

## CHAPTER 8

# Conclusions

*I have yet to see any problem, however complicated, which, when you looked at it in the right way, did not become still more complicated.*  
*Poul Anderson (New Scientist, 25 Sept., 1969, p638)*

### **8.1 Characterisation and modification of native *D. nodosus* plasmid, pDN1 for the development of a transformation system**

A number of genes encoding potential virulence determinants have been identified in *D. nodosus*, however there is no transformation system, which precludes direct testing of the role of these and other genes in virulence. In an effort to address this problem, in this work, a native *D. nodosus* plasmid pDN1 was isolated, sequenced, characterised, and modified to contain appropriate antibiotic resistance markers and a multiple cloning site. Derivatives of the native *D. nodosus* plasmid were subsequently used in transformation experiments with the aim of developing a transformation system for *D. nodosus* so that the role of *vap* and other virulence associated genes in virulence could be determined directly. The development of such a transformation system is dependent upon a large number of empirical factors, and although numerous parameters were varied in transformation experiments no transformants were obtained. Future experiments should investigate other mechanisms by which *D. nodosus* might be transformed, and particularly the potential for pDN1 to be utilised for the development of a conjugative transfer system should be investigated.

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## 8.2 Northern blot analysis of the *vap* genes in *D. nodosus*

In the absence of a transformation system for *D. nodosus* one is relegated to employing more indirect methods in order to establish whether the *vap* genes of *D. nodosus* have a role in virulence. Previous investigations have concentrated on analyses at the DNA level. Southern blot experiments indicated that (i) multiple copies of the *vap* genes are not required for virulence; (ii) that the arrangement of the *vap* genes was similar in benign and virulent strains of *D. nodosus*; and (iii) that the presence or absence of certain *vap* genes, did not determine whether a given strain exhibited a benign or virulent phenotype (Bloomfield *et al.*, 1997). In this study, northern blot experiments were undertaken to determine whether the other *vap* genes are expressed at the RNA level in the virulent and/or benign strains in which they are present. The results suggest that the *vap* genes (in general) are expressed in the virulent and benign strains in which they are present, and although differential expression of the *vap* genes was observed, the differences were not related to the virulence of the isolates. In addition, the transcripts detected in these analyses correlated well with those predicted from analyses undertaken at the DNA level. It was confirmed that *vapB* and *vapC* are expressed as an operon, as are *toxA* and *vapA*, whilst *vapD* is not. Furthermore, the results indicate that *vapE* is transcribed from two transcriptional start sites, and one of these messages includes *vapH* and *vapG*. The arrangement and analyses of the DNA sequence of *vapHG* suggests that the *vap* element contains a superinfection immunity region, like that of defective bacteriophage P4.

## 8.3 Further characterisation of the *intB* element in *D. nodosus*

It was previously proposed that a genetic element, called the *intB* element was present adjacent to the *attR* site of *vap* region 3 of *D. nodosus* virulent strain A198 (Bloomfield *et al.*, 1997). It was unknown whether sequences adjacent to *intB*, *regA*, and

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*gepA* corresponded to part of an integrated element or otherwise. In an effort to further characterise the *intB* element, chromosome walking to the right of *gepC* was undertaken, and a sequence of 4.3 kb was determined. Five potential open reading frames designated *gepC*, *gepD*, *gepE*, *gepF* and *gepG* were identified. *gepD* and *gepE* appear to encode components of a sulfate binding-protein dependent ABC importer complex whilst *gepF* is likely to encode a thiamine biosynthesis protein. These results suggest that these genes are bacterial housekeeping genes rather than genes of an integrated genetic element. The prevalence, arrangement and integrity of the *intB* element in seventeen strains of *D. nodosus* was also investigated and results suggest that at least ten strains (A198, 1311, 1311A, AC3577, D1172, C305, 819, 3138, 1469, 1493) contain a truncated copy of a primordial *intB* element which consists of *intB*, *regA* and *gepA*. The remaining seven strains (H1215, H1204, 1169, AC390, 2483, G1220, B1006) studied do not contain *gepA*, and *regA* and *gepB* are not adjacent in these strains. Thus, it has been proposed that sequences separating *regA* and *gepB* in these seven strains may be part of another inserted sequence or be the product of a genomic rearrangement which resulted in the deletion of *gepA*.

