Genomics update

New feel for new phyla

Michael Y. Galperin*
National Center for Biotechnology Information, National Library of Medicine, National Institutes of Health, Bethesda, MD 20894, USA.

According to the dictionary, the Latin term 'phylum' comes from Greek phylon (φυλόν), which means 'race, tribe or clan' and is unrelated to either philia (φιλία) meaning 'love, affection' or to the 'feel', which comes from Old English felan 'to touch'. These similarly sounding words illustrate a key problem of systematic microbiology: How can we extract useful information from short sequence fragments and not be swayed by superficial similarities? One of the most useful approaches has been binning together sequences from related microorganisms, even if the nature of these organisms remained unknown. This resulted in a number of candidate microbial phyla that still have no cultivated representatives (Hugenholtz et al., 1998). Extensive sequencing has been the only way to get a 'feel' of these organisms, find out at least some information about their physiology and distribution in the environment. The ultimate goal, of course, is to get a complete genome sequence of the previously uncharacterized organism and use the power of comparative genome analysis to deduce its features.

The past 2 months have been marked by the release of complete genome sequences from first representatives of two new phyla, Verrucomicrobia and Candidate division Termite group 1 (Table 1). The first one is now represented by three different genomes, the second one – by two.

The phylum Verrucomicrobia, first recognized as a separate bacterial lineage more than 20 years ago (Albrecht et al., 1987; Hedlund et al., 1997), remains poorly characterized. Environmental sampling revealed representatives of this phylum in a wide range of environments, including soils, seawater, hot springs and human gastrointestinal tract (Wagner and Horn, 2006). However, few members of Verrucomicrobia have been isolated in pure culture and, until recently, there were few sequences from this phylum. To address this deficiency, JGI scientists have launched genome sequencing of five members of Verrucomicrobia (see http://www.jgi.doe.gov/sequencing/why/CSP2006/Verrucomicrobia.html). Genomes of two organisms (Akkermansia muciniphila and Opitutus terrae) have now been completed and three more genomes released in the draft form (Bacterium Ellin514, 7.5 Mbp, GenBank accession number ABOX00000000, Opitutaceae bacterium TAV2, 4.9 Mbp, ABEA00000000; and Verrucomicrobiurn spinosum, 8.2 Mbp, ABIZ00000000). A genome of one more member of Verrucomicrobia, an extremely acidophilic methanotroph Methylacidiphilum infernorum, has been sequenced at the University of Hawaii (Hou et al., 2008).

Akkermansia muciniphila is a strictly anaerobic bacterium, originally isolated from a human fecal sample, that can use gastric mucin as carbon, energy and nitrogen source (Derrien et al., 2004). It has been named after Dutch microbiologist Antoon D.L. Akkermans, professor at Wageningen University and a pioneer in studying molecular ecology of bacterial communities (see http://www.mib.wur.nl/UK/AF/). Recent studies showed that A. muciniphila is a common inhabitant of the human intestinal tract, comprising up to 1% of the total bacteria in the intestine (Derrien et al., 2008). It grows optimally at 37°C and is capable of fermenting glucose, N-acetylgulosamine and N-acetylgalactosamine. The genome size of A. muciniphila is far smaller than those of other verrucomicrobia (see above), suggesting a massive gene loss in the course of adaptation to the life in nutrient-rich human intestine.

Another sequenced member of Verrucomicrobia, O. terrae, is also a strictly anaerobic saccharolytic bacterium. It was isolated from a rice paddy soil microcosm, obtained from rice fields in Vercelli, Italy (Chin et al., 2001). Opitutus terrae can metabolize various mono-, di- and polysaccharides, fermenting them into acetate and propionate.

