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MEETING REVIEWS

Vibrio2005: the First International Conference on the Biology of Vibrios

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The First International Conference on the Biology of Vibrios was held at Ghent University, Ghent, Belgium, from 6 to 8 November 2005. One hundred thirty participants from 32 countries attended this meeting (Fig. 1). It was held in an impressive, refurbished medieval monastery, Het Pand, originally established in 1228 by Dominican monks in the heart of the historical city of Ghent. Het Pand is an exceptional venue with rooms with spacious arched ceilings, stone walls, and very beautiful windows. The goal of the meeting was to discuss the various types of research under way that is focused on vibrios, including their biodiversity, ecology, genomics, proteomics, bioinformatics, pathogenesis, and epidemiology. The meeting was also designed to coincide with the eminent publication of *The Biology of Vibrios*, an ASM Press book which covers the topics in vibrio research also presented at Vibrio2005. R. R. Colwell highlighted, in her keynote lecture, that some 20 years ago, not more than a half dozen researchers would have attended such a meeting. Now it is understood that vibrios play important roles in the health of humans and many different marine hosts, in addition to being an abundant and virtually ubiquitous component of the aquatic microbiota. Vibrios contain nearly all known bacterial genetic elements, including (super)integrons, episomes, plasmids, transposons, and bacteriophages, making them an attractive model for the study of genome plasticity.

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TAXONOMY, BIODIVERSITY, AND BIOCOMPLEXITY

One highlight of the Conference was the keynote address by R. Colwell on the global role of vibrios. Colwell spoke of utilizing a unifying scientific approach to the study of vibrios, referred to as biocomplexity, which integrates findings from the atomic level to the environmental level (7, 8). The convergence of people with expertise in several complementary areas, such as biology, epidemiology, mathematics, medicine, and geography, with the aim of modeling environmental changes may be used as a tool for predictive/preemptive medicine. The combination of remote sensing and molecular biological techniques may offer researchers the opportunity of studying vibrios from a macroscale perspective and lead to correlations between the presence and abundance of particular species with given environmental parameters, e.g., the presence of chlorophyll and nutrients, sea surface temperature, and sea level (18). Future studies may be devised to determine the role of specific species in the health of marine life, such as in the process of coral (bleaching) disease.

The concept of the word "species" for vibrios generated considerable debate among conference attendees, in light of the seemingly extremely high rates of horizontal gene transfer and recombination occurring between related *Vibrio* species, e.g., *V. harveyi*, *V. tubiashii*, and *V. splendidus*. For example, Martin Polz (MIT) quantitatively analyzed the annual dynamics of *V. splendidus* within coastal bacterioplankton by a combination of culture-independent and -dependent techniques.

FIG. 1. Group photo.

That study suggested that the *V. splendidus* group consists of at least 1,000 distinct genotypes, each of which occurs at extremely low environmental concentrations (on average, <1 cell/ml). Moreover, the genomes show extensive neutral allelic diversity and size variation (39), and the phylogenetic trees constructed with different genetic markers from these strains were not congruent, suggesting high levels of homologous recombination.

Clearly a question to be addressed in future studies is what constitutes a species of vibrio in nature. Following genetic analysis of large collections of isolates, it becomes clear that the standard polyphasic taxonomy (15, 37) may not be sufficient to describe and differentiate species of vibrios. The use of multilocus sequence analysis (MLSA) was highlighted by different researchers as a means to develop a better, more automatable, and portable taxonomic tool. A new prototype taxonomy of vibrios based on the sequencing of multiple housekeeping genes was presented by Fabiano Thompson of UNICAMP (38). A number of biodiversity studies based on MLSA were presented, including the analysis of fish symbionts by Paul Dunlap of the University of Michigan (2, 13) and the analysis of vibrios associated with sea anemones (*Actinia* sp.) by Ed Feil of the University of Bath. Paul Dunlap explored the question of cospeciation in symbiotic luminescent vibrios of deep-sea fish. He found nearly identical *Photobacterium kishitanii* strains in several different fish species, including members of the Acropomatidae, Chlorophthalmidae, Macrouridae, Moridae, and Trachichthyidae. This fact could be taken as evidence against the cospeciation hypothesis proposed for this *Photobacterium* species and its hosts.

