NAIST-IS-DD0661206

Doctoral Dissertation

Evaluation of predicted protein complexes emerged from protein interaction network and proposition of prediction method toward topological structure of protein complexes

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February 4, 2010

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A Doctoral Dissertation
submitted to the Graduate School of Information Science,
Nara Institute of Science and Technology
in partial fulfillment of the requirements for the degree of
Doctor of Engineering.

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Abstract

Proteins interact with other proteins or biomolecules to perform their functions, and protein complexes are the fundamental functional units of these macromolecular systems: protein interactions play a key role in many cellular processes. Therefore, elucidating protein-protein interactions (PPIs) leads to understanding the protein functions required for various biological processes in cells. More or less over the past 10 years, vast amount of PPI data have been generated by high-throughput methods for detecting protein interactions. However, there being no complete and accurate detection method, each experimental strategy generates a significant number of false-negatives and false-positives. Additionally, experimental methods which identify protein complexes such as affinity purification-mass spectrometry (MS) equally detect direct and non-direct interactions i.e. “bait-prey” and “prey-prey” interactions. These false-positives and confusion non-direct interactions with direct interactions are serious problems because they cause erroneous results and misleading conclusions.

The goal of this dissertation based on above background is to predict and evaluate certain protein complexes, more specifically i) to predict members of protein complexes and to evaluate that by annotation and ii) to propose a method to predict the topological structure of protein complexes. In analysis on human PPI network presented in Chapter 2, totally, 1,264 protein complexes were predicted by finding densely connected regions with their cluster properties in the network, and these predicted complexes were annotated and evaluated using integrated data such as literatures and research papers, ternary structures, description of proteins, localizations, expression profiles etc. The study on Arabidopsis interactome of

Chapter 3 proposes a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs). As the first step, I extracted 312 statistically significant DDIs out of 1,162 DDIs underlying 3,118 protein-protein interactions (PPIs). Next, 67 protein complexes were obtained by protein interaction network analysis. Finally, I discussed the topological structure of protein complexes based on DDI information extracted in the first step.

Keywords:
topological structure of protein complexes, protein-protein interactions (PPIs), domain-domain interactions (DDIs), graph theory, false-positive and false-negative, "bait-prey" and "prey-prey" interactions

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.*Doctoral Dissertation, Department of Bioinformatics and Genomics, Graduate School of Information Science, Nara Institute of Science and Technology, NAIST-IS-DD0661206, February 4, 2010.

Acknowledgements

First of all, I wish to express my deepest gratitude to **Professor Shigehiko Kanaya**, who has been the adviser for the research described in this dissertation. Regardless of his busy schedule, he has supported my wishes through many kinds of efforts for the accomplishment of this dissertation. I could have never got such wonderful experiences without his warmest supports. I never forget his warmest assistance for me.

I would also like to thank **Associate Professor Md. Altaf-Ul-Amin** for his valuable suggestions and comments, and reviewing my papers and this dissertation, to **Assistant Professor Hiroki Takahashi** and **Professor Naotake Ogasawara** for their suggestions and comments, and review of this dissertation.

I'm highly thankful to the members of Comparative genomics laboratory, especially **Mr. Masayoshi Wada**, who really supported domain detection by InterProScan, and **Ms. Aki Hirai**, who constantly supported my clerical ministrations.

I'm sincerely thankful to the members of now-defunct JBIRC (Japan Biological Information Research Center), particularly **Dr. Shingo Kikugawa**, who and I designed and performed human PPI analysis together, **Dr. Yoshiharu Sato**, **Dr. Katsuhiko Murakami**, and **Team Leader Tadashi Imanishi**. This organization gave me the opportunity to research human PPI.

Finally, I would like to offer deep and special thanks to my family. **My parents** and **my sister** babysat my baby son. Under their supporting, I have been able to spend considerable time on this work. And, above all, **Naoko**, who is my wife, understood my wish for taking the doctorate, and she has always warmly encouraged me to accomplish my work and this dissertation. Without her understanding and supporting, I couldn't have got this opportunity and achieved this work beside my business. I must never forget this appreciation of her supporting in my life.