The third verrucomicrobial genome represents one of the recently characterized methanotrophic strains, mentioned in this column 4 months ago. Three different groups reported independent isolation of extremely acidophilic methanotrophs belonging to the phylum Verrucomicrobia from a methane-emitting geothermal field in New
1928 Genomics update

Table 1. Recently completed microbial genomes (April–May 2008).

| Species name                   | Taxonomy                          | GenBank accession | Genome size (bp) | Proteins (total) | Sequencing centre | Reference               |
|-------------------------------|-----------------------------------|-------------------|------------------|------------------|-------------------|-------------------------|
| **New organisms**             |                                   |                   |                  |                  |                   |                         |
| Akkermansia muciniphila       | Verrucomicrobia                   | CP001071          | 2 664 102        | 2138             | JGI               | Unpublished             |
| Methylocystis capsulatus      | Verrucomicrobia                   | CP000972          | 2 287 145        | 2473             | U. Hawaii         | Hou et al. (2008)       |
| Optitutus terra               | Verrucomicrobia                   | CP001032          | 5 957 605        | 4812             | JGI               | Unpublished             |
| Uncultured Termite group 1    | Candidate                         | AP009510          | 1 148 570 (total)| 776              | RIKEN             | Hongo et al. (2008)     |
| Elusimicrobiium minutum       | Candidate division TG1            | CP001055          | 1 643 562        | 1529             | JGI               | Unpublished             |
| Corynebacterium urealyticum   | Actinobacteria                    | AM942444          | 2 369 219        | 2024             | Bielefeld U.      | Tauch et al. (2008)     |
| Mycobacterium marinum         | Actinobacteria                    | CP000854          | 6 636 827        | 5452             | Sanger Institute  | Stinear et al. (2008)   |
| Streptomyces griseus          | Actinobacteria                    | CP000895          | 23 317           |                  |                  |                         |
| Nostoc punctiforme            | Cyanobacteria                     | CP001037-CP001042 | 9 059 191 (total)| 6690             | JGI               | Unpublished             |
| Candidatus Phytosoma           | Firmicutes                        | AM422018          | 879 959          | 684              | MPIMG             | Tran- Nguyen et al. (2008) |
| Exiguobacterium sibiricum     | Firmicutes                        | CP001022          | 3 034 136        | 3015             | JGI               | Unpublished             |
| Lactobacillus fermentum       | Firmicutes                        | CP001023          | 4 885            |                  |                  |                         |
| Beijerinckia indica           | α-Proteobacteria                  | AP008937          | 2 098 685        | 1843             | Kitasato U.       | Morita et al. (2008)    |
| Burkholderia phymatum         | β-Proteobacteria                  | CP001043-CP001046 | 8 676 562 (total)| 7496             | JGI               | Unpublished             |
| Burkholderia phytofirmans     | β-Proteobacteria                  | CP001052          | 4 467 537        | 7241             | JGI               | Unpublished             |
| Stenotrophomonas maltophilia  | γ-Proteobacteria                  | AM743169          | 4 851 126        | 4430             | Sanger Institute  | Crossman et al. (2008)  |
| Borrelia hermsii              | Spirochaetes                      | CP000048          | 922 307          | 819              | RML-NIAID         | Unpublished             |
| Borrelia turicatae            | Spirochaetes                      | CP000049          | 917 330          | 820              | RML-NIAID         | Unpublished             |
| New strains                   |                                   |                   |                  |                  |                  |                         |
| Porphyromonas gingivalis      | Bacteroidetes                     | AP009380          | 2 354 886        | 2090             | Kitasato U.       | Naito et al. (2008)     |
| Clostridium botulinum B str.  | Firmicutes                        | CP001056          | 3 800 327        | 3527             | JGI               | Unpublished             |
| Eklund 17B                    | Firmicutes                        | CP001057          | 47 642           |                  |                  |                         |
| Clostridium botulinum E3 str. | Firmicutes                        | CP001078          | 3 659 644        |                  | JGI               | Unpublished             |
| Alaska E43                    | Firmicutes                        | CP001033          | 2 209 198        | 2206             | BGI               | Unpublished             |
| Lactococcus reuteri           | Firmicutes                        | AP007281          | 2 039 414        | 1820             | Kitasato U.       | Morita et al. (2008)    |
| F275 JCM1112                  | Firmicutes                        | CP001033          | 2 209 198        | 2206             | BGI               | Unpublished             |
| Streptococcus pneumoniae      | Firmicutes                        | CP000888          | 1 161 449        |                  |                  |                         |
| Brucella abortus S19          | α-Proteobacteria                  | CP000887          | 2 122 487        | 3000             | VBI               | Crasta et al. (2008)    |
| Orientia tsutsugamushi str.   | α-Proteobacteria                  | CP000888          | 2 008 987        | 1967             | Kitasato U.       | Nakayama et al. (2008)  |
| MC40-6                        | β-Proteobacteria                  | CP001025          | 7 642 536        | 6697             | JGI               | Unpublished             |
| Acinetobacter baumannii       | γ-Proteobacteria                  | CP000885          | 3 904 116        | 3759             | CNR-ISS           | Iacono et al. (2008)    |
| ACICU                         | Firmicutes                        | CP001063          | 28 279           |                  |                  |                         |
| Francisella tularensis ssp.   | γ-Proteobacteria                  | CP000915          | 1 893 866        | 1406             | JGI               | Unpublished             |
| Shigella boydii CDC 3083–94   | γ-Proteobacteria                  | CP001058-CP001063 | 4 86 (total)     | 4557             | JCVI              | Unpublished             |
| Xanthomonas oryzae pv. oryzae | γ-Proteobacteria                  | CP001063          | 5 240 075        | 4988             | JCVI              | Salzberg et al. (2008)  |
| Xylella fastidiosa M23        | γ-Proteobacteria                  | CP001011          | 2 535 690        | 2201             | JGI               | Unpublished             |
| Yersinia pseudotuberculosis   | γ-Proteobacteria                  | CP001048-CP001049 | 4 695 619        | 4237             | JGI               | Unpublished             |
| Helicobacter pylori Shi470    | ε-Proteobacteria                  | CP001072          | 1 608 547        | 1567             | Wash U.           | Unpublished             |

