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Proteomic analysis of Chilo iridescent virus

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ABSTRACT

In this first proteomic analysis of an invertebrate iridovirus, 46 viral proteins were detected in the virions of Chilo iridescent virus (CIV) based on the detection of 2 or more distinct peptides; an additional 8 proteins were found based on a single peptide. Thirty-six of the 54 identified proteins have homologs in another invertebrate and/or in one or more vertebrate iridoviruses. The genes for 5 of the identified proteins, 22L (putative helicase), 118L, 142R (putative RNaseIII), 274L (major capsid protein) and 295L, are shared by all iridoviruses for which the complete nucleotide sequence is known and may therefore be considered as iridovirus core genes. Three identified proteins have homologs only in ascoviruses. The remaining 15 identified proteins are so far unique to CIV. In addition to broadening our insight in the structure and assembly of CIV virions, this knowledge is pivotal to unravel the initial steps in the infection process.

Introduction

Chilo iridescent virus (CIV), also known as Invertebrate iridovirus 6, belongs to the family Iridoviridae and is the type species of the genus Iridovirus (Fauquet et al., 2005; Williams, 1996; Williams et al, 2005; Willis, 1990). Iridoviruses are large, cytoplasmic, icosahedral viruses with a linear double-stranded DNA genome, which is both circularly permuted and terminally redundant (Darai et al., 1983; Goorha and Murti, 1982). The CIV virion consists of an unusual three layer structure containing an outer proteinaceous capsid, an intermediate lipid membrane, and a core DNA–protein complex containing the 212, 482 bp genome (Jakob et al., 2001; Williams, 1996; Williams et al., 2005). Up to now, thirteen complete sequences of iridovirus genomes have been published, including CIV (Huang et al., 2009; Williams et al., 2005). The availability of the CIV sequence facilitates the identification and functional analysis of the proteome of CIV virions. Replication of CIV occurs in the nucleus of infected cells and the assembly takes place in the cytoplasm (Goorha and Murti, 1982).

Many questions remain to be answered concerning the structure and scaffolding of the virus particles, the nature of virus–host interactions and the initial steps in virus infection, including the mechanism behind the onset of transcription of CIV genes. Viral structural proteins are likely to play crucial roles in these processes. Initiation of viral transcription for instance requires one or more virion proteins, since CIV DNA alone is not infectious, similar to what has been shown for the vertebrate iridovirus Frog virus 3 (Willis and Granoff, 1985). In previous studies, efforts have been made to characterize the polypeptides in CIV virions by one- or two-dimensional SDS-PAGE. The presence of 21–28 polypeptides was revealed by one-dimensional SDS-PAGE, while 35 polypeptides were observed in two-dimensional SDS-PAGE (Barray and Devauchelle, 1979, 1985; Cerutti and Devauchelle, 1985; Kelly and Tinsley, 1972; Orange and Devauchelle, 1987). The size of these polypeptides ranged from 11 to 300 kDa. However, most of these proteins were not further characterized and it is unknown, except for the major capsid protein MCP, by which CIV genes they are encoded.

In the current study we identified the CIV virion proteins by a proteomic approach, based on a combination of one-dimensional SDS-PAGE and Liquid Chromatography/Mass Spectrometry/Liquid Spectrometry (LC-MS/MS). The data obtained were analyzed by searches against a CIV ORF database. This provided a fast and highly sensitive method for the identification of genes through the sequences of the encoded proteins (Pandey and Mann, 2000).