February 2010

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Chapter 1 Introduction

1.1. Dissertation outline

Chapter 1 explains the background and the problem of protein-protein interaction (PPI) analysis, and indicates the goal of this dissertation. Section 1.2 explains detection method of PPIs and Section 1.3 elucidates problems of PPIs analysis caused by PPI detection method especially focused on the affinity purification-MS, which is one of the PPI detection methods. Section 1.4 gives some suggestive ideas for a common approach of studies of this dissertation. Taking these matters into consideration, Section 1.5 indicates the goal of this dissertation. Aiming to the goal of this dissertation, I tried two kinds of studies: i) predicting members of protein complexes in human and evaluating that by annotation (in Chapter 2) and ii) proposing a method to predict the topological structure of protein complexes by determining statistically significant domain-domain interactions (in Chapter 3).

Chapter 2 considers integrating PPI data from public PPI databases and predicting protein complexes, and evaluating the predicted complexes by annotation using integrated data such as such as literatures and research papers, ternary structures, descriptions of protein, localizations, expression profiles etc.

Chapter 3 proposes a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs). It is important to discuss the topological structure of protein complexes, because high-throughput methods for detecting protein interactions generate a significant number of false-positives, and additionally, the affinity purification-MS detects non-direct interactions: “prey-prey” interactions.

Finally, in Chapter 4 concluding remarks of this dissertation are described.

1.2. Protein-protein interaction and the detection

Proteins interact with other proteins or biomolecules to perform their functions, and protein complexes are the fundamental functional units of these macromolecular systems: protein interactions play a key role in many cellular processes. Therefore, comprehensive analysis of protein-protein interactions (PPIs) provides a valuable framework for understanding the protein functions required for various biological processes in cells.

To elucidate complete picture of PPIs in several organism, more or less over the past 10 years, vast amount of PPIs data have been generated by high-throughput methods for detecting protein interactions (Uetz et al. 2000; Ito et al. 2001; Ho et al. 2002; Gavin et al. 2002). Protein interactions can be analyzed by different genetic, biochemical, and physical methods, which are listed in Table 1.1 (Shoemaker and Panchenko 2007). Although a number of methods are available for high-throughput analysis of PPIs, the most commonly used are the yeast two-hybrid (Y2H) method and the combinatorial method of protein complex purification and protein identification by mass spectrometry (MS) (affinity purification-MS). The mechanisms of these two representative methods (Y2H and affinity purification-MS) are respectively outlined below.

Table 1.1 Different experimental methods of PPI detection**.**

High-throughput techniques are indicated with pluses (second column), and those which can provide information on interactions in vivo are shown in the third column. Fourth column indicates whether the method supplies data on physically interacting proteins in a complex ("complex") or only pairwise interactions ("binary"). Methods inferring interactions through functional association are shown as well. The type of protein interaction characterization is shown in the last column.

Method	High-Throughput Approach	Living Cell Assay	Type of Interactions	Type of Characterization
Y2H	+	In vivo	Physical interactions (binary)	Identification
Affinity purification-MS	+	In vitro	Physical interaction (complex)	Identification
DNA microarrays/Gene coexpression	+	In vitro	Functional association	Identification
Protein microarrays	+	In vitro	Physical interaction (complex)	Identification
Synthetic lethality	+	In vivo	Functional association	Identification
Phage display	+	In vitro	Physical interaction (complex)	Identification
X-ray crystallography, NMR spectroscopy	−	In vitro	Physical interaction (complex)	Structural and biological characterization
Fluorescence resonance energy transfer	−	In vivo	Physical interactions (binary)	Biological characterization
Surface plasmon resonance	−	In vitro	Physical interaction (complex)	Kinetic, dynamic Biological
Atomic force microscopy	−	In vitro	Physical interactions (binary)	Mechanical, dynamic characterization
Electron microscopy	−	In vitro	Physical interaction (complex)	Structural and biological

1.2.1. Yeast two-hybrid (Y2H) method

Yeast two-hybrid (Y2H) method analyzes the physical interaction between two proteins by detecting the expression of the reporter gene (Shoemaker and Panchenko 2007) (Figure 1.1). The premise behind the test is the activation of downstream reporter gene(s) by the binding of a transcription factor onto an upstream activating sequence (UAS). In Y2H method, the transcription factor is split into two separate fragments, called the binding domain (BD) and activating domain (AD). The BD is the domain responsible for binding to the UAS and the AD is the domain responsible for activation of transcription. For the purposes of testing the interactions, a protein of interest is fused to BD ("bait"). This chimeric protein is cloned in an expression plasmid, which is then transfected into a yeast cell. A similar procedure creates a chimeric sequence of another protein fused to AD ("prey"). If two proteins physically interact, the reporter gene is activated and expressed, and then the expression is detected. The most broadly used Y2H method is GAL4/LexA-based, where the GAL4 protein controls in yeast the expression of the LacZ gene encoding beta-galactosidase, though numerous variations of Y2H have been developed including systems with several reporter genes.

