hypothesis, the scaffold protein PBIP1, which anchors Plk1 at kinetochores, is degraded in prometaphase in a ubiquitin-dependent fashion [10]. Both Plk1 and PRC1 are substrates of the anaphase-promoting complex (APC) [12]. In the case of Plk1, its slow ubiquitination by the APC ensures that it is not degraded prematurely [13]. It is tempting to speculate that formation of a complex between PRC1 and Plk1 stimulates the ubiquitination of both proteins, and thereby limits the duration of their activity at the central spindle.

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Bacterial Endosymbionts: Genome Reduction in a Hot Spot

Prokaryotic symbionts are common in invertebrates and play an essential metabolic role in deep-sea hydrothermal vent communities. Complete genome sequences of bacterial endosymbionts of two deep-sea clams are providing new insights into evolutionary genome reduction.

Christopher E. Lane

Since the discovery of the Pacific deep-sea hydrothermal vents and the subsequent description of the abundant life existing there [1], the biotic community of this unique habitat has fascinated scientists and non-scientists, alike. Over 500 species of metazoans live around these seeps of hot, mineral-rich water, raising the question of how so much biodiversity is able to survive in an environment devoid of the solar energy that drives life on the surface of the planet. The answer: environmental and symbiotic chemoautotrophic bacteria.

2007 has been a banner year for advancing our understanding of the interactions between deep-sea invertebrates and bacterial symbionts. The genome sequence of the endosymbiont isolated from the deep-sea clam, *Calyptogena okutanii*, reported recently in *Current Biology* by Kuwahara *et al.* [2], is the second for a deep-sea endosymbiont and the third genome-level study completed this year, expanding our understanding of the essential contribution of bacteria to the fauna of deep-sea thermal seeps. Given the coding capacity of the bacterial endosymbiont of *C. okutanii*, it would not be expected to be able to persist outside its clam host. The *C. okutanii* endosymbiont has lost genes for motility, stress responses and DNA recombination and repair. The loss of essential genes for a free-living lifestyle, combined with evidence for the transmission of the endosymbiont from one generation to the next via the clam's eggs [3], indicates that the *C. okutanii* endosymbiont is in the process of genome reduction whereby it has become dependent on its host.

The majority of metazoans surrounding hydrothermal vents depend on the sulphur oxidizing activity of chemoautotrophic bacteria for nutrients, either directly through endosymbiotic associations or indirectly by feeding on them [4]. The uptake, retention and ultimate enslavement of prokaryotic (or in some cases, eukaryotic) cells is a common evolutionary strategy for eukaryotes, allowing them to exploit new resources. The plastids and mitochondria are the textbook examples of this, whereby the endosymbionts have been entirely incorporated into the cellular machinery of their 'hosts'. Organelles are, of course, an extreme case of reduction in which massive numbers of genes have been transferred to the nucleus and their products are targeted back to the organelle [5]. More recently acquired symbionts, however, are like windows on the process of reduction and incorporation, and

Table 1. Genome statistics for various γ-proteobacteria employing a variety of lifestyles.

Organism	*C. okutanii* symbiont	*Ruthia magnifica*	*Riftia* symbiont	*Buchnera aphidicola*	*Thiomicrospira crunogena*
Lifestyle	Intracellular endosymbiont[1]	Intracellular endosymbiont[1]	Symbiont[2]	Intracellular endosymbiont[1]	Free-living
Host organism	*Calyptogena okutanii*	*Calyptogena magnifica*	*Riftia pachyptila*	*Cinara cedri*	None
Genome size	1.02 Mb	1.2 Mb	3.3 Mb	0.6 Mb	2.4 Mb
G+C content	31.6%	34%	NA	26%	43%
Total # of genes	975	1248	NA	608	2199

[1]Vertically transmitted between generations via the eggs of the host.
[2]Environmentally transmitted and sequestered anew each generation.

from this perspective, the hydrothermal vent biota provides an exciting opportunity for comparisons of multiple independent acquisitions of bacterial symbionts with different relationships with their hosts.

The proteome [6] of the symbiotic gut inhabitant of the hallmark organism of hydrothermal vent research, the tube worm (*Riftia pachyptila*), provided the first glimpse into the biology of the host–symbiont relationship from a deep-sea invertebrate. Subsequent reports of the genome sequences of endosymbionts isolated from the gill tissue of two hydrothermal vent-associated clams of the genus *Calyptogena* — *Ruthia magnifica* from *C. magnifica* [7] and the endosymbiont of *C. okutanii* [2] — have provided comparative data. Not surprisingly, the clam endosymbionts are more alike in their genome size, coding capacity and interaction with the host than either is to the tube worm symbiont (Table 1).

The most striking correlation from the comparisons of the available genomic data is between genome size and lifestyle. The clam endosymbionts live in specialized cells of the gill (bacteriocytes) and are vertically transmitted from one generation to the next via the clam's eggs. In contrast, the tube worm, *Riftia*, acquires its symbiont environmentally and sequesters it within a vestigial gut. The intracellular clam endosymbionts contain genomes about one third the size of the environmentally transmitted *Riftia* symbiont genome and less than half the size of their closest known free-living relative, *Thiomicrospira crunogena* (Table 1). Whereas the complete genome sequence of the *Riftia* symbiont is not available, its larger size is most likely related to the presence of pathways necessary for the free-living portion of its life cycle, along with a complex cross-membrane transport system to shuttle fixed carbon to the host. The *Riftia* symbiont has been shown to actively transport nutrients to the host (reviewed in [8]), but the genome of the *C. okutanii* endosymbiont does not encode transporters for the export of metabolic products [2]. The mechanism by which nutrients are provided to the host is not entirely clear, but Kuwahara *et al.* [2] postulate that the clam digests the endosymbiont, much like has been demonstrated in deep-sea mussels [9].

