilus* isolated from a supposedly sterile environment of the spacecraft assembly facility in Pasadena, California, a marine bacterium that degrades nitramine explosives and two enterobacteria that are commonly found in soil and water habitats but can also infect humans, particularly newborns, causing sepsis and neonatal meningitis.

The largest of the recently sequenced genomes comes from the early-diverging amitochondrial eukaryote Giardia lamblia (Morrison et al., 2007). Like most other eukaryotic genomes, it has been released in a draft form that consists of 306 contigs, representing 5 chromosomes of G. lamblia. In accordance with earlier reports, G. lamblia encodes a simplified archaeal-like DNA replication machinery, a yeast-like machinery for transcription synthesis and RNA processing and a limited set of largely bacterial-like metabolic enzymes. Since G. lamblia is an intestinal parasite, its primitive features could be equally well rationalized as either an ancestral state of the eukaryotic cell or as a result of a later adaptation to the parasitic lifestyle. So, although the genome of G. lamblia is certainly an important step towards understanding the origin and early evolution of the eukaryotic cell, genomes of other early-diverging eukaryotes would be needed to allow meaningful comparative analysis.

Ignicoccus hospitalis, isolated from a submarine hydrothermal vent to the north of Iceland and originally organism in its own right. It is an obligately anaerobic hyperthermophilic chemolitoautotroph that uses CO2 as a source of carbon and derives energy from reducing elemental sulfur with H₂ as the sole electron donor (Paper et al., 2007). It belongs to a recently described genus that forms a deeply branching lineage within the crenarchaeal family Desulfurococcaceae (Huber et al., 2000) and has an outer membrane (Näther and Rachel, 2004) and an unusual pathway of autotrophic CO₂ fixation (Jahn et al., 2007). Still, Ignicoccus never attracted as much attention as the tiny (~400 nm) coccoidal cells of Nanoarchaeum equitans found on its surface. Based on its unique 16S rRNA sequence and the extremely small size of its genome (less than 0.5 Mbp), N. equitans was assigned to a separate phylum of archaea, the Nanoarchaeota (Huber et al., 2002). Subsequent genome sequencing revealed an extremely reduced genome of only 491 kb with 536 protein-coding genes (Waters et al., 2003). These genes encoded the components of information processing and DNA repair machinery, but not enzymes of lipid, cofactor, amino acid, or nucleotide biosynthesis. These observations showed that N. equitans must acquire most of its biosynthetic precursors from its host and cannot exist without it, establishing its interaction with I. hospitalis as a kind of symbiotic or parasitic relationship. Although the lack of the core metabolic genes suggested that N. equitans was a highly evolved organism, adapted to the parasitic lifestyle, an analysis of its ribosomal genes supported its deep branching at the base of the archaeal phylogenetic tree (Huber et al., 2003; Waters et al., 2003). Subsequent analysis led some researchers to position N. equitans near the root of the universal Tree of Life (Di Giulio, 2007), while others argued that it simply belongs to a fast-evolving lineage within the Euryarchaeota (Brochier et al., 2005; Makarova and Koonin, 2005). The genome of *I. hospitalis* is expected to shed light on the mechanisms and evolutionary history of its association with N. equitans. In addition, it should show whether I. hospitalis acquired any of its metabolic genes through lateral gene transfer from N. equitans. However, for a better resolution of ancestral archaeal phylogeny, we should probably wait for the upcoming release by the JGI of the genome of

described as Ignicoccus sp. KIN4/I, is an interesting

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Table 1. Recently completed microbial genomes (August-September 2007).