For screening entire genomes, the Y2H method has been advanced into two main approaches: matrix-based and library-based. In the *matrix approach*, a matrix of "prey" clones is created where each clone expresses a particular "prey" protein in one well of a plate. Then each "bait" strain is mated with an array of "prey" strains, and those diploids where two chimeric proteins interact are selected based on the expression of a reporter gene and the position on a plate. In the *library approach*, each “bait”s is screened against an undefined “prey” library containing random cDNA fragments or open reading frames (ORFs). Diploid positives are selected based on their ability to grow on specific substrates; and interacting proteins are determined by DNA sequencing.

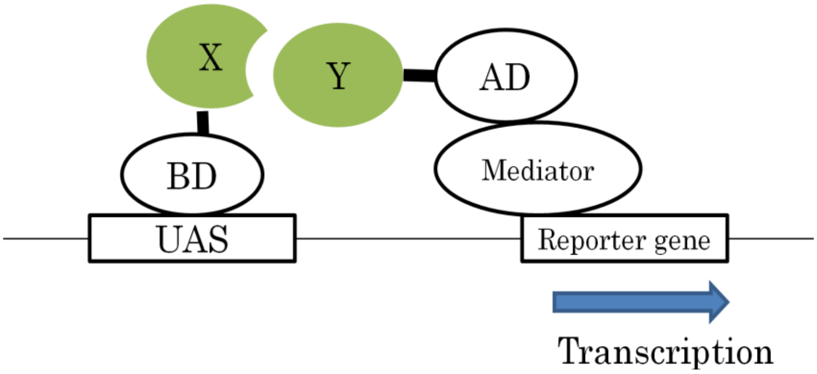


Figure 1.1 Y2H method illustration.

Yeast two-hybrid (Y2H) method analyzes the physical interaction between proteins X (“bait”) and Y (“prey”) by detecting the expression of the reporter gene. If two proteins physically interact, the reporter gene is activated and expressed.

1.2.2. Affinity purification-MS method

The affinity purification-MS is the combinatorial method of protein complex purification and protein identification by mass spectrometry (MS), i.e., a protein complex is purified by affinity purification, and then proteins in the complex are identified by mass spectrometry (MS).

The open reading frame (ORF) of a target protein is fused with the DNA sequences encoding the “tag” such as FLAG (Ho et al. 2002), TAP-tag (Gavin et al. 2002) or His-tag (Arifuzzaman et al. 2006), and expressed where it can form native complexes with other proteins. For purification, target protein complexes are fixed in affinity column through the tag of the target protein, and the contaminants are washed out. After washing, the target protein complex is released from affinity column by breaking away the interaction between the tag of target protein and affinity column. The components of each protein complex are screened by polyacrylamide gel electrophoresis, cleaved to fragments by proteases, and identified using subsequent analysis of the fragments by MS. The principle of the MS method is to produce ions which can be detected based on their mass-to-charge ratios, thereby allowing the identification of polypeptide sequences. The problem of converting protein/peptide molecules from the condensed phase into ions in the gas phase is solved by using Electrospray Ionization (ESI) and Matrix Assisted Laser Desorption Ionization (MALDI). Different algorithms have been developed to analyze mass spectra and to identify proteins by their sequence (Shoemaker and Panchenko 2007).

