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Further investigation revealed that the bias in usage of nucleotides extends further than just individual bases: A further extension to this is the use of codon preference; different genomes have different patterns of preferred codons, and looking for deviations from the norm can be a profitable way of finding candidate horizontally transferred genes. For some reason, probably a mutational asymmetry in the replication fork, there tend to be more G residues on the leading strand than the lagging strand Lobry, Significant deviations from this plot may either indicate recent insertions of DNA, or recent rearrangements, such as the largescale insertion sequence IS -element mediated inversions seen in the genome of Yersinia pestis Parkhill et al. For each of these measurements, there are several provisos that must be considered. Obviously, they will not detect DNA that has been acquired from a very similar genomic background. In addition, each of these properties is imposed in some way on the genomic sequence e. The final, and most important, proviso is that not all biases in genomic DNA are due to horizontal acquisition. Sequence constraints can also play a strong role in producing perturbations in any of these measurements. Such constrains include preferential coding for specific amino-acid subsets, such as those in large hydrophobic proteins, and small basic ribosomal proteins; indeed, the major ribosomal protein operon often shows the largest deviation in dinucleotide signature in many bacterial genomes. Large repetitive proteins containing a short or biased amino-acid repeat will often also give strong nucleotide and codon bias signals the Gly-rich repetitive PGRS proteins of Mycobacterium tuberculosis are particularly noteworthy in this regard; Cole et al. Investigations of potential horizontally acquired islands in genomes should, therefore, be extended to include other possible indicators; large mobile islands, especially those carrying pathogenicity genes, may often carry mobility determinants, such as phage integrases or transposases. Those with phage-derived mobility genes may also be adjacent to tRNA genes, a common integration site for prophage. In closely related syntenic 20 Figure 1. Anomalies in large-scale nucleotide plots. The three large anomalies caused by genomic rearrangements are indicated with black bars. This analysis is usually facilitated by attempting to classify functionally all of the predicted gene products for which some kind of function can be inferred. The first attempt to produce a comprehensive hierarchical functional classification of the gene products of a single organism was for E. Classifying genes in this way allows the rapid identification of proteins required for known biochemical pathways, and the clustering of genes involved in specific cellular activities, such as host interaction. One-dimensional hierarchical classification schemes of this type do, however, suffer somewhat from the fact that gene products are only placed in one category, when they may participate in many different pathways or functions. Many analysis teams are now migrating to more complex classification schemes, the most common of which is the Gene Ontology http: A good example of this comes from the genome sequencing of Mycobacterium tuberculosis Cole et al. Subsequent laboratory investigation of these genes indicated that they were expressed under anaerobic conditions Hutter and Dick, , and might well be important for the virulence of the organism Weber et al. Several excellent collections of metabolic pathway information are available to assist in metabolic reconstruction attempts, and good examples of these are the Kyoto Encyclopaedia of Genes and Genomes KEGG; http: Other tools exist, such as WIT http: Obviously the metabolism of any microbe can only be reconstructed as far as the biochemical knowledge of current model organisms allows. Genomic analysis cannot, on its own, predict completely novel metabolic capabilities, although it may be able to suggest routes for experimental investigation. It should always be remembered that the metabolism of any organism may be significantly different from current models, and any attempt to investigate novel systems by comparison with these may risk imposing an apparent uniformity that is not a true reflection of the capabilities of the organism under study. Whilst the results of most programs and techniques used can be trusted most of the time, the