#### **8.4 Identification and characterisation of part of an *intD* element from *D. nodosus***

It was proposed that a sequence previously separating the *pnpA* gene and *intB<sub>N</sub>* in the original laboratory strain of C305 (C3051) was lost, or moved position, generating our current laboratory strain of C305 (C3052). In order to investigate the nature, origin and prevalence of the sequences that separated *pnpA* and *intB<sub>N</sub>* in strain C3051, a 3.7 kb sequence from the lambda clone  $\lambda$ GB300 (Bloomfield, 1997) was determined. Within these *intD* element sequences six putative open reading frames were identified which share similarity to mobilisation genes from non-conjugative and conjugative plasmids, and

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transposons. In addition, putative *oriV* and *oriT* regions were identified. This work confirmed that these *intD* element sequences had been lost rather than moved elsewhere in the C305 genome. Southern blot analyses of seventeen other strains of *D. nodosus* indicated that eleven strains contained none of the sequences which so far define the *intD* element, whilst four strains (1311, AC3577, B1006, D1172) contain only part of it, and only two strains (819, 3138) contain all the of *intD* element sequences tested. These results indicate clearly that the *intD* element was acquired horizontally *via* the integration of a mobilisable and possibly conjugative plasmid or transposon into the *D. nodosus* genome. Furthermore, the results suggest that the *intD* element may have a significant role in the acquisition and dissemination of other genetic elements in *D. nodosus*.

## 8.5 Characterisation of an *intC* element in *D. nodosus*

The presence of a new genetic element in *D. nodosus* strain C305, designated the *intC* element was postulated previously (Bloomfield, 1997). In an effort to determine whether genes that were adjacent to an integrase gene, *intC*, were a part of *intC* element, Southern blot analyses and PCR experiments were undertaken in seventeen different strains of *D. nodosus*. The results revealed that where genes *orf242* and *orf171* are present, they are always immediately adjacent to a copy of the *intC* gene, and therefore constitute part of a single genetic element. This was further supported by the observation that *intC*, *orf242*, and *orf171* were lost together, in strain 1311. Analyses revealed that only two strains of *D. nodosus* do not contain sequences that so far define the *intC* element.

A significant step forward was made in understanding how virulence might be regulated in *D. nodosus* when the spontaneous loss of the *intC* element and the *intD* element in one strain of *D. nodosus* was observed to result in the loss of protease

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thermostability, a virulence factor in *D. nodosus*. The subsequent analysis of the integration sites for the *vap*, *intB* and *intC* elements in seventeen strains of *D. nodosus*, and the studies of the prevalence and integrity of these elements in these strains, suggests that in *D. nodosus*, virulence may be modulated by the site-specific integration of genetic elements. Mechanisms by which the *vap*, *intC* and *intB* elements might modulate virulence were postulated, and thus further studies should be undertaken in order to determine which of mechanism/s are correct. The proposal that genetic elements which appear to carry no classical virulence determinants may modulate virulence by the site-specific integration of horizontally transferred and interacting genetic elements is unlikely to be a novel mechanism of virulence gene regulation, and has significant implications for footrot eradication programs currently in p ace in Australia, and consequently is worthy of further investigations.

## 8.6 General Conclusions

Bacterial evolution and the genetics of bacterial virulence is intertwined with the transfer and acquisition of mobile genetic elements such as plasmids, phages, transposons and conjugative transposons (Mahan, Slauch & Mekalanos, 1996), and the *D. nodosus* genome provides a good example of this. The ability to acquire complex traits in a single step, rather than by undergoing the natural selection of genes, such as those involved in virulence, for many generations provides a rapid mechanism for changes in bacterial-host interactions (Meccas & Strauss, 1996). In *D. nodosus* to date, numerous genetic elements have been identified and at least partially characterised, including the *vap* element (Cheetham *et al.*, 1995; Katz, Stružnell & Rood, 1992; Katz *et al.*, 1994), the *intB* element (Bloomfield *et al.*, 1997), the *intC* element (Whittle *et al.*, unpublished), the *intD* element (Chapter 6), plasmid pDN1 (Chapter 3), native bacteriophage DinoHI (Bloomfield, 1997), the *vrl* region (Haring *et al.*, 1995; Katz *et al.*, 1991), and another element, the *intE*

element has been postulated (Chapter 7). Five of these elements (*vap*, *intB*, *intC*, *intD* and *intE* elements) have been identified primarily because they integrate into the same position of the *D. nodosus* chromosome as the *vap* element. Analyses of these elements have indicated that many of these *D. nodosus* elements are chimeric, in that they contain features common to plasmids, phages, transposons and conjugative transposons, all at the same time.

It has previously been established that the acquisition of novel genetic elements may have a significant impact on the host genome, since their integration can facilitate DNA rearrangements *via* homologous recombination between different sites in the genome, resulting in deletion, inversion and fusion events. In addition, the acquisition of novel genetic elements can affect the virulence of the host organism.