Clearly the path toward an automated taxonomic database will be through the use of gene sequences and World Wide Web resources (http://lmg.ugent.be/bnserver/MLSA/Vibrionaceae/). We encourage the use of *recA*, *pyrH*, *rpoA*, *atpA*, and *obg* as markers in future biodiversity, biogeography, taxonomic and evolutionary studies. As contingencies, we suggest the use of *uvrB*, *thd*, *serS*, *pheS*, *ligA*, *hsp60*, *mdh*, and *adk*. While data gathered in recent MLSA studies show that the species of vibrios may be delineated at a cutoff level of around 94% sequence similarity (see, e.g., reference 38), additional analyses using collections of fresh isolates are needed in order to shed light on the forces leading to diversification in vibrios.

Another important issue raised for discussion concerned the crucial role of institutional culture collections as repositories of important collections of vibrios in underpinning ecological and biotechnological studies worldwide. The facilities of international reference collections, such as the LMG Bacteria Collection at Ghent University (http://bccm.belspo.be/index.htm), the CAIM collection (www.ciad.mx/caim), and the Brazilian Collection of Environmental and Industrial Microorganisms (http://webdrm.cpqba.unicamp.br/), must be relied upon for the deposition of biological material to guarantee that important laboratory collections of vibrios do not become lost with time. This is a fundamental problem, since strain availability has not always been guaranteed by authors in recent biodiversity studies, which may compromise the reproduction of the observations and the success of future research in a variety of topics.

ECOLOGY

A general theme emerged at the meeting that environmentally relevant investigations will need to move out of the laboratory for study of vibrios in the field, and ideally, these investigations should be coupled with temporal studies (i.e., with observations measured in hours, in days, across seasons, from year to year, and throughout a decade); this type of approach is still rare and needs to be encouraged. Daniel Keymer of Stanford University compared the genomes and

phenotypes of *Vibrio cholerae* strains along the coast of California for 18 months and was able to link these data with 30 physical-chemical and biological environmental parameters, such as temperature and the presence of dissolved nutrients. In the isolates, genes involved in chemosensing, cell envelope biosynthesis, and binding and transport of nutrients varied depending on these parameters, suggesting that different *V. cholerae* populations dominate in different seasons.

Diane McDougald of the University of New South Wales presented data on the pivotal role of quorum sensing in the regulation of biofilm formation, virulence, and protection against protozoan grazing (20). She suggested that the use of quorum signaling molecules (e.g., furanones) could open up new avenues for the control of infectious disease (29). Consistent with this possibility, Tom Defoirdt of Ghent University showed that virulence may be attenuated in *V. harveyi* by using such molecules, allowing for new and more environmentally friendly treatments for vibriosis in the shrimp farming industry (11).

Further analyses of the effects of environmental parameters on vibrio behavior was presented by James Oliver (University of North Carolina at Charlotte), who utilized membrane diffusion chambers to study gene expression of clinical and environmental *Vibrio vulnificus* strains in estuarine settings (34, 35). He detected the expression of virulence genes, such as hemolysin (*vvhA*) and capsule (*wza* and *wzb*), during the starvation-survival state in cold estuarine waters (ca. 5°C) that are conducive to a viable but nonculturable state. In contrast, catalase (*katG*) was expressed only in warm estuarine waters (>20°C). Since catalase plays a key role in the culturability of *V. vulnificus* in complex (H_2O_2-rich) media, the loss of catalase activity may be considered a cold shock response that contributes to the viable but nonculturable state. Hege S. Tunjo of the Norwegian School of Veterinary Science reported that *Vibrio salmonicida*, a fish pathogen, adheres more promptly to host fish cells at low temperatures and salt concentrations than at high temperatures and salt concentrations, indicating a feature of this cold water pathogen that is adaptive to these environmental parameters.