Results

To identify the virion proteins of CIV, the proteins of purified virion particles were separated by one-dimensional SDS-PAGE. Staining of the gel with colloidal blue revealed at least 21 proteins ranging from 10 to 250 kDa (Fig. 1) much in line to what has been found previously (Barray and Devauchelle, 1979, 1985; Cerutti and Devauchelle, 1985; Kelly and Tinsley, 1972; Orange and Devauchelle, 1987). The gel lane was divided into 6 slices containing proteins with a molecular mass lower than 26 kDa, ranging from 26–34 kDa, 34–43 kDa, 43–55 kDa or 55–95 kDa and higher than 95 kDa, respectively. The proteins were digested with trypsin and analyzed by LC-MS/MS. A decoy database strategy (Elias and Gygi, 2007) was used which, after applying the appropriate filters,
resulted in 89 protein hits: 54 CIV proteins, 34 contaminants and 1 decoy hit giving a False Discovery Rate of 1.1%. Out of the 54 CIV proteins, 46 of the more abundant proteins were identified with 2 or more peptides (Table 1), while relatively small proteins like ORFs 342R, 227L or 104L as well as some less abundant proteins could be identified with one peptide only (Table 2). The proteins with one hit were manually verified to correlate well to the theoretical b+y ion spectrum and to be unique for one protein only (see also Supplementary Material S1).

The proteins identified are indicated in Fig. 1. A genomic map of CIV ORFs that encode polypeptides represented in the proteome of CIV particles is shown in Fig. 2. For individual CIV virion proteins, 2.7% to 70% of the amino acid sequence was covered with peptides retrieved from the analysis. The major capsid protein (MCP) encoded by ORF 274L is one of the most abundant CIV proteins (Barray and Devauchelle, 1979, 1985; Cerutti and Devauchelle, 1985; Kelly and Tinsley, 1972) and this is clearly re-
have evolved from invertebrate iridoviruses (Stasiak et al., 2003). The kinase, and ATPase III, and led to the hypothesis that ascoviruses may have homology to an entomopoxvirus gene (Table 1, Fig. 2). These results underscore the evolutionary distance of iridoviruses from both baculoviruses and entomopoxviruses and the closer relation to ascoviruses. Despite the proposed close evolutionary relation between the symbiotic ascoviruses, but not in other iridoviruses (209T, 422L and 374R). One of these (422L) is the only CIV virion ORF with a baculovirus homolog in the 34 ORFs with all iridoviruses: 022L, 118L, 142L, 274L (MCP) and 295L, and these may be considered to belong to the major capsid protein activity (Tan et al., 2009b) is notable in the CIV genome. Three of the identified CIV virion ORFs are found in one or more ascoviruses, but not in other iridoviruses (209T, 422L and 374R). One of these (422L) is the only CIV virion ORF with a baculovirus homolog (Cydia pomonella granulovirus ORF34). The gene products of six of the eleven SfAV1a homologs were also found in the proteome of SfAV1a virions (Tan et al., 2009a). A homolog of the SfAV1a virion protein P64, which was recently shown to be a major DNA binding protein with proposed DNA condensing activity (Tan et al., 2009b) is not encoded in the CIV genome. (DpAV4a). The gene products of six of the eleven SfAV1a homologs were also found in the proteome of SfAV1a virions (Tan et al., 2009a). A homolog of the SfAV1a virion protein P64, which was recently shown to be a major DNA binding protein with proposed DNA condensing activity (Tan et al., 2009b) is not encoded in the CIV genome. Three of the identified CIV virion ORFs are found in one or more ascoviruses, but not in other iridoviruses (209T, 422L and 374R). One of these (422L) is the only CIV virion ORF with a baculovirus homolog (Cydia pomonella granulovirus ORF34; genus Betabaculovirus). ORF 337L shares thirteen viral protein homologs with Singapore grouper iridovirus (SGIV) virion proteins identified by two independent mass spectrometric approaches (Chen et al., 2008; Song et al., 2004). Fifteen of the 34 ORFs with homologs in IV3, also have homologs in one or more vertebrate iridoviruses. The CIV proteome shares five ORFs with all iridoviruses: 022L, 118L, 142L, 274L (MCP) and 295L, and these may be considered to belong to the iridovirus core genes. The Rana gryllus iridovirus (RGI) ORF 53R, which is a homolog of the putative core gene 118L, has been shown to encode a novel iridovirus envelope protein (Zhao et al., 2008). The CIV proteome shares thirteen viral protein homologs with Singapore grouper iridovirus (SGIV) virion proteins identified by two independent mass spectrometric approaches (Chen et al., 2008; Song et al., 2004). Previous phylogenetic studies on ascoviruses were based on comparative analyses of the capsid protein, DNA polymerase, thymidine kinase, and ATPase III, and led to the hypothesis that ascoviruses may have evolved from invertebrate iridoviruses (Stasiak et al., 2003). The proteomic analysis of CIV performed here showed that 16 ORFs encoding CIV virion proteins have homologs in one or more ascoviruses (Asgari et al., 2007; Bideshi et al., 2006; Bigot et al., 2008; Stasiak et al., 2000; Wang et al., 2006). Nine CIV structural proteins have homologs in Heliothis virescens ascovirus 3e (HvAV3e), thirteen have homologs in Trichoplusia ni ascovirus 2c (TnAV2c), eleven in Spodoptera frugiperda ascovirus (SfAV1a) and six in Diadromus pulchellus ascovirus 4a (DpAV4a). The gene products of six of the eleven SfAV1a homologs were also found in the proteome of SfAV1a virions (Tan et al., 2009a). A homolog of the SfAV1a virion protein P64, which was recently shown to be a major DNA binding protein with proposed DNA condensing activity (Tan et al., 2009b) is not encoded in the CIV genome. (DpAV4a). The gene products of six of the eleven SfAV1a homologs were also found in the proteome of SfAV1a virions (Tan et al., 2009a). A homolog of the SfAV1a virion protein P64, which was recently shown to be a major DNA binding protein with proposed DNA condensing activity (Tan et al., 2009b) is not encoded in the CIV genome. (DpAV4a). The gene products of six of the eleven SfAV1a homologs were also found in the proteome of SfAV1a virions (Tan et al., 2009a). A homolog of the SfAV1a virion protein P64, which was recently shown to be a major DNA binding protein with proposed DNA condensing activity (Tan et al., 2009b) is not encoded in the CIV genome.
ascovirus DpAv4a and Chilo iridescent virus (Bigot et al., 2009) the number of CIV virion proteins with homologs in DpAv4a is limited in comparison to the other ascoviruses.