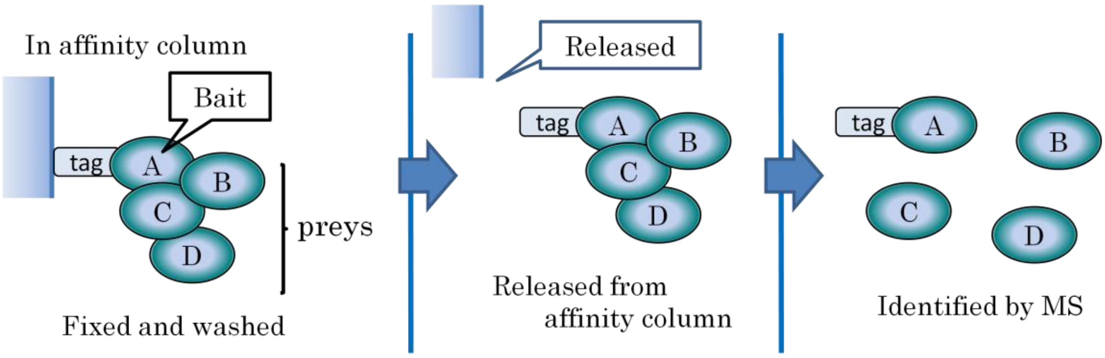


Figure 1.2 Affinity purification-MS illustration.

Target protein with tag is expressed in cells and form protein complexes. Protein complexes is fixed in affinity column and washed, then released from affinity column. And each protein in complexes is identified by MS.

1.3. Problems of PPIs analysis

1.3.1. Problems of false-negative and false-positive

The first genome-wide PPIs studies of a free-living organism using the yeast two-hybrid (Y2H) method have been published by Uetz and coworkers and Ito and collaborators using the yeast *Saccharomyces cerevisiae* (Uetz et al. 2000; Ito et al. 2001). Soon after these analyses, Ho and coworkers and Gavin and colleagues used the combinatorial method of protein complex purification and protein identification by mass spectrometry (MS), so-called affinity purification-MS (Ho et al. 2002; Gavin et al. 2002).

These two different experimental approaches for detecting protein interactions have already taught us one important lesson. That is two data sets obtained from Y2H and affinity purification-MS are strikingly different but are also highly complementary, i.e., each experimental strategy generates false-negatives and these two experimental methods have propensity to detect different kind of protein interactions: Y2H more often find transient interactions, whereas affinity purification-MS identifies stable interactions such as those in protein complexes (Titz et al. 2004). This variation is caused by the differences in mechanisms of protein interaction detection. Y2H test an interaction of pairs of proteins, and can detect transient interactions, but not detecting highly cooperative and weak interactions which constitute a protein complex. And, artificial domain fused to “bait” protein or “prey” protein in Y2H, i.e., the binding domain (BD) or activating domain (AD) of transcription factor, may interrupt the interactions between “bait” and “prey”. On the other hand, in affinity purification-MS, major bottleneck for MS analysis is low abundance of proteins. Proteins that are only weakly associated with protein complexes such as in transient interactions tend to be lost in the process of protein complexes purification.

Furthermore, each experimental strategy generates not only false-negatives but also a significant number of false-positives (Titz et al. 2004). False-positives are usually a more serious problem because they cause erroneous results and misleading conclusions, making PPI analysis complicated and difficult. In Y2H studies, some “bait” constructs activate the reporter gene without interacting with a “prey” and so may generate large numbers of technical false-positives, and over-expression can be a result of non-specific interactions. Moreover, some proteins might specifically interact when they are co-expressed in the yeast, although in reality they are never present in the same cell at the same time. Conversely, in affinity purification-MS, too weak washing during purification can generate technical false-positives: exquisite balance of washing strength is required because too weak washing may generate technical false-positives and too strong washing may generate technical false-negatives. Continuously, it is undeniable that tag of target protein might directly interacts with “prey” proteins, and as is the case with Y2H, some “bait” proteins might specifically interact with “prey” proteins when “bait” proteins are forced-expressed in a host cell, although in reality they are never present in the same cell at the same time.

Affinity purification-MS is a powerful method of studying PPIs, however, in addition to above problems of technical false-positives, it has critical problems about handling the data caused by fundamental principle of affinity purification-MS. That would be described the next section.