Species name	Taxonomy	GenBank accession	Genome size, bp	Proteins (total)	Sequencing centre ^a	Reference
New organisms						
Giardia lamblia	Eukaryota, Diplomonadida	AACB02000000	11 700 000	6470	MBL	Morrison <i>et al.</i> (2007)
Ignicoccus hospitalis	Crenarchaeota	CP000816	1 297 538	1434	JGI	Unpublished
Roseiflexus castenholzii	Chloroflexi	CP000804	5 723 298	4330	JGI	Unpublished
Bacillus pumilus	Firmicutes	CP000813	3 704 465	3681	Baylor	Gioia et al. (2007)
Streptococcus gordonii	Firmicutes	CP000725	2 196 662	2051	JCVI	Unpublished
Rickettsia akari	α -Proteobacteria	CP000847	1 231 060	1259	U. Iowa	Unpublished
Rickettsia canadensis	α -Proteobacteria	CP000409	1 159 772	1093	U. Iowa	Eremeeva <i>et al.</i> (2005)
Rickettsia massiliae	α -Proteobacteria	CP000683	1 360 898	980	CNRS- Marseille	Blanc <i>et al.</i> (2007a)
		CP000684	15 286			
Rickettsia rickettsii	α -Proteobacteria	CP000848	1 257 710	1345	U. Iowa	Unpublished
Citrobacter koseri	γ-Proteobacteria	CP000822	4 720 462	5031	WashU	Unpublished
		CP000823	9 294			
		CP000824	5 601			
Enterobacter sakazakii	γ-Proteobacteria	CP000783	4 368 373	4442	WashU	Unpublished
		CP000785	131 196			
		CP000784	31 208			
Serratia proteamaculans	γ-Proteobacteria	CP000826	5 448 853	4942	JGI	Unpublished
		CP000827	46 804			
Shewanella pealeana	γ-Proteobacteria	CP000851	5 174 581	4241	JGI	Unpublished
Shewanella sediminis	γ-Proteobacteria	CP000821	5 517 674	4497	JGI	Unpublished
Vibrio harveyi	γ-Proteobacteria	CP000789	3 765 351	6064	WashU	Unpublished
		CP000790	2 204 018			
		CP000791	89 008			
Arcobacter butzleri	ε -Proteobacteria	CP000361	2 341 251	2259	USDA-ARS	Kaakoush <i>et al.</i> (2007)
Campylobacter concisus	ε -Proteobacteria	CP000792	2 052 007	1985	JCVI	Unpublished
		CP000793	30 949			
		CP000794	16 457			
Thermotoga lettingae	Thermotogae	CP000812	2 135 342	2040	JGI	Unpublished
New strains						
Prochlorococcus marinus str. MIT 9215	Cyanobacteria	CP000825	1 738 790	1983	JGI	Unpublished
Staphylococcus aureus subsp. aureus Mu3	Firmicutes	AP009324	2 880 168	2698	Juntendo U.	Unpublished
Rickettsia bellii OSU 85-389	α -Proteobacteria	CP000849	1 528 980	1476	U. Iowa	Unpublished
Escherichia coli E24377A	γ-Proteobacteria	CP000795-	5 249 288	4997	JCVI	Unpublished
		CP000801	(total)			-
Escherichia coli HS	γ-Proteobacteria	CP000802	4 643 538	4384	JCVI	Unpublished
Francisella tularensis subsp. holarctica FTA	γ-Proteobacteria	CP000803	1 890 909	2079	JGI	Unpublished
Campylobacter jejuni subsp. jejuni 81116	ε -Proteobacteria	CP000814	1 628 115	1626	IFR-Norwich	Pearson <i>et al.</i> (2007)

^a Sequencing centre names are abbreviated as follows: Baylor, Human Genome Sequencing Center, Baylor College of Medicine, Houston, Texas, USA; CNRS-Marseille, CNRS-UPR 2589, Institut de Biologie Structurale et Microbiologie, Marseille, France; IFR-Norwich, Institute of Food Research, Norwich Research Park, Norwich, U.K.; JCVI, J. Craig Venter Institute, Rockville, Maryland, USA; JGI, US Department of Energy Joint Genome Institute, Walnut Creek, California, USA; Juntendo U., Department of Bacteriology at Juntendo University, Bunkyo-ku, Tokyo, Japan; MBL, Marine Biological Laboratory, Woods Hole, Massachusetts, USA; U. Iowa, Environmental Health Sciences Research Center, The University of Iowa, Iowa City, Iowa, USA; USDA-ARS, US Department of Agriculture, Agricultural Research Service, Western Regional Research Center, Albany, California, USA; WashU, Washington University School of Medicine, St. Louis, Missouri, USA.

Korarchaeota OPF1-KOR, a representative of yet another ancient lineage, *Korarchaeota*, which is currently under embargo (see http://genome.jgi-psf.org/mic_cur1.html).