Although the morphology of the virions of members of the family Ascoviridae differs considerably from that of viruses of the family Iridoviridae, evidence is mounting that the ascoviruses and iridoviruses shared a common ancestor. Phylogenetic analyses based on proteins found in most enveloped dsDNA viruses provide strong evidence that ascoviruses evolved from iridoviruses, despite the marked differences in the characteristics of the virions belonging to these two families and differences in their cytopathology (Bigot et al., 2008). The conservation of structural proteins between CIV and ascoviruses further supports the hypothesis of common ancestry.

In conclusion, this is the first detailed study towards the determination of the virion proteins of an invertebrate iridovirus. This study will contribute to a better understanding of the molecular mechanisms underlying CIV virion assembly, CIV entry into cells, the initial steps of early iridovirus gene expression and the cell to cell movement of this virus.

Materials and methods

Preparation of virus particles and gel electrophoresis

CIV was propagated in larvae of the wax moth, Galleria mellonella, isolated as described by Marina et al. (1999) and further purified by 25–65% sucrose density gradient centrifugation. The purified CIV particles were checked for quality by transmission electron microscopy and quantified by UV spectroscopy. The purified particles were denatured and the proteins were separated by 12% one-dimensional SDS-PAGE. The gel was stained with colloidal blue and the gel lane containing the virion proteins was cut into six segments based on a comparison with molecular markers. Each gel piece was sliced and dehydrated with acetonitrile (100%) (ACN). After vacuum drying, the gel segments were incubated in 10 mM dithiothreitol in 50 mM ammonium bicarbonate (ABC buffer) at 57 °C for 1 h and subsequently in 55 mM iodoacetamide (Sigma) in ABC buffer at room temperature for 1 h. After a final wash step with ABC buffer the gel material was dried.