Are the tube worm symbiont, with its large genome and extensive proteome, and clam endosymbionts, which lack essential genes and contain a reduced genome, simply snapshots from the inevitable road trip between mutualistic association and fully integrated organelle? Mitochondria and plastids display massive genome reduction, in both size and coding capacity, compared with the modern-day equivalent of their putative ancestors, alpha-proteobacteria and cyanobacteria, respectively. Additionally, reduced genomes generally have certain characteristics, such as lower G+C content and elevated mutational rates, compared to non-endosymbiotic genomes [10]. Similar processes have been studied in detail in other intracellular bacterial endosymbionts, such as *Buchnera* and *Wolbachia* in aphids, and appear to also be at work on the genomes of deep-sea endosymbionts (Table 1). Detailed comparisons, both within and between lineages including free-living and endosymbiotic members, will undoubtedly shed light on interesting parallels and help elucidate the mechanisms behind symbiont genome reduction and adaptation to an intracellular environment.

Equally interesting should be analyses of the variations in host–symbiont interactions. Although the endosymbiontic relationships of both aphids and *Calyptogena* are of similar antiquity [11,12], the genome of *Buchnera* is substantially more reduced than that of the *C. okutanii* endosymbiont. This is believed to be related to the complexity of sulfide oxidation and the number of products the *C. okutanii* endosymbiont provides [7]. The aphid hosts of *Buchnera* depend on the endosymbiont for the production of essential amino acids, while the host supplies sugars and non-essential amino acids for *Buchnera*. In contrast, the genomic sequence from the *C. magnifica* endosymbont, *Ruthia*, indicates that it has complete pathways for the synthesis of all 20 amino acids, whereas the *C. okutanii* endosymbiont is missing only a single gene from two of the 20 pathways and may replace these with alternative genes within its genome. The *C. okutanii* endosymbiont genome also encodes full sets of genes for the production of various cofactors, fatty acids and nucleotides. These represent an essential contribution to the host because *C. okutanii* has only a vestigial gut and greatly reduced filtering ability [13], making it dependent on the endosymbiont for its nutrients.

Further evidence for the importance of this relationship for the survival of *Calyptogena* comes from the adaptations the clam has made to accommodate the endosymbiont. Sulphur-oxidizing bacteria require sulfide as an electron donor and oxygen as an acceptor (or nitrate in anoxic conditions) to fix carbon. But sulfide and oxygen can react spontaneously, making it difficult for a single-celled organism to obtain both from the environment at the same time [13]. *Calyptogena* overcomes this barrier for its endosymbionts by arranging the bacteriocytes in the outermost layer of gill epithelial cells, so that they contact both the oxygen (or nitrate)-rich water and the sulfide accumulated in the blood of the clam [14]. *Calyptogena* sequesters the sulfide by pushing its highly vascularized foot into the substrate, where it can access mineral rich water from the vents while keeping its inhalant siphon in the ambient seawater above.

The relationship between *C. okutanii* and its endosymbiont is clearly essential for the survival of both organisms and manifests itself at multiple levels of organization. The genome sequence of the endosymbiont provides an intriguing window into the biology behind this interaction and how it affects both the clam and the symbiont. As we explore more deep-sea host–symbiont systems it will be fascinating to determine the extent of endosymbiont genome reduction and the parallels between the process of symbiont reduction on land and in the depths of the ocean.

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Evolution: Reducible Complexity — The Case for Bacterial Flagella

A recent paper, which will surely figure centrally in the debate between evolutionists and Intelligent Design creationists, proposes a (perhaps too simple) scheme for the evolution of bacterial flagella.

W. Ford Doolittle and Olga Zhaxybayeva

Advocates of Intelligent Design (ID) hold that some biological structures are 'irreducibly complex', made up of parts that would be useless by themselves, and requiring for their assembly an intelligent designer. The bacterial flagellum is one such structure, the 21st Century microbial equivalent of the vertebrate eye — the origin of which Darwin himself admitted was a test case for his theory. Arguments about whether a flagellum could have been cobbled together, step by step, from antecedent proteins that had at each stage some sort of partial or alternative use figured large in the 2005 Dover, Pennsylvania trial over the teaching of ID as science in public schools.

That trial went against the antievolutionists, Judge Jones ruling that ID theory "cannot uncouple itself from its creationist, and thus religious, antecedents". This decision has not, of course, put paid to the creationist movement, so efforts by evolutionists to elaborate and test evolutionary scenarios for flagella continue to have political currency as well as scientific interest.

Last October, Pallen and Matzke [1] summarized in a review much of the relevant knowledge. Bacterial flagella are, in fact, diverse in composition (and quite distinct from archaeal analogs), but concerning eight axial bacterial proteins these authors inferred that "the flagellar