1.3.2. Problems of affinity purification-MS Data

An experimental method which identifies protein complexes such as affinity purification-MS, in the strict sense, detects all proteins in multiple complexes with a target protein (“bait”), but does not detect only direct PPIs. Isolation of protein complexes in these experimental procedure allow the purification of the “bait” together with all of the “prey” proteins that belong to the same multi-protein complexes. The problem seems to lie in the fact that every “prey” protein doesn’t directly interacts with the “bait” protein; rather, the topological structure of the complex will include both “bait-prey” and “prey-prey” interactions (Hakes et al. 2007). It implies that the topological structure of the protein complexes cannot be determined from the individual experiments only. In case that proteins A, B, C and D are identified in isolation as a protein complex using protein *A* with a tag as a “bait”, it is difficult to conclude what is the true topological structure of the complex out of the four sample cases as shown in **Figure 1.3** i)～iv): if we presume that the topological structure of protein complexes is linear, the order of proteins cannot be decide (the case i) or ii)). In addition, first of all, it is not determinable that topological structure of protein complexes is linear or non-linear (the case i), ii) or iii)). Furthermore, the member of protein complexes cannot be determined, i.e., the all of proteins identified by MS can construct a single complex or multiple complexes (the case i)~iii) or iv)).

Though understanding the topological structure of protein complexes is necessary in order to obtain useful information about them, little attention has been given by the bioinformatics researchers to decipher the topological structure of the protein complexes. Also the experimental technologies used to detect PPIs do not focus on this matter.

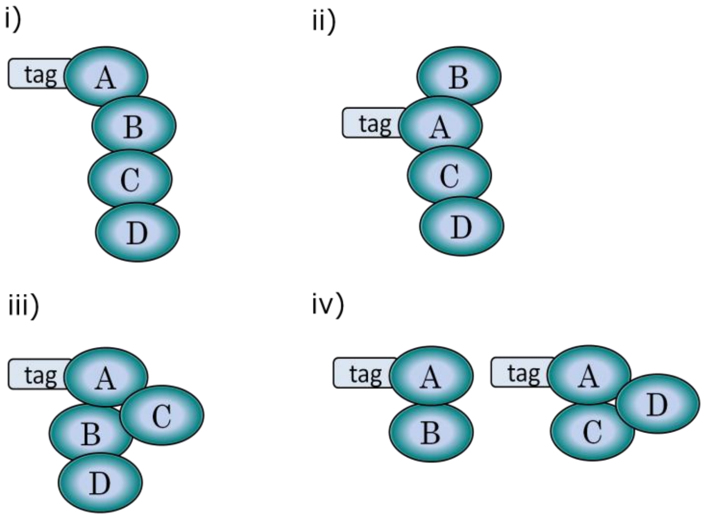


Figure 1.3 Topological structure diversity of protein complexes

Some topologies of protein complexes are conceivable in case that proteins A, B, C and D are identified by MS after affinity purification.

1.4. Suggestive ideas for approach of this dissertation

1.4.1. Handling of affinity purification-MS data

Generally, in practice to analyze PPIs of affinity purification-MS data, pairwise interactions are assigned by applying either a “spoke model” or “matrix model” to each complex (**Figure 1.4**). In a spoke model, only interactions of a “bait” and each “prey” are applied to pairwise interactions, while in a matrix model, all possible interactions among a “bait” and all “preys” are applied to pairwise interactions.

Here, we would think which model (spoke model or matrix model) should be adopted in this study using **Figure 1.5**. In the case of i) in **Figure 1.5**, proteins A~F construct a single protein complex, while in the case of ii), proteins construct multiple protein complexes (proteins A, B, C, D complex and proteins A, E, F complex). In the case of adopting matrix model, not only case i) but also case ii) results in obtaining complete graph in that a “bait” protein A interacts with “preys” proteins B~F. Conversely, in the case of adopting spoke model, each two case i) and ii) results in obtaining specific graph by integration of pairwise interactions of each “bait” proteins A~F and corresponding “prey” proteins. That is graphs after integration of applying spoke model of affinity purification-MS data for each “bait” protein in protein complexes can represent specific topologies depending on the separation patterns of protein complexes. Therefore, in the study of this dissertation, I adopted spoke model.

The following issue, in example of **Figure 1.5**, is how to determine the members of protein complexes from respectively specific topologies of graph. In the case of i), a single complex composed of proteins A~F should be predicted, while in the case of ii), multiple complexes composed of proteins A, B, C, D and proteins A, E, F should be predicted from the topology of graph. **Figure 1.5** demonstrates clusters of proteins densely interacting each other would correspond to protein complexes. In next section, clustering of nodes focusing the density in the graph theory would be described, in order to predict members of protein complexes from these topologies depending on the separation patterns of protein complexes.