Trypsin digestion and LC-MS/MS

In-gel protein digestions were performed using sequencing grade modified porcine trypsin (Promega, Madison, WI) in ABC buffer at 37 °C for 15 h, after which the digests were centrifuged at 6000 g. The supernatants were collected, and the remaining gel pieces were extracted with 5% trifluoroacetic acid (TFA) and then with 15% ACN /1% TFA. The extracts were combined with the supernatants of the original digests, vacuum-dried, and the dried material was dissolved in 20 μl 0.1% formic acid in water. The peptides resulting from this digestion were analyzed by LC-MS/MS. To this aim, 18 μl of the samples were concentrated over a 0.10×32 mm Prontosil 300-5-C18H (Bischoff, Germany) pre-

Table 2

| ORF NCBI Accession No | Molecular mass (kDa) | Peptide sequence | Protein coverage (% by amino acids) | MH+ (ppm) | Delta m/z (ppm) | z | Xcorr |
|----------------------|----------------------|-----------------|------------------------------------|-----------|----------------|---|-------|
| 317L AAK82178        | 43.95                | IVNLIPQGQFQAK   | 3.11                               | 1455.832  | −0.30          | 2 | 1.77  |
| 130R AAB94451        | 23.18                | ICFSEQPPLDFSNIK | 7.46                               | 1812.847  | 1.04           | 2 | 2.86  |
| 307L AAK82168        | 22.86                | LKPLGYNLSIQ     | 5.58                               | 1245.720  | 0.33           | 2 | 1.81  |
| 395R AAK82255        | 17.28                | YAINNENQYR      | 6.62                               | 1284.597  | −0.72          | 2 | 2.54  |
| 010R AAK81948        | 12.84                | TGSMVCSSTR      | 8.33                               | 1065.471  | 3.19           | 2 | 2.34  |
| 342R AAK82203        | 9.33                 | IQAQNYATMGCLN-QCSQR* | 21.59                          | 2156.055  | 2.74           | 2 | 3.73  |
| 227L AAK82088        | 7.72                 | TFAVEVPR*       | 14.30                              | 1095.583  | 1.49           | 2 | 2.61  |
| 104L AAB94434        | 7.05                 | RVACSPR*        | 12.30                              | 845.441   | 2.01           | 2 | 2.78  |

* The same peptide was measured multiple times in different gel slices.

Fig. 2. Linearized genomic presentation of the 54 CIV structural protein ORFs determined by LC-MS/MS. Arrows indicate the positions and the direction of gene transcription (R or L). Red arrows are ORFs unique to CIV, green arrows represent ORFs present in all sequenced iridovirus genomes. The yellow and the white ORFs, have an entomopox- and baculovirus homolog, respectively. The remaining ORFs are indicated in blue. Genomic positions are indicated on the right in base pair number.
**Table 3**

List of CIV virion proteins identified by LC-MS/MS ordered by mass with homolog in other iridoviruses and/or ascoviruses.¹