annotator must always be aware of potential problems. It is important to be guided by biological knowledge and understanding, and not solely by bioinformatic analysis, in order to gain a true insight into the meaning of the genomic information available. Basic local alignment search tool. The InterPro database, an integrated documentation resource for protein families, domains and functional sites. The Gene Ontology Consortium. The Pfam protein families database. H27 , is synthesized via a precursor molecule. The relationship between base composition and codon usage in bacterial genes and its use for the simple and reliable identification of protein-coding sequences. Computers Chemistry 17, Deciphering the biology of Mycobacterium tuberculosis from the complete genome sequence. Archaeal shikimate kinase, a new member of the GHMP-kinase family. Profile hidden Markov models. Horizontal gene transfer among microbial genomes: Nucleotide sequence analysis of a type 1 fimbrial gene of Streptococcus sanguis FW Combining diverse evidence for gene recognition in completely sequenced bacterial genomes. Structure of an alanine transfer ribonucleic acid. Detecting anomalous gene clusters and pathogenicity islands in diverse bacterial genomes. Dinucleotide relative abundance extremes: Horizontal gene transfer in prokaryotes: Reconciling the many faces of lateral gene transfer. Asymmetric substitution patterns in the two DNA strands of bacteria. Detecting protein function and protein-protein interactions from genome sequences. Complete genome sequence of Salmonella enterica serovar Typhimurium LT2. Codon usage tabulated from international DNA sequence databases: A general method applicable to the search for similarities in the amino acid sequence of two proteins. The new gene mukB codes for a kd protein with coiled-coil domains involved in chromosome partitioning of E. Lateral gene transfer and the nature of bacterial innovation. Use of contiguity on the chromosome to predict functional coupling. The genome sequence of the food-borne pathogen Campylobacter jejuni reveals hypervariable sequences. Complete genome sequence of a multiple drug resistant Salmonella enterica serovar Typhi CT Genome sequence of Yersinia pestis, the causative agent of plague. Improved tools for biological sequence comparison. Assigning protein functions by comparative genome analysis: Genome sequence of enterohaemorrhagic Escherichia coli O Functions of the gene products of Escherichia coli. Escherichia coli gene products: In Escherichia coli and Salmonella: Cellular and Molecular Biology Neidhardt, F. Computational identification of noncoding RNAs in E. Identification of common molecular subsequences. A dot-matrix program with dynamic threshold control suited for genomic DNA and protein sequence analysis. Crystal structure of the N-terminal domain of MukB: Identification of novel small RNAs using comparative genomics and microarrays. Chaperonin turned insect toxin. At the time of writing, 57 complete bacterial genome sequences have been published, together with 13 archaeal sequences, but a further prokaryotic genomesequencing projects are under way Genomes OnLine Database; Bernal et al. This means that within a few years we will have over prokaryotic genome sequences, releasing roughly protein-coding gene sequences into the public databases. How are we to make sense of all this information? One way is to exploit the range of high-throughput functional genomics approaches described elsewhere in this volume. Another is to try to use the sequence data themselves to devise hypotheses that can be tested in the laboratory and that can inform our view of the biology of the organism s from which they came. It then often becomes clear that assumptions about what is typical of a bacterial system, based on observations in a single model organism, are simplistic or even erroneous when placed in the context of an analysis drawing on dozens or hundreds of genome sequences, for example, the archetypal sortase gene in Staphylococcus aureus is rather atypical in not clustering with genes of its substrates Pallen et al. Several impediments limit our ability to draw the clearest and bestinformed conclusions from the sequence data. Any attempt to formulate novel hypotheses should aim to draw on this best, most current data, but searching all the unfinished genome projects individually is very time consuming. With that in mind, several attempts have been made to gather up these sequences into a single searchable database Tateno et al. These not only save time by allowing many in-progress sequences to be searched simultaneously and by facilitating follow-up of hits by easy sequence retrieval but, in the case of ViruloGenome, also allow more sensitive searches through, for example, position-specific iterative basic local alignment sequence tool PSI-BLAST searches over more comprehensive databases. Use of unfinished

sequence data can bring other problems. Broadbased analyses of protein families can often add value to a genome sequence, for example, our analysis of sortase-like proteins and their substrates has been cited in some definitive genome sequence papers Hoskins et al. However, publication of analyses of extended regions of a genome could jeopardize the publication of a definitive description of the sequence by those who did the hard work in completing it Marshall, For this reason, careful attention should be paid to acceptable use policies associated with the data and, when in doubt, it is advisable to contact the owners of the sequence. Also, one must always remember that any analyses on incomplete genome sequences and their predicted proteins must be considered tentative until the genome is complete. Although an incomplete genome sequence is better than none, Parkhill has stressed the importance of finishing genome sequences as crucial genes may lurk in the gaps. Even finished genome sequence data present problems in that annotation is usually superficial, is often misleading and is sometimes plain wrong Bork and Koonin, ; Galperin and Koonin, ; Brenner, ; Dandekar et al. This is not surprising, given that sequence

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One way is to exploit the range of high-throughput functional genomics approaches described elsewhere in this volume. Another is to try to use the sequence data themselves to devise hypotheses that can be tested in the laboratory and that can inform our view of the biology of the organism(s) from which they came.