GENOMICS

The origin of the two chromosomes in vibrios was addressed by John Heidelberg (TIGR). He argued that an ancestral protovibrio with a single (large) chromosome captured a mega-plasmid, which, in turn, evolved into the small chromosome (17). Comparative genomic analysis of the complete genome sequences for several *V. cholerae* strains, both clinical and environmental isolates, is under way and is defining what constitutes a pathogenic strain. At least 15 whole-genome sequencing projects of vibrios are under way, opening up the possibility of massive advances in the understanding of the biology of these microbes through bioinformatics tools (http://www.tigr.org/tigr-scripts/CMR2/CMRHomePage.spl). Dave Ussery (the Technical University of Denmark) described several excellent tools available from the Center for Biological Sequence Analysis for mining current data sets and comparing whole-genome sequences (http://www.cbs.dtu.dk/researchgroups/compmicro.php).

Using whole-genome sequence information of *V. vulnificus*, Anne-Marie Quirke (National University of Ireland) detected massive genome plasticity among a collection of 28 isolates from different continents. Both clinical and environmental isolates harbored genomic islands, with particular genes encoding integrases, multidrug efflux pumps, and hydrolases found associated specifically with the clinical genomic islands. One mechanism of lateral gene transfer affecting the genomes of vibrios is the integron gene capture system (5, 21, 30). Yan Boucher (Macquarie University) reported that the gene cassette content conservation of integrons is very limited, even within the same species. He found a high functional diversity (i.e., plasmid addiction, phage relatedness, metabolism, and information processing) among cassettes recovered from vibrios isolated from aquaculture facilities and surface seawater despite the fact that 70% of these elements could not be assigned a function. A similar proportion of gene cassettes of unknown function were found in a survey of 1,500 cassettes from marine sediments at Halifax Harbor.

Another mechanism for lateral gene transfer is bacteriophages. The toxigenic conversion of *V. cholerae* by CTXϕ is a well-known example of lateral gene transfer (41), but phage-mediated gene transfer that confers new phenotypic attributes is likely to be common in many vibrios. John Paul III (University of South Florida) pointed out that vibriophage genomes evolve modularly and independently of the host. Phages may infect completely unrelated hosts (e.g., the KVP40 can infect several different *Vibrio* species) (27), and most phages that infect noncholera vibrios belong to the families *Podoviridae* and *Myoviridae*. One example of a phage conferring virulence attributes to its host is the *V. harveyi* Myovirus-like lysogenic phage, which encodes hemolysins and an *N*-6-adenine methyltransferase (ADP-ribosylating toxin) (24). Another potential virulence-associated phage is the newly described phage ϕHSIC of *Vibrio pelagius*, which encodes a hemagglutinin related to streptococcal hemagglutinin.

Bacteriophages can also have a major impact on disease epidemiology by controlling the prevalence of pathogenic strains in the environment. Shah M. Faruque (ICDDRB, Bangladesh) discussed the epidemiology of cholera in light of his recent findings on the role of lytic phages in the dynamic cycle of cholera epidemics in Bangladesh. He presented a model of the initiation and cessation of epidemics driven by the actions of phages (14). In this model, lytic phages are proposed to be amplified within the human host and then shed into the environment, where they reduce the abundance of *V. cholerae*, resulting in the end of the epidemics. New epidemics occur due to the appearance of new variants of *V. cholerae* resistant to this dominant lytic phage.

INTERACTIONS WITH HOST ORGANISMS

One of the best-studied relationships of a vibrio with a host organism is the symbiotic relationship between *Vibrio fischeri* and the squid *Eupyrmna scolopes*. The process of *V. fischeri* colonizing the squid light organ and becoming bioluminescent is a fascinating interplay of vibrio and host responses, and the recent completion of the whole-genome sequence of the bacterium (31), as well as an EST library of the host light organ, is likely to dramatically enhance our understanding of this symbiosis. Amy Schaefer of the University of Washington highlighted the use of whole-genome microarrays to unravel the

complex symbiotic relationship between *V. fischeri* and *E. scolopes*. She found that *V. fischeri* has a chitin utilization pathway similar to that previously described for *V. cholerae* (22) and that this pathway is upregulated during squid colonization. This led to the identification of chitin provided by the squid functioning as both a key nutrient and a chemotactic signal guiding the movement of *V. fischeri* into the light organ. Interestingly, Michael Miller (Stanford University) reported that environmental and clinical *V. cholerae* strains become naturally competent after growth on chitin (23), suggesting that growth within the marine environment on its natural hosts may stimulate horizontal gene transfer.