Sequencing centre names are abbreviated as follows: BGI, Beijing Genomics Institute, Beijing, China; Bielefeld U., Centrum für Biotechnologie, Universität Bielefeld, Bielefeld, Germany; CNR-ISS, Institute for Biomedical Technologies, National Research Council, Milan, and Istituto Superiore di Sanità, Rome, Italy; JCVI, J. Craig Venter Institute (formerly TIGR), Rockville, Maryland, USA; JGI, US Department of Energy Joint Genome Institute, Walnut Creek, California, USA; Kitasato U. Kitasato Institute for Life Science, Kitasato University, Tokyo, Japan; MPIMG, Max Planck Institute for Molecular Genetics, Berlin, Germany; RIKEN, Genomic Sciences Center, RIKEN, Kanagawa, Japan; RML-NIAID, Rocky Mountain Laboratories, National Institutes of Allergy and Infectious Disease, National Institutes of Health, Hamilton, Montana, USA; Sanger Institute, The Wellcome Trust Sanger Institute, Wellcome Trust Genome Campus, Hinxton, Cambridgeshire, UK; U. Hawaii, Advanced Studies in Genomics, Proteomics and Bioinformatics, University of Hawaii at Manoa, Honolulu, Hawaii, USA; VBI, Virginia Bioinformatics Institute at Virginia Tech, Blacksburg, Virginia, USA; Wash U., Washington University Medical School, St. Louis, Missouri, USA.

Journal compilation © 2008 Society for Applied Microbiology and Blackwell Publishing Ltd, Environmental Microbiology, 10, 1927–1933

No claim to original US government works
Zealand, a Solfatara volcano mudpot in Italy, and from an acidic hot spring in Kamchatka, Russia (Dunfield et al., 2007; Pol et al., 2007; Islam et al., 2008). These three isolates were all thermophiles capable of growing aerobically at 55–60°C with methane as the sole carbon source. They had 98% identical rRNA sequences, indicating that they belong to the same genus, for which the name ‘Methylacidiphilum’ is being proposed. The complete genome sequence of the New Zealand isolate has now been published (Hou et al., 2008). Methylacidiphilum infernorum is an autotrophic bacterium whose 2.3 Mbp genome is even smaller than that of A. munciniphila. Signs of genome streamlining during adaptation to its unique ecological niche are seen in the organization of central metabolism of M. infernorum, including its C1-utilization pathways, simple signal transduction machinery and a limited set of transcriptional regulators (Hou et al., 2008).