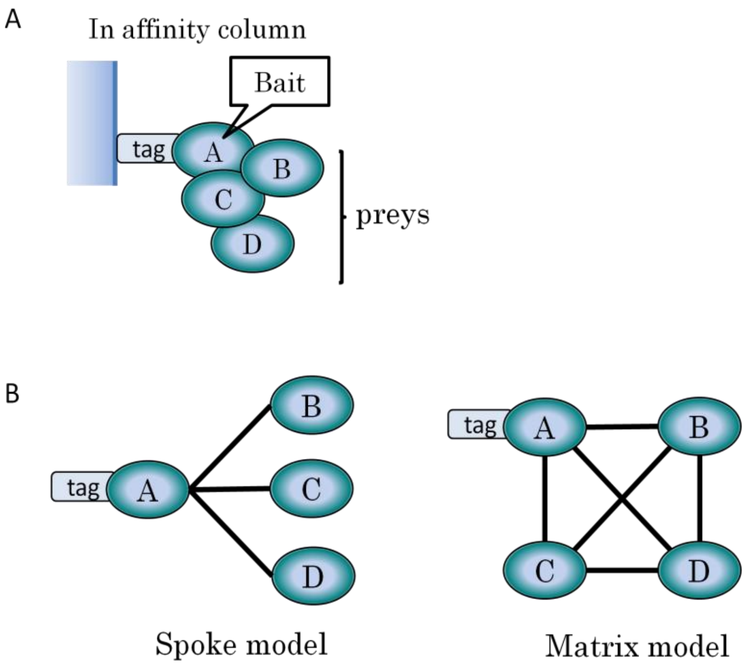


Figure 1.4 PPIs models generated from affinity purification-MS data

Two models (spoke model and matrix model) can be generally applied when pairwise interactions are assigned from affinity purification-MS data.

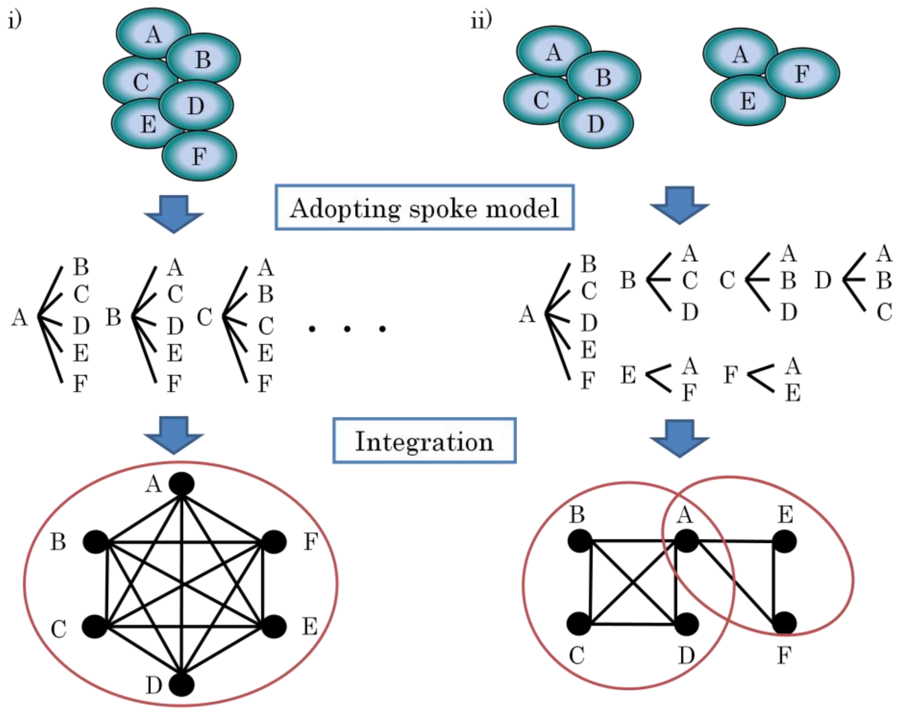


Figure 1.5 Advantages of adopting spoke model for affinity purification-MS data

Graphs after integration of applying spoke model of affinity purification-MS data for each "bait" protein in protein complexes can represent specific topological structure depending on the separation pattern of protein complexes.