| Invertebrate | Vertebrate | Lympoviroidea | Megaloviroidea | Ascoviridae |
|--------------|------------|----------------|----------------|-------------|
| Irido-virus  | Chlorido-virus | Ranavirus       | LCDVvirus      | ISKNV       |
| CIV          | III         | ATTV            | LCDV-C         | ISKNV       |
| 443L         | 91L         | 72R             | 234R           | 76L         |
| 295L         | 16L         | 45R             | 92R            | 72L         |
| 179L         | 32L         | 41L             | 29L            | 75L         |
| 022L         | 67L         | 57L             | 45R            | 144R        |
| 261L         | 91L         | 27L             | 110R           | 93R         |
| 209L         |             | 78L             | 76L            | 84L         |
| 390L         | 01L, 8L     | 80L             | 59L            | 128L        |
| 268L         | 74L         | 30L             | 63L            | 96R         |
| 149L         | 113L        | 11L             | 61L            | 161R        |
| 232R         | 84L         | 21R             | 85L            | 90R         |
| 439L         | 35R         |                 | 110R           | 141R        |
| 361L         | 24L         |                 | 114L           | 140R        |
| 380R         | 10L         |                 | 111L           | 101R        |
| 213R         | 51L         |                 |                | 114R        |
| 118L         | 6R          |                 |                | 118R        |
| 158L         | 69L         | 53L             | 35L            | 157L        |
| 274L         | 14L         | 55R             | 7L             | 51L         |
| 229L         | 46R         | 88L             | 8L             | 150L        |
| 337L         | 47R         | 49L             | 8L             | 151L        |
| 329R         | 59R         | 157R            | 8L             | 154R        |
| 219L         | 36R, 91L    | 35R             | 85L            | 158R        |
| 142R         | 101R        | 28R             | 85R            | 161R        |
| 155L         | 113L        | 85L             | 83R            | 168R        |
| 401R         | 68R         | 85L             | 85R            | 26R         |
| 117L         | 107R        | 111L            | 85R            | 94R         |
| 415R         | 18L         | 113L            | 85R            | 22R         |
| 309L         | 63R         | 83L             | 83R            | 181L        |
| 422L         |             | 20R             | 85R            | 109R        |
| 307L         | 33L         | 038L            | 16L            | 109R        |
| 378R         | 100L        | 123R            | 23R            | 100R        |
| 355R         | 104L        | 152L            | 43L            | 103L        |
| 374R         |             | 98L             | 43L            | 109L        |
| 203L         | 85L         | 98L             | 83L            | 109L        |
| 395R         | 1L          | 85L             | 85R            | 109L        |
| 453L         | 41R         | 32R             | 85R            | 114R        |
| 366R         | 63R         | 32R             | 85R            | 114R        |
| 010R         | 43R         | 35R             | 85R            | 114R        |
| 342R         | 115R        |                 |                | 114R        |

¹ORFs in bold are conserved in all analyzed iridovirus- and ascovirus genomes.

The a-d indices for the ascovirus ORFs refer to the following species:

- HvAV3 (Jancovich et al., 2003)
- TFV (Tidona and Darai, 1997)
- ISKNV (Tsai et al., 2005)
- STIV (Huang et al., 2009)
- LCDV-C (Wang et al., 2006)
- ATV (Asgari et al., 2007)
- Diadromus pulchellus ascovirus 4a (Wang et al., 2006)
- Spodoptera frugiperda ascovirus 1a (Bideshi et al., 2006)

The peptide mass tolerance for peptide precursor ions was set to 10 ppm (0.010% m/z 1000 amu) and for MS/MS fragment ions to 0.5 Da. An Invertebrate iridescent virus 6 protein database was used for the analysis (AF303741; created July 31, 2001; downloaded from www.ncbi.nlm.nih.gov/sites/entrez) after adding a list of commonly observed contaminants like: BSA (P02769, bovine serum albumin precursor), trypsin (P00760, bovine), trypsin (P00761, porcin), keratin K22E (P35908, human), keratin K1C9 (P35527, human), keratin K22E (P35908, human), keratin K1C9 (P35527, human). A decoy database was created by adding the reversed sequences using the program SequenceReverser from the MaxQuant package (Cox and Mann, 2008). The names of the other viruses are abbreviated as follows: CIV, Chilo iridescent virus (Jakob et al., 2001); IV3, Aedes taeniorhynchus iridescent virus (Delhox et al., 2006); ATV, Ambystoma tigrinum stebbensi virus (Jancovich et al., 2003); TVP, Tiger frog virus (He et al., 2002); FV3, Frog virus 3 (Tan et al., 2004); SGV, Singapore group iridovirus (Song et al., 2004); GIV, Grouper iridovirus (Tsai et al., 2005); STIV, Soft-shelled turtle iridovirus (Huang et al., 2009); LCDV-C, Lymphocystis disease virus – isolate China (Zhang et al., 2004); LCDV-1, Lymphocystis disease virus 1 (Tidona and Darai, 1997); ISKNV, Infectious spleen and kidney necrosis virus (He et al., 2001); RBIV, Rock bream iridovirus (Do et al., 2004); OSGIV, Orange-spotted grouper iridovirus (Li et al., 2005).
charge state 2+, Xcorr > 3.3 for charge state 3+ and Xcorr > 3.5 for charge state 4+ (Peng et al., 2003). Only those proteins that showed a Bioworks Score factor (SF) larger then 0.6 were considered.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jvirol.2010.05.038.

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