Roseiflexus castenholzii is a facultatively anaerobic moderately thermophilic filamentous phototrophic bacterium that belongs to the phylum *Chloroflexi*, also known as *green non-sulfur bacteria*, which unifies filamentous bacteria that lack peptidoglycan in their cell walls (Meissner *et al.*, 1988). This is the 5th completely sequenced genome from that phylum, coming on the

heels of the genome of *Roseiflexus* sp. strain RS-1 that has been released by the JGI earlier this year and three genomes of *Dehalococcoides* spp. The genome of *Chloroflexus aurantiacus*, the best-studied representative of the *Chloroflexi*, is available in GenBank (accession no. AAAH00000000) in an unfinished form. The sequenced strain *Roseiflexus castenholzii* DSM 13941 has been isolated from a red-colored bacterial mat developed in Nakabusa hot spring near Nagano, Japan (Hanada *et al.*, 2002). Although similar to *C. aurantiacus* in many

Journal compilation © 2007 Society for Applied Microbiology and Blackwell Publishing Ltd, *Environmental Microbiology*, 9, 2905–2910 No claim to original US government works features, including the cell shape, gliding motility and the ability to perform anoxygenic photosynthesis, *R. castenholzii* does not contain chlorosomes or bacteriochlorophyll *c*; its major photosynthetic pigment is bacteriochlorophyll *a. Roseiflexus castenholzii* also differs from other members of the family *Chloroflexaceae* in that its cells are actually red, owing to the high amount of γ -carotene (Hanada *et al.*, 2002). The organization of genes encoding the photosynthetic reaction center and the lightharvesting proteins of *R. castenholzii* differs from that in *C. aurantiacus* (Yamada *et al.*, 2005), which could help in understanding the evolution of anoxygenic photosynthesis and photosynthesis in general.

The next organism in the list (Table 1), Bacillus pumilus, is a common Gram-positive soil bacterium that is often associated with plant roots and has been studied primarily because of its role in plant defense against fungal and nematode parasites. Bacillus pumilus is often found in various foods and on some occasions has been identified as a source of food poisoning. The ability of *B. pumilis* to survive standard sterilization procedures has been attributed the high resistance of its spores to gamma irradiation and common solvents. These properties have become subject of intense interest in 1999-2002 when spores of B. pumilis and several other bacilli were isolated from the spacecraft surfaces at the Spacecraft Assembly Facility of the NASA Jet Propulsion Laboratory in Pasadena, California (Kempf et al., 2005). One of the strains, B. pumilus SAFR-032, isolated from a clean-room airlock, demonstrated unusually high resistance to UV radiation and was even able to withstand UV irradiation in the 200 to 400 nm range at the levels that were expected to be found on the surface of Mars (Newcombe et al., 2005). Although direct exposure to extremely short-wavelength (10-100 nm) UV irradiation that exists in high vacuum appears to effectively kill both spores and vegetative cells (Saffary et al., 2002), these data revived the idea that such spores could survive space travel under the surface of basalt rocks and be brought to Earth from other planets (Benardini et al., 2003). The complete genome of B. pumilus strain SAFR-032 has now been sequenced and its adaptations to UV irradiation and peroxide stress analyzed in detail (Gioia et al., 2007). Surprisingly, B. pumilus SAFR-032 encoded essentially the same set of genes related to DNA repair and H₂O₂ resistance as far less UV-resistant B. subtilis and B. licheniformis (Gioia et al., 2007). Still, certain differences in gene order and deduced protein sequences were identified and will be subject of further analysis. This observation is somewhat similar to the results of the just-published comparative analysis of the complete genomes of Deinococcus radiodurans and Deinococcus geothermalis (Makarova et al., 2007), which did not reveal any specific genes responsible for the extreme radioresistance of these two organisms. Anyway, whether or not *B. pumilus* could have come from other planets – or whether or not our space probes could contaminate the Martian atmosphere along the lines outlined by Ray Bradbury – the extreme resistance of this organism to sterilization protocols deserves a careful consideration.

The second Gram-positive bacterium on the list, *Strep-tococcus gordonii*, is a normal inhabitant of human oral cavity. It has been implicated in the development of dental caries and gum disease. From the oral cavity, *S. gordonii* can spread to the bloodstream, causing bacterial endocarditis. The sequenced strain *S. gordonii* Challis is commonly used as a model organism and is relatively well studied.