1.4.2. Graph clustering software, DPClus

A PPI network can be represented as a graph in that nodes indicate proteins and edges indicate interactions. The discussion of foregoing section suggest that the densely connected clusters in a protein interaction network generated from affinity purification-MS data should be predicted as protein complexes. DPClus is a graph clustering software that can extract densely connected clusters in a network using an algorithm that is based on density and periphery tracking of clusters (Altaf-Ul-Amin et al. 2006). While using DPClus, it is necessary to provide a value of minimum density for the generated clusters (d), a minimum value for cluster property for the nature of periphery tracking (cp), and a minimum number of nodes in a cluster.

Here, in an undirected simple graph G=(N, E) that consists of an finite set of nodes N and a finite set of edges E, density d_k and cluster property cp_{nk} are respectively defined below.

The ***density*** d_k of any cluster k is the ratio of the number of edges present in the cluster ($|E_k|$) and maximum possible number of edges in the cluster ($|E_k|$) and the maximum possible number of edges in cluster ($|E_k|_{\max}$), and is represented by (1). $|N_k|$ is the size of the cluster, i.e. the number of nodes in the cluster. The density of a cluster is a real number ranging from 0 to 1.

$$d_k = \frac{|E_k|}{|E_k|_{\max}} = \frac{2 \times |E_k|}{|N_k| \times (|N_k| - 1)} \qquad (1)$$

The ***cluster property*** cp_{nk} of any node n with respect to any cluster k of density d_k and size$|N_k|$ is defined by (2). $|E_{nk}|$ is the total number of edges between the node n and each of the nodes of cluster k. The cluster property is a real number ranging from 0 to 1.

$$cp_{nk} = \frac{|E_{nk}|}{d_k \times |N_k|} \qquad (2)$$

In the cluster formation process, the cluster starts as a single node which is selected as cluster seed in the target graph, and then grows gradually by adding nodes one by one from its priority neighbors. The neighbors of a cluster are the nodes connected to any node of the cluster but not part of the cluster. In adding nodes of the cluster formation, the density d_k and the cluster property cp_{nk} are checked to determine that the node should be added or not to a cluster.

1.5. The goal of this dissertation

The goal of this dissertation based on above background is to predict certain protein complexes, more specifically i) to predict members of protein complexes and to evaluate that by annotation and ii) to propose a method to predict the topological structure of protein complexes. Analysis on human PPI network is presented in Chapter 2, which predicts certain new protein complexes in the PPI network. Protein complexes are predicted by finding densely connected regions with their cluster properties in the network, and these predicted complexes are annotated and evaluated using integrated data such as literatures and research papers, ternary structures, descriptions of protein, localizations, expression profiles etc. The study on *Arabidopsis* PPI network of Chapter 3 proposes a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs).

Chapter 2

Prediction and evaluation of human protein complexes from the integrated protein interaction network

2.1. Abstract

Background: Comprehensive analysis of PPIs provides a valuable framework for understanding the protein functions required for various biological processes in cells, and in recent years, a number of well-organized public PPI databases have become available. However, overlap ratio of PPI data entities across databases is relatively low, so that we only have a partial map of the whole interactome space from each PPI databases, and it is essential to integrate PPI data in order to fill in as many holes in the interactome space as possible. And, the next important issue for the elucidation of the functional organization of the proteome is the extraction of information about protein complex formation and function from the PPI network.

Results: Here, I report the first attempt of comprehensive annotation of human protein complexes identified from the network of integrated protein-protein interactions (PPIs). I predicted 1,264 human protein complexes from protein interaction network emerged from 32,198 PPIs composed of 9,268 proteins by integrating PPI data from six databases. In addition, the predicted 1,264 protein complexes were evaluated by annotating with reference

papers. Out of these annotated complexes, 136 complexes were perfect matches to experimentally defined complexes, 405 complexes had at least two proteins common to the experimentally defined complexes, and 723 hypothetical complexes were predicted as protein complexes but had no evidence of paper supporting to construct protein complexes. To assess the quality of our protein complex annotation, I estimated the enrichment and the ratio of consistency of Gene Ontology (GO) terms among members of a complex. Next, I compared the expression profiles of the protein members in each complex. Furthermore, the ratio of duplicated genes in a complex was evaluated. Finally, I found 78 hypothetical proteins that were annotated as members of 82 complexes that included several well-known complexes.