Advanced Search Abstract Next-generation sequencing technologies have had a dramatic impact in the field of genomic research through the provision of a low cost, high-throughput alternative to traditional capillary sequencers. These new sequencing methods have surpassed their original scope and now provide a range of utility-based applications, which allow for a more comprehensive analysis of the structure and content of microbial genomes than was previously possible. With the commercialization of a third generation of sequencing technologies imminent, we discuss the applications of current next-generation sequencing methods and explore their impact on and contribution to microbial genome research. Craig Venter Institute http: The complete sequences of these first bacterial genomes were quickly followed by the larger genomes of Bacillus subtilis [6] and Escherichia coli [7] and the genomes of the eukaryotes Saccharomyces cerevisiae [8], Caenorhabditis elegans [9], Arabidopsis thaliana [10], Drosophila melanogaster [11] and ultimately the human genome [12 , 13]. However, despite advances in sequencing methodologies, sequencing cost remained relatively high and prohibitively expensive for most research groups. The high cost per base and low throughput of the traditional slab gel or capillary electrophoresis CE sequencing platforms prompted the development of so-called next-generation sequencing NGS technologies that provided a much greater throughput at a substantially lower cost [14]. The technical details of NGS technologies have been extensively reviewed elsewhere [14â€”16] and are not discussed here. Instead, this review will summarize recent developments of NGS, and explore their contribution to the field of microbial genomics. Furthermore, this review focuses on the application of NGS technologies to the sequencing and analysis of bacterial genomes, the genome sequencing and genome analysis of viruses and other nonprokaryotic microbes is not discussed. However, since an additional bacterial genome sequences have been completed, published and deposited in online databases Figure 1. As of 12 October , complete and draft Bacterial, Archaeal and Eukaryal genomes have been deposited online of which are bacterial Figure 1. A Published genome sequences for the three domains of life as of April B Distribution of completed and on-going genome projects amongst the three domains. C Phylogenetic distribution of bacterial genome sequencing projects. View large Download slide Published genomes. Prior to the development of NGS technologies, sequencing methodologies based on the Sanger sequencing chemistry dominated the genome sequencing industry. Automated Sanger capillary-based sequencing technologies, which rely on clone libraries, were too expensive, time consuming and labor intensive for the routine sequencing of bacterial genomes [17]. Consequently, bacterial sequencing projects focused on model organisms or those with practical applications, i. Resequencing Using NGS technologies to sequence bacterial genomes was not without attendant problems. Early in the development of NGS technologies read lengths were short, ranging between 35 bp Illumina and bp Roche ; significantly shorter than the bp obtainable with automated capillary sequencers. De novo genome assembly with short read technologies results in highly fragmented assemblies, because of the reduction in assembly quality with decreasing read lengths [21]. In assemblies derived from NGS reads, all gaps are typically as a direct result of unresolved repeats [22]. With short reads, repetitive segments longer than the read length become more common, which increases the complexity of the assembly problem resulting in more fragmented assemblies. Consequently, it was believed that NGS-derived short read sequencing data would be unsuitable for de novo genome assembly. However, the low cost and high-throughput of these platforms was ideally suited to the resequencing of whole genomes. Forty years of genome sequencing has resulted in an abundance of publically available genome sequences stored in online databases. This catalog of genomesâ€”containing representatives from nearly all phylaâ€”provides a bank of reference species to which reads are aligned to reconstruct the

genome of the target organism [23 , 24]. Accurately resequencing a genome requires that the reads must be long enough to allow for their correct mapping to the reference genome. Additionally, the number of reads which map to the reference increases with increasing read length, stabilizing at read lengths of approximately 40 nt [21 , 25]. The emergence of multidrug-resistant strains poses a particular global health risk. In active infections, M. However, in latent infection, it was believed that it was unlikely the bacterium would develop new mutations and treatment typically involved one antibiotic, isoniazid. In a recent study which sequenced and compared M. The authors suggest, based on the pattern of polymorphisms they detected, that the in vivo mutation rate is due to DNA oxidation. Moreover, treatment of latent infections with only isoniazid poses a significant risk and could result in the emergence of isoniazid-resistant strains. This study illustrates the power of microbial genome NGS for informing clinical practice. De novo sequencing and assembly Despite short read lengths, NGS technologies have been and continue to be successfully applied in de novo bacterial genome sequencing projects. The de novo NGS of the kb genome of M. Sixteen of the 25 gaps were as a direct result of unresolved repeats, highlighting the difficulties posed by these regions during the assembly process. The read lengths and throughput of NGS technologies have steadily increased since Increasing read length improves assembly quality by reducing the number of gaps and increasing contig size [21 , 22 ,

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Functional Microbial Genomics provides in-depth accounts from scientists working with these new technologies explaining both the techniques and the ways in which they have been applied to the study of gene function in different microbial species.

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