The past two months brought 5 new genomes of Rickettsia spp. (Table 1), doubling the total number of complete rickettsial genomes. This genus, named after Howard Taylor Ricketts (1871–1910), who described the first bacterium of this group exactly 100 years ago, consists of arthropod-borne α -*Proteobacteria*, some of which are important pathogens. Human diseases caused by rickettsiae include epidemic typhus (caused primarily by Rickettsia prowazekii and Rickettsia typhi), scrub typhus (Rickettsia tsutsugamushi), the Rocky Mountain spotted fever (Rickettsia rickettsii), Mediterranean spotted fever (Rickettsia conorii), and rickettsialpox (Rickettsia akari). Rickettsiae are obligately intracellular pathogens that are transmitted to their vertebrate hosts by ticks, mites or lice. In 2005 and 2006, Annals of the New York Academy of Sciences dedicated two special volumes to the anniversary of the Ricketts' discovery and the current research of rickettsiae (Hechemy et al., 2005, 2006). Analysis of rickettsial genomes has been used to uncover the principles of their evolution (Blanc et al., 2007b) and their relation to the mitochondria (Andersson et al., 1998). Now, analysis of the Rickettsia massiliae genome revealed a mobile genetic element containing tra gene cluster, shared with Rickettsia bellii (Blanc et al., 2007a). This work suggests that lateral gene transfer could have played an important role in the evolution of obligate intracellular bacteria.

The list of the recently sequenced γ -proteobacterial genomes includes 5 representatives of the family *Enterobacteriaceae*, as well as two marine bacteria, and a new strain of tularemia-causing *Francisella tularensis* (Table 1). Two of these, *Citrobacter koseri* (formerly *Citrobacter diversus*) and *Enterobacter sakazakii*, are common environmental organisms, found in soil, water and sewage samples. Although these organisms are often isolated from human feces, they are usually considered to be part of normal gut flora. However, they can turn into dangerous pathogens, particularly for infants. Thus, *C. koseri* is an opportunistic pathogen of the central nervous system that causes sepsis and meningitis in newborn

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children and in immuno-compromised adults (Doran, 1999). The sequenced strain *C. koseri* ATCC BAA-895 was isolated in 1983 from a case of neonatal meningitis. Similarly, *E. sakazakii* has been repeatedly isolated from infant formula, milk powder, cereals and other sources, and implicated in a number of foodborne diseases causing severe meningitis or enteritis (Nazarowec-White and Farber, 1997; Drudy *et al.*, 2006). The sequenced strain *E. sakazakii* ATCC BAA-894 was isolated from the cerebrospinal fluid in the case of fatal neonatal meningitis in an infant fed with a commercial powdered milk formula in Tennessee in 2001.

The third sequenced member of the *Enterobacteriaceae*, *Serratia proteamaculans*, is a common plant endophyte, isolated from the roots of the poplar tree (Moore *et al.*, 2006). This organism appears to promote plant growth, although the nature of the specific compounds involved in this process remains unknown. The availability of *S. proteamaculans* genome sequence should give a boost to the studies of bacteria-to-plant signals.

The two newly sequenced strains of Escherichia coli represent the extreme diversity of this species. Escherichia coli strain E24377A (serotype O139:H28) is an enterotoxigenic strain, capable of causing traveler's diarrhea, a nasty disease familiar to most international travelers. This strain produces two types of pili, used for colonization of the surface of small intestine, as well as heat-stable and heat-labile enterotoxins that are largely responsible for its virulence. Genome sequencing reveals a 5-Mb chromosome and 6 plasmids, ranging in size from 5 to 79 kb. These plasmids carry a number of uncharacterized genes, at least some of which might be involved in virulence. In contrast, Escherichia coli strain HS appears to be able to colonize the human gastrointestinal tract without causing any obvious disease and is a good model organism to study the colonization mechanisms.