Some genetic elements including plasmids, bacteriophage (Waldor, 1998), transposons and pathogenicity islands harbour classical virulence determinants (Hacker *et al.*, 1997; Ott, 1993). Classical virulence factors are defined in the literature as all those factors that contribute to infection and disease without having essential cell structure or metabolic (“housekeeping”) functions (Mahan *et al.*, 1996; Ott, 1993). Examples of classical virulence factors include genes involved in adherence to host tissues, toxin production, invasion into host cells and resistance to host defence mechanisms, and acquisition of iron. It is ultimately the coordinated action of a subset of these virulence factors at the appropriate time that result in pathogenesis (Falkow, 1981).

However, integrated genetic elements do not have to carry classical virulence factors in order to affect the expression of virulence-associated genes. The integration of genetic elements can also result in alterations in gene expression by encoding outward facing promoter sequences that can consequently affect the expression of adjacent genes (Craig, 1996; Craig & Kleckner, 1987; Dorman, 1994; Ou *et al.*, 1988). Also the

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integration of a mobile element can alter gene expression *via* altering the location of the genes in a genome and by affecting local topology (Dorman, 1995). More recently elements have been identified that disrupt the expression of tRNA genes after excision. Since these tRNA genes are required for housekeeping and virulence-associated functions their disruption also alters the virulence of the isolate (Blum *et al.*, 1994; Hacker *et al.*, 1997; Ritter *et al.*, 1995; Ritter *et al.*, 1997).

In this work, it has been proposed that genetic elements carrying none of the aforementioned classical virulence determinants appear to be able to modulate virulence in *D. nodosus* by affecting the expression of "housekeeping" genes encoding tRNA molecules (*tRNA<sup>ser</sup><sub>GCU</sub>* and *tRNA<sup>ser</sup><sub>GGA</sub>*), polynucleotide phosphorylase (*pnpA*), and a putative global repressor of virulence (*glpA*), which are adjacent to the predominant integration sites for these elements. It is likely that the potential role of such genes in virulence is often overlooked because they are not classical virulence factors. In addition, their role in virulence is likely to be difficult to identify, since such genes are involved in many cell processes, some of which may include virulence-associated functions, and so they have pleiotropic effects on the phenotype of an organism. In addition, such genes are present in both virulent and benign strains and hence would not be identified by subtractive hybridisation.

All of the *D. nodosus* elements studied in this work satisfy most of the criteria for classification as pathogenicity islands (Pais) (Hacker *et al.*, 1997). They all integrate into the 3'-end of tRNA<sup>ser</sup> genes (*tRNA<sup>ser</sup><sub>GCU</sub>* or *tRNA<sup>ser</sup><sub>GGA</sub>*), are flanked by direct repeats and appear to have been acquired by the integration of an element which has features common to bacteriophages and plasmids. All except the *vap* element, which contains a toxin/antidote plasmid maintenance system, appear to be unstable, and the *vap* (40.6%) and *intD* (31.8%) elements appear to have lower G + C contents than the *D. nodosus* chromosome (45%) (Holdeman, Kelley & Moore, 1984). Except for the *vap* element

however, work done herein shows that the other elements are not preferentially associated with more virulent strains of *D. nodosus*. Furthermore even the *vap* region does not appear to contain classical virulence factors like other Pais (Hacker *et al.*, 1997), though it is possible they have a role in virulence *via* carrying regulatory genes which affect the expression of existing virulence determinants. Since the *D. nodosus* elements are like Pais except that they do not appear to carry classical virulence determinants, they may be of value in understanding Pais in general, and so broaden our knowledge about evolutionary mechanisms involved in creating new pathogens.

It is likely that the current interest in pathogenicity islands may lead to the identification of numerous other integrated genetic elements, that like the *D. nodosus* elements, carry no classical virulence factor but have an affect on expression of genes adjacent to the integration site.

The putative ability of *D. nodosus* to modulate virulence by moving or losing certain genetic elements at appropriate times in growth and/or infection may be important for microbial-host interactions in general. Death of a host does not provide an optimal rate of transmission and survival, and so microorganisms that are well adapted to their host should exhibit reduced virulence, and one mechanism by which they may achieve this is by optimisation of virulence gene regulation according to their environment. One way by which virulence gene expression might be optimised could be by stimulating the reversible movement and/or transfer of genetic elements at appropriate times.

Further investigations aimed at identifying factors that regulate or initiate the movement of these genetic elements in nature may yield insights into whether such rearrangements are random biological events, or whether the rearrangement of these genetic elements are triggered by the same environmental signals that switch classical virulence factors on or off. If the later is the case, this would support the idea that the



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movement of genetic elements may be a regulatory mechanism employed by pathogens in general to regulate the expression of virulence-associated genes.

Since many virulence factors are expressed in response to environmental stresses due to changes in temperature, pH, osmolarity, anaerobiosis, or specific chemicals (Dorman, 1994), it is possible that the movement or excision of genetic elements is associated with the expression of virulence also, since it has been established that agents that cause cell stress *via* causing DNA damage or inhibition of DNA replication also cause prophage induction (Birge, 1994). Prophages in turn, are also known to induce the excision of pathogenicity islands (Lindsay *et al.*, 1998; Waldor, 1998).