Verrucomicrobial genomes are very interesting from the evolutionary standpoint. Phylogenetic analysis of M. infernorum proteins confirmed earlier conclusions on the proximity of Verrucomicrobia and Chlamydiae (Hugenholtz et al., 1998; Griffiths and Gupta, 2007), which are often treated as a single Chlamydiae/Verrucomicrobia group. It also provided support for specific association of Chlamydiae/Verrucomicrobia with Planctomycetes and Lentisphaerae, and two candidate phyla; Poribacteria and OP3, referred to as Planctomycetes/Verrucomicrobia/Chlamydiae superphylum (Wagner and Horn, 2006). However, genome analysis did not support the idea of a potential evolutionary relationship between Verrucomicrobia and eukaryotes, which had been prompted by the discovery of tubulin in members of the genus Prosthecobacter, also belonging to the Verrucomicrobia (Jenkins et al., 2002; Staley et al., 2005). The genome of M. infernorum did not encode tubulin or, for that matter, close homologues of any other signature eukaryotic proteins (Hou et al., 2008). Tubulin genes were missing also in A. munciniphila and O. terrae genomes. These results argue against bacterial origin of tubulin and suggest that Prosthecobacter acquired tubulin genes through lateral gene transfer from some eukaryotic cells after its divergence from other verrucomicrobial lineages.

The second new phylum with recently sequenced genomes, candidate division ‘Termite group I’ (TG-1), includes no cultivated representatives (however, see below) and has been defined on the basis of rRNA sequences obtained by environmental sampling (Hugenholtz et al., 1998). Representatives of one TG-1 lineage, the so-called ‘Endomicrobia’, are abundant in the termite gut, where they are found as intracellular symbionts of various wood-feeding protozoa (Stingl et al., 2005; Ikeda-Ohtsubo et al., 2007). TG-1 representatives can also be detected in many other habitats, including rice soil, river sediment and cow rumen (Herlemann et al., 2007b; Ohkuma et al., 2007). Although there have been no physiological studies of any TG-1 member, the conditions inside the termite gut suggest that they are obligately anaerobic bacteria that gain energy by fermentation of wood-derived carbohydrates.

Now, after many years of having just bits and pieces of TG-1 sequences, we suddenly have two completely sequenced genomes of TG-1 members. The first of them comes from bacterial phylotype Rs-D17, a member of the “Endomicrobia”, which is found specifically within the cells of the cellulolytic flagellate Trichonympha agilis that inhabits the gut of the termite Reticulitermes speratus (Hongoh et al., 2008). By using as the DNA source only ~10³ bacterial cells isolated from a single cell of T. agilis, it became possible to obtain sufficiently pure and uniform population to perform the sequencing and assembly of Rs-D17 genome. The reconstructed genome consists of a circular 1.1 Mbp chromosome and three plasmids of 11.6, 5.7 and 5.3 kb. It shows clear signs of genome streamlining, including presence of numerous pseudogenes and partial or complete loss of certain metabolic pathways. Still, cells of Rs-D17 appear to be able to synthesize at least 15 amino acids, purines and pyrimidines (Hongoh et al., 2008). The authors suggest that Rs-D17 serves as an intracellular symbiont of T. agilis, supplying the host protist cell with amino acids and vitamins more or less the same way as it happens in Buchnera-aphid symbiosis.