Shewanella sediminis strain HAW-EB3 is a recently described marine γ -proteobacterium with potential use in bioremediation (Zhao et al., 2005). It has been isolated from the sediment of Emerald Basin, a former military dumping site of unexploded ordnance located in the Atlantic Ocean, 50 miles from the Halifax Harbor in Nova Scotia, Canada, at the depth of 215 m. This site is heavily contaminated with hexahydro-1,3,5-trinitro-1,3,5-triazine, which is used as an explosive agent and also as a rodenticide and is known under the trade names RDX, hexogen, hexolite, and cyclonite (see http://pubchem. ncbi.nlm.nih.gov/summary/summary.cgi?cid=8490 for the chemical formula and references). The isolated strain S. sediminis HAW-EB3 was able to degrade hexogen anaerobically at 10°C, suggesting that it could be used in remediation of various nitramine compounds (Zhao et al., 2004). Given that other Shewanella spp. reduce Cr(VI), U(VI), and other toxic metals, these organisms demonstrate a very impressive ability to clean up after humans.

Another new species of Shewanella isolated from the Emerald Basin, Shewanella halifaxensis (Zhao et al., 2006), turned out to be a relative of the souid symbiont Shewanella pealeana, which prompted sequencing of that genome as well. Shewanella pealeana inhabits accessory nidamental gland, an oval secretory organ in the female reproductive system of the squid Loligo pealei (Leonardo et al., 1999). This gland is remarkable for turning from colorless to red-orange during sexual maturation of the squid, most likely owing to accumulation of carotenoid pigments in the bacterial community inhabiting it (Barbieri et al., 2001). Although the exact function of accessory nidamental gland is unknown, it is believed to participate in the formation of egg capsular sheath, which contains a dense culture of bacteria that may protect cephalopod eggs from predators. Shewanella pealeana is a facultatively anaerobic, psychrotolerant bacterium that can grow anaerobically on lactate using elemental sulfur, iron, manganese, nitrate, fumarate, trimethylamine-N-oxide, or thiosulfate as electron acceptors (Leonardo et al., 1999). Comparison of this genome with 13 other completely sequenced genomes of Shewanella spp. should provide interesting clues into coevolution of S. pealeana and squid cells.

Vibrio harveyi is a widespread marine bacterium, often found associated with marine animals, such as octopi and shrimp. For a number of years, it has been a favorite model organism to study regulation of bioluminescence by quorum sensing (Dunlap, 1999). It has a very complex regulatory system (Waters and Bassler, 2006) that should now become much easier to comprehend.

The three new ε -proteobacterial genomes in the current list all come from the family Campylobacteriaceae. Arcobacter butzleri is an aerotolerant waterborne campylobacterium that is commonly found in pigs, cattle, sheep, and poultry, as well as in surface, drinking, and well water and in processed meat (Snelling et al., 2006). Consumption of contaminated water or infected poultry may lead to human infection. The sequenced strain A. butzleri RM4018 was isolated from a case of human gastroenteritis. Meanwhile, the Campylobacter sequencing project at the JCVI released the genome of the gastrointestinal clinical isolate Campylobacter concisus, the first genome from that species, whereas the Institute of Food Research in Norwich, UK, sequenced the genome of the commonly used laboratory strain Campylobacter jejuni subsp. jejuni 81116, which is infective for chicken (Pearson et al., 2007). This brings to 17 the total number of completely sequenced genomes of representatives of the families Campylobacteriaceae and Helicobacteriaceae, including genomes of two free-living bacteria, Thiomicrospira denitrificans and Wolinella succinogenes.

Journal compilation © 2007 Society for Applied Microbiology and Blackwell Publishing Ltd, *Environmental Microbiology*, 9, 2905–2910 No claim to original US government works Given the recent progress in sequencing the genomes of free-living ε -proteobacteria of unclear phylogenetic status that inhabit deep-sea thermal vents (Nakagawa *et al.*, 2005; 2007), this class of *Proteobacteria* is finally achieving reasonable genome coverage.

The *Thermotogales* sequencing project at the JGI released the complete genome of yet another representative of this early-branching bacterial phylum. *Thermotoga lettingae* strain TMO was isolated in 2002 from a sulfate-reducing bioreactor operated at 65°C with methanol as the sole carbon and energy source (Balk *et al.*, 2002). *Thermotoga lettingae* fermented methanol to acetate, CO_2 and H_2 . In the presence of electron acceptors, such as thiosulfate, elemental sulfur, or Fe(III), it was able to degrade methanol to CO_2 and H_2 (Balk *et al.*, 2002). The unique ability of *T. lettingae* to utilize methanol near its boiling point of 64.7°C makes it a very attractive object for biotechnology.

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