A number of species are best known for their deleterious effect on host organisms, and some of these pathogenic mechanisms were highlighted. Tetsuya Iida (Osaka University) has characterized two distinct type III secretion systems (TTSSs) found in *Vibrio parahaemolyticus*, a human pathogen. TTSSs are known to secrete effector proteins directly into host cells, and Iida's studies implicate TTSS1 in cytotoxicity, while TTSS2 appears to be involved in enterotoxicity (19, 25, 26). Iida detected TTSSs in clinical and environmental strains of several *Vibrio* species, suggesting that this may be a common pathogenic mechanism among virulent vibrios. One of the most prominent attributes of most vibrios is the polar flagellum, and Karl Klose (University of Texas at San Antonio) has found that the flagellar regulatory system controls not only flagellar synthesis but also nonflagellar genes, including those involved in virulence (9, 10, 28). The mechanism(s) by which the flagellum regulates these nonflagellar genes appears to be complex and likely involves GGDEF proteins, which synthesize cyclic diguanylate and are known to affect *V. cholerae* virulence and biofilm formation (6, 36, 40). Another example of cyclic diguanylate involvement in biofilm formation was presented by Rosana Ferreira (University of Iowa), who showed that signaling by a GGDEF/EAL-containing protein regulates the expression of biofilm-related polysaccharide genes in *Vibrio parahaemolyticus* (4, 16).

The potential of vibrios to cause disease in aquatic (marine) organisms was emphasized throughout the meeting. Jorge Crosa (Oregon Health and Science University) highlighted the role of the siderophore anguibactin in the virulence of the fish pathogen *Vibrio anguillarum*. The gene encoding anguibactin and surrounding genes are nearly identical to those found in the human pathogen *Acinetobacter baumannii* that encode acinetobactin, suggesting possible horizontal gene transfer between these pathogenic bacteria (1, 12). Vibrios have also been found to cause significant disease in nonvertebrate marine hosts. Colin Munn (University of Plymouth) described the pathogenic potential of *Vibrio coralliilyticus* toward corals and sea fans in both Australia and the United Kingdom, while Tomoo Sawabe (Hokkaido University) identified *V. harveyi* as the etiological agent of recent mass mortality among the Japanese abalone *Haliotis discus hannai*. This bacterium has gained notoriety as a cause of heavy mortalities in peneid shrimp in South America and South East Asia. Christine Paillard (IFREMER) showed *Vibrio tapetis* virulence toward clam (*Ruditapes philippinarum*) hemocytes, probably due to the action of a hemolysin. Yan Labreuche (IFREMER) demonstrated that the virulence of *Vibrio aestuarianus* toward the oyster *Crassostrea gigas* is related to the expression of a zinc metalloprotease with homology to the H/A protease of *V. cholerae*, which has been implicated in virulence in humans (32, 33, 3). Thus, these two *Vibrio* species apparently utilize the same protease to cause disease in oysters and humans.

CONCLUDING REMARKS

The Vibrio2005 meeting succeeded in bringing together scientists working on diverse aspects of the biology of vibrios, and this resulted in the participants recognizing and highlighting the shared attributes of this large and important group of marine bacteria. The meeting enabled an appreciation for the genomic plasticity, host adaptability, and environmental responsiveness of this fascinating group of organisms. Due to the importance of continued and renewed efforts toward a better understanding of the biology of vibrios and the success of the present meeting, the scientific committee established the Association of Vibrio Biologists (AVIB; http://www.vibriobiology.net/). The main goals of the association are to promote collaboration on vibrio research and to disseminate information on the latest breakthroughs and insights in vibrio research through biannual meetings.

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