The second TG-1-related genome comes from Elusimicrobium minutum Pei191, the first cultivated representative of this phylum, which still remains to be formally described. According to Andreas Brune and colleagues at Max Planck Institute for Terrestrial Microbiology in Marburg, Germany, E. minutum is an obligately anaerobic ultra-microbacterium (0.2–0.3 μm in diameter) that was isolated from sterile-filtered gut homogenates of the larva of humivorous scarab beetle Pachnoda ephippia (Coleoptera: Scarabaeidae; see Egert et al., 2003; Lemke et al., 2003). This organism grows heterotrophically on glucose and produces acetate, hydrogen and ethanol as major products (Herlemann et al., 2007a). It belongs to the so-called ‘Intestinal Cluster’, which represents a distinct lineage of TG-1-affiliated microorganisms present in arthropod guts and in the cow rumen (Herlemann et al., 2007b). The relatively small genome size of both E. minutum and Rs-D17 may reflect their adaptation to gut environment and is not necessarily representative of the whole TG-1 group.

There have also been interesting genomes among relatively well-known bacterial phyla. Actinobacteria, for example, are represented by three new genomes coming from opportunistic human pathogens Corynebacterium urealyticum and Mycobacterium marinum and the soil bacterium Streptomyces griseus, the original producer of streptomycin.
Although \textit{C. urealyticum} is part of the natural flora of human skin, it often colonizes the urinary tract, causing a variety of urinary tract infections. Presence of \textit{C. urealyticum} in urine samples correlates with elevated pH and presence of struvite (magnesium ammonium phosphate hexahydrate) stones. The sequenced strain \textit{C. urealyticum} DSM7109 was originally isolated from a patient with alkaline-encrusted cystitis. Its growth requires presence of exogenous lipids, explained by the absence of a fatty acid synthase gene and presence of a robust system for degradation of exogenous fatty acids (Tauch \textit{et al}., 2008). Presence of several antibiotic-resistance determinants suggests high incidents of lateral gene transfers, which lead to the accumulation of multidrug-resistant strains.

\textit{Mycobacterium marinum} is close relative of \textit{M. tuberculosis} that causes a tuberculosis-like disease in fish and amphibia. Owing to its lower temperature optimum (25–35°C) and a much faster growth than \textit{M. tuberculosis}, it is often used as a convenient experimental model to study tuberculosis in humans (Tobin and Ramakrishnan, 2008). However, \textit{M. marinum} can also infect humans, causing granulomatous skin disease. Comparison of mycobacterial genomes suggests that evolution of \textit{M. tuberculosis} from a \textit{M. marinum}-like ancestral form included reduction in the genome size, accompanied by specialization toward human host and the loss of the ability to survive in the environment (Stinear \textit{et al}., 2008).

The sequenced strain of \textit{S. griseus}, IFO 13350, came from the Waksman laboratory at Rutgers University and is one of the original strains used for production of streptomycin (Ohnishi \textit{et al}., 2008). Analysis of its genome revealed a significant degree of colinearity with genomes of \textit{Streptomyces coelicolor} A3(2) and \textit{Streptomyces avermitilis} with at least 45% of proteins shared by all three genomes. It also identified 34 clusters of genes encoding polyketide synthases and non-ribosomal peptide synthetases. Some of these clusters are responsible for production of known secondary metabolites (streptomycin, grixazone, melanin, carotenoids, siderophores, lantibiotics), products of others remain unknown (Ohnishi \textit{et al}., 2008).

\textit{Nostoc punctiforme} is a nitrogen-fixing terrestrial filamentous cyanobacterium that is closely related to \textit{Anabaena (Nostoc)} PCC 7120. This organism can exist in a free state but readily forms symbioses with a wide variety of plants and fungi. It is a favourite model organism for studies of cyanobacterial growth, metabolism, cell development and symbiotic behaviour (Meeks \textit{et al}., 2001; 2002; Meeks, 2006). \textit{Nostoc punctiforme} has one of the most complex developmental programs known in bacteria: in addition to usual vegetative cells, it is capable of producing three kinds of differentiated cells: (i) hetero-
among others, the geographic location and time of the sample collection (plus depth or altitude, if appropriate) and properties of the habitat (temperature, pH, salinity, pressure, light intensity, dissolved organic carbon, dissolved oxygen, phosphate, nitrate, sulfates, sulfides, and so on). While this sounds like a sensible recommendation, this paper does not clearly articulate the penalties, if any, for non-compliance. Besides, what should one do with the isolate for which such data are unavailable, refrain from sequencing the genome or delay the release of the genome sequence until such data become available? Strict adherence to the MIGS standards would have prevented or greatly delayed public release of the genome of *E. minutum*, discussed above, as well as many other genomes sequenced at the JGI and other institutions.