The observation that these *D. nodosus* elements were acquired horizontally, suggests that these elements also have the capacity to be transferred from one bacterium to another. This is supported by the presence of *cis* elements required for autonomous replication and conjugative transfer, the identification of putative mobilisation and conjugative transfer genes, and the identification of a circular intermediate in the case of the *vap* element. In addition, at least two of these elements, the *intD* and *intC* elements, can be lost or move concomitantly in at least two strains of *D. nodosus*. It is unclear by what mechanism the *D. nodosus* elements are transferred however it may involve specialised transduction by a helper bacteriophage or conjugative transfer mediated by a co-resident conjugative element such as the *intD* element, or by both of these mechanisms. Further investigations of how *D. nodosus* elements are transferred may give us further insight into evolution of bacteria *via* horizontal transfer mechanisms in general.

The similarities and differences between different *D. nodosus* elements is also very interesting. Five of these *D. nodosus* elements (*vap*, *intB*, *intC*, *intD* and *intE* elements) recognise the same target sites for integration in the genome, next to *askA* and *pnpA* respectively. It is therefore perhaps not surprising that the integrase genes of the *vap*, *intB*,

*intC* and *intD* elements (*intE* has not been isolated) are more highly related to each other than to integrase genes from other elements. The similarity between these elements is not confined to the integrase genes, as certain sequences within these elements are also highly related. The *intD* element contains 102 bp repeats and a putative *oriT* which are also present in the *vap* element. The *intC* element contains a putative immunity region, like the *vap* element. The presence of homologous sequences in these elements also greatly enhances the potential for recombination between these elements. Perhaps this is why so many variants of these elements appear to be present in *D. nodosus* genomes.

To illustrate this point, there are three copies of the *vap* regions in *D. nodosus* strain A198, however all three copies are clearly different from each other. Furthermore within these regions the sequences of these genes diverge differentially. The copy of *vapD* in region 1 has 100% identity to the copy in region 3, and yet *vapE'* has only 67% identity to *vapE*. It is difficult to explain this differential divergence, unless these *vap* elements are actually different but related genetic elements. Restriction fragment length polymorphisms are also associated with the *intC* element sequences, and the *intD* element in different strains of *D. nodosus*, suggesting that there may also be variations within these elements.

The sequence similarity between these elements together with the observation that these five *D. nodosus* elements integrate preferentially into the same two positions of the *D. nodosus* chromosome, suggests that these *D. nodosus* elements may interact with each other. These elements could form heterogenous concatemers both in the *D. nodosus* chromosome and in transfer. Such interactions might favour survival of these elements in the host genome, since integration into one or two positions of the *D. nodosus* chromosome would be less likely to be deleterious to the host organism. It is ironic that despite the apparent fluidity of the *D. nodosus* genome, and the presence of so many pieces of foreign DNA, *D. nodosus* seems to be very difficult to transform with plasmid DNA.

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If as suggested, *D. nodosus* elements do interact, are transferred as concatemers and modulate virulence *via* site-specific integration in the recipient chromosome, this has significant implications for the eradication and control of footrot. A benign strain of *D. nodosus* could be converted to a virulent strain, and *vice versa*. The idea that a virulent strain could reversibly become a benign strain is significant, since footrot eradication programs only employ measures by which to control the spread of virulent strains of *D. nodosus*. Programs are not aimed at controlling the spread of benign strains.

Recent advances in microbial ecology have now started to consider microorganisms in terms of communities, that communicate *via* the secretion of environmental sensing molecules such as acylated-homoserine lactones (AHLs). It is known that footrot is characterised by a mixed bacterial infection of the hoof, and although it is only when *D. nodosus* is applied to the hoof in pure culture that the disease progresses, it has been proposed that the infection may involve symbiosis (Beveridge, 1941). However, the role of other organisms in the progression of footrot has not yet been investigated. Given that intercellular communicating molecules like AHLs are being identified in an increasing number of microorganisms, it is likely that intercellular communication between *D. nodosus* cells and those from other symbiotic microorganisms at the site of infection are likely to have some role in pathogenesis. Perhaps as we learn more about these interactions, the study of bacteria present in an infection as a community, in addition to the study of pure cultures of a microorganism, may become important in the study of pathogens and pathogenesis in the future.

It is hoped that the analysis of bacterial genome organisation, and, in particular, the investigation of the deletion and integration of genetic elements, as has been begun in *D. nodosus*, will ultimately contribute to a better understanding of microbial evolution, and the complex multifactorial nature of bacterial pathogenesis, both in *D. nodosus* and in microorganisms in general.

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