The second paper (Mons et al., 2008), whose authors include, among others, Wikipedia founders Jimmy Wales and Erik Moeller, announces creation of a Wiki-based system called WikiProteins, intended for ‘community annotation of biomedical concepts and their interactions’. The core of the system is based on ‘protein concepts’ (in plain language, extended protein annotations) from Swiss-Prot and on Unified Medical Language System (UMLS®) concepts for computer processing of natural language-based biomedical information (see http://www.nlm.nih.gov/pubs/factsheets/umls.html). In the future, WikiProteins are expected to incorporate the Gene Ontology (GO) vocabulary and a variety of other databases. This sounds like a very promising undertaking, and the whole paper (which is freely available online with a variety of colourful links and pop-up windows) deserves a careful reading, even if the idea of ‘collaborative knowledge discovery’ might seem too far-fetched to most readers of this journal.

In conclusion, a correction: in the previous Genomics Update (Galperin, 2008), I confused properties of two methylo trophs. *Methylobacterium* spp. 4-46 is a symbiont of the legume *Lotononis bainesii*, whereas *Methylobacterium radiotolerans* is not known for symbiosis. I thank Benjamin Gourion (ETH Zürich) and Ludmila Chistoserdova (University of Washington) for pointing out this mistake.

Acknowledgements

M.Y.G. is supported by the Intramural Research Program of the NIH, National Library of Medicine. The author’s opinions do not reflect the views of NCBI, NLM or the National Institutes of Health.

References

Albrecht, W., Fischer, A., Smida, J., and Stackebrandt, E. (1987) *Verrucomicrobi um spinosum*, an eubacterium representing an ancient line of descent. *Syst Appl Microbiol* 10: 57–62.

Chin, K.J., Liesack, W., and Janssen, P.H. (2001) *Opitutus terrae* gen. nov., sp. nov., to accommodate novel strains of the division ‘*Verrucomicrobia*’ isolated from rice paddy soil. *Int J Syst Evol Microbiol* 51: 1965–1968.

Crasta, O.R., Folkerts, O., Fei, Z., Mane, S.P., Evans, C., Martino-Catt, S., et al. (2008) Genome sequence of *Brucella abortus* vaccine strain S19 compared to virulent strains yields candidate virulence genes. *PLoS ONE* 3: e2193.

Crossman, L.C., Gould, V.C., Dow, J.M., Vernikos, G.S., Okazaki, A., Sebaglia, M., et al. (2008) The complete genome, comparative and functional analysis of *Stenotrophomonas maltophilia* reveals an organism heavily shielded by drug resistance determinants. *Genome Biol* 9: R74.

Davis, R.E., Dally, E.L., Gundersen, D.E., Lee, I.M., and Habili, N. (1997) ‘*Candidatus* Phytoplasma australiensi*, a new phytoplasma taxon associated with Australian grapevine yellows. *Int J Syst Bacteriol* 47: 262–269.

Derrien, M., Vaughan, E.E., Plugge, C.M., and de Vos, W.M. (2004) *Akkermansia muciniphila* gen. nov., sp. nov., a human intestinal mucin-degrading bacterium. *Int J Syst Evol Microbiol* 54: 1469–1476.

Derrien, M., Collado, M.C., Ben-Amor, K., Salminen, S., and de Vos, W.M. (2008) The mucin degrader *Akkermansia muciniphila* is an abundant resident of the human intestinal tract. *Appl Environ Microbiol* 74: 1646–1648.

Dunfield, P.F., Khmelenina, V.N., Suzina, N.E., Trotsenko, Y.A., and Dedysh, S.N. (2003) *Methylcocc lla silvestris* sp. nov., a novel methanotroph isolated from an acidic forest cambisol. *Int J Syst Evol Microbiol* 53: 1231–1239.

Derrien, P.F., Yuryev, A., Senin, P., Sminova, A.V., Stott, M.B., Hou, S., et al. (2007) Methane oxidation by an extremely acidophilic bacterium of the phylum *Verrucomicrobia*. *Nature* 450: 879–882.

Egert, M., Wagner, B., Lemke, T., Brune, A., and Friedrich, M.W. (2003) Microbial community structure in midgut and hindgut of the humus-feeding larva of *Pachnoda ephippiata* (Coleoptera: Scarabaeidae). *Appl Environ Microbiol* 69: 6659–6668.

Elliott, G.N., Chen, W.M., Chou, J.H., Wang, H.C., Sheu, S.Y., Perin, L., et al. (2007) *Burkholderia phymatum* is a highly effective nitrogen-fixing symbiont of *Mimos a* spp. and fixes nitrogen ex planta. *New Phytol* 173: 168–180.

Field, D., Garrity, G., Gray, T., Morrison, N., Selengut, J., Sterk, P., et al. (2008) The minimum information about a genome sequence (MIGS) specification. *Nat Biotechnol* 26: 541–547.

Galperin, M.Y. (2008) Genomes of model organisms: know thy tools. *Environ Microbiol* 10: 1383–1391.

Griffiths, E., and Gupta, R.S. (2007) Phylogeny and shared conserved inserts in proteins provide evidence that *Verru comicrob ia* are the closest known free-living relatives of chlamydiae. *Microbiology* 153: 2648–2654.

Hedlund, B.P., Gosink, J.J., and Staley, J.T. (1997) *Verrucomicrobia* division nov., a new division of the bacteria containing three new species of *Prosthecobacter*. *Antonie Van Leeuwenhoek* 72: 29–38.

Herlemann, D.P., Geissinger, O., and Brune, A. (2007a)
Diversity and environmental distribution of the termite group I phylum, and isolation of *Elusimicrobi um minutum* gen. nov. sp. nov. In Second Annual DOE Joint Genome Institute User Meeting, March 28–30, 2007. Walnut Creek, CA, USA: US DoE Office of Science, p. 29. [http://www.jgi.doe.gov/meetings/usermtg07/]

Herlemann, D.P., Geissinger, O., and Brune, A. (2007b) The 1932

Herlemann, D.P., Geissinger, O., and Brune, A. (2007b) The 1932

Morita, H., Toh, H., Fukuda, S., Horikawa, H., Oshima, K., Suzuki, T., et al. (2008) Comparative genome analysis of Lactobacillus reuteri and Lactobacillus fermentum reveal a genomic island for reuterin and cobalamin production. *DNA Res* 15, in press. doi: 10.1093/dnares/dsn009.

Naito, M., Hirakawa, H., Yamashita, A., Ohara, N., Shoji, M., Yuki tate, H., et al. (2008) Determination of the genome sequence of *Porphyromonas gingivalis* strain ATCC 33277 and genomic comparison with strain W83 revealed extensive genome rearrangements in *P. gingivalis*. *DNA Res* 15, in press. doi: 10.1093/dnares/dsn013.

Nakayama, K., Yamashita, A., Kurokawa, K., Morimoto, T., Ogawa, M., Fukuhara, M., et al. (2008) The whole-genome sequencing of the obligate intracellular bacterium *Orientia tsutsugamushi* revealed massive gene amplification during reductive genome evolution. *DNA Res* 15, in press. doi: 10.1093/dnares/dsn011.

Okhuma, M., Sato, T., Noda, S., Ui, S., Kudo, T., and Hongoh, Y. (2007) The candidate phylum ‘Termite Group 1’ of bacteria: phylogenetic diversity, distribution, and endosymbiotic members of various gut flagellated protists. *FEMS Microbiol Ecol* 60: 467–476.

Ohnishi, Y., Ishikawa, J., Hara, H., Suzuki, H., Ikenoya, M., Ikeda, H., et al. (2008) Genome sequence of the streptomycin-producing microorganism *Streptomyces griseus* IFO 13350. *J Bacteriol* 190: 4050–4060.

Pol, A., Heijmans, K., Harhangi, H.R., Tedesco, D., Jetten, M.S., and Op den Camp, H.J. (2007) Methanotrophy below pH 1 by a new *Verrucomicrobia* species. *Nature* 450: 874–878.

Rodrigues, D.F., Goris, J., Vishnivetska, T., Gilichinsky, D., Thomashow, M.F., and Tiedje, J.M. (2006) Characterization of *Exiguobacterium* isolates from the Siberian permafrost. Description of *Exiguobacterium sibiricum* sp. nov. *Extremophiles* 10: 285–294.

Salzberg, S.L., Sommer, D.D., Schatz, M.C., Philippy, A.M., Rabinowicz, P.D., Tsuge, S., et al. (2008) Genome sequence and rapid evolution of the rice pathogen *Xanthomonas oryzae* pv. oryzae PX099A. *BMC Genomics* 9: 204.

Sessitsch, A., Coenye, T., Sturz, A.V., Vandamme, P., Barka, E.A., Salles, J.F., et al. (2005) *Burkholderia phytofirmans* sp. nov., a novel plant-associated bacterium with plant-beneficial properties. *Int J Syst Evol Microbiol* 55: 1187–1192.

Staley, J.T., Bouzek, H., and Jenkins, C. (2005) Eukaryotic signature proteins of *Prosthecobacter dejongeii* and *Gemmata* sp. Wa-1 as revealed by *in silico* analysis. *FEMS Microbiol Lett* 243: 9–14.

Stinear, T.P., Seemann, T., Harrison, P.F., Jenkin, G.A., Davies, J.K., Johnson, P.D., et al. (2008) Insights from the complete genome sequence of *Mycobacterium marinum* on the evolution of *Mycobacterium tuberculosis*. *Genome Res* 18: 729–741.

Stingl, U., Radek, R., Yang, H., and Brune, A. (2005) *Endomicrobia* : cytoplasmic symbionts of termite gut protozoa form a separate phylum of prokaryotes. *Appl Environ Microbiol* 71: 1473–1479.

Tauch, A., Trost, E., Tilmik, A., Ludewig, U., Schneiker, S., Goesmann, A., et al. (2008) The lifestyle of *Corynebacterium urealyticum* derived from its complete genome sequence established by pyrosequencing. *J Biotechnol* 135, in press. doi: 10.1016/j.jbiotec.2008.02.009.
Tobin, D.M., and Ramakrishnan, L. (2008) Comparative pathogenesis of Mycobacterium marinum and Mycobacterium tuberculosis. *Cell Microbiol* 10: 1027–1039.

Tran-Nguyen, L.T.T., Kube, M., Schneider, B., Reinhardt, R., and Gibb, K.S. (2008) Comparative genome analysis of ‘Candidatus Phytoplasma australiense’ (subgroup tuf-Australia I; rp-A) and ‘Ca. Phytoplasma asteris’ strains OY-M and AY-WB. *J Bacteriol* 190: 3979–3991.

Vishnivetskaya, T.A., Siletzky, R., Jefferies, N., Tiedje, J.M., and Kathariou, S. (2007) Effect of low temperature and culture media on the growth and freeze-thawing tolerance of Exiguobacterium strains. *Cryobiology* 54: 234–240.

Wagner, M., and Horn, M. (2006) The Planctomycetes, Verrucomicrobia, Chlamydiae and sister phyla comprise a superphylum with biotechnological and medical relevance. *Curr Opin Biotechnol* 17: 241–249.