Conclusion: I predicted and annotated 1,264 human protein complexes. GO analysis increased the reliability of both complex prediction and manual annotation. The analysis of expression profiles and duplicated genes made it clear that protein members in larger complexes tend to express similarly and are mutually paralogous in a complex. Comprehensive protein complex prediction and annotation will provide strong functional clues about hypothetical proteins. I constructed a new database “PPI view” to provide this large annotation of human protein complexes. PPI view is available at http://hinvitational.jp/hinv/ppi/

2.2. Introduction

Proteins interact with other proteins or biomolecules to perform their functions, and protein complexes are the fundamental functional units of these macromolecular systems.

Comprehensive analysis of PPIs provides a valuable framework for understanding the protein functions required for various biological processes in cells. Moreover, it can offer annotation clues for proteins with unknown function (Hishigaki et al. 2001; Kemmeren et al. 2002; Titz et al. 2004). The next important issue for the elucidation of the functional organization of the proteome is the extraction of information about protein complex formation and function from the PPI network.

In recent years, a number of well-organized public PPI databases have become available such as BIND (Biomolecular Interaction Network Database) (Bader et al. 2000; 2003), DIP (Database of Interacting Proteins) (Xenarios et al. 2002), MINT (Molecular INTeraction database) (Zanzoni et al. 2002; Chatr-aryamontri et al. 2007), HPRD (Human Protein Reference Database) (Peri et al. 2003), IntAct (Hermjakob et al. 2004), and GNP (Genome Network Project Y2H data; http://genomenetwork.nig.ac.jp/).

However, in the current PPI data, main focuses are on protein-binding partners or binary protein interactions. Knowledge about how gene products form a complex, interactions among complexes, or protein interconnectivity in a complex are still scarce. In addition, overlap ratio of PPI data entities across databases is relatively low, so that we only have a partial map of the whole interactome space, thus limiting the broader application of systems modeling. Therefore, it is essential to integrate PPI data in order to fill in as many holes in the interactome space as possible.

In this study, I integrated human PPI data from the databases. I then predicted human protein complexes from the integrated PPI data set by finding densely connected regions with cluster properties in the PPI network based on the graph theory that were previously reported by Altaf-Ul-Amin et al. (2006). After prediction, these predicted protein complexes were manually annotated by experienced annotators according to our standardized procedures utilizing literature mining and the wealth of annotation data from the human full-length cDNA database "H-Invitational Database (H-InvDB)", which have been developed by Imanishi et al. (2004) and Yamasaki et al. (2008). By using the data from H-InvDB, several analyses of the annotated complexes were performed, which should increase the validity of our annotation. This is the first attempt of comprehensive annotation of human protein complexes identified from the network of PPIs.

2.3. Materials and Methods

2.3.1. Integration of PPI data onto the H-InvDB proteins

We used XML and flat files from PPI databases; BIND, DIP, MINT, HPRD, IntAct, and GNP on October 25, 2007. These databases excepting GNP stored experimentally determined PPIs from many organisms through literature curation, but GNP had original Y2H experimental data on humans, and any computationally predicted PPIs were excluded from this study. A standardized interaction data model is needed to store PPI data from different sources. With reference to the method described in the Atlas biological data warehouse (Shah et al. 2005), I designed data loading applications for each PPI database and a relational data storage system compliant with the Proteomics Standards Initiative Molecular Interaction Standard (PSI-MI) controlled vocabulary (Hermjakob et al. 2004), which is a community standard XML format for the presentation of protein interaction data. This system allowed me to unify data from different sources. I used only human PPIs in this study but did not use cross-species PPI data such as human proteins interacting with mouse proteins or data with ambiguous taxonomic labels such as “Mammalia”, commonly seen in the HPRD download file. I downloaded all protein sequences from GenBank (Benson et al. 2007), RefSeq (Pruitt et al. 2007), and UniProt (The UniProt Consortium 2007) databases by their accession numbers, removed redundancies and assigned them to H-InvDB proteins using BLASTCLUST (Altschul et al. 1997; Wheeler et al. 2007) with a threshold of 98% sequence similarity in 95% alignment length coverage for both sequences.

2.3.2. Parameter optimizations of DPClus in prediction of protein complexes

In a PPI network, nodes represent proteins and edges represent interactions. DPClus can detect clusters of a network that are separated by sparse regions, keeping track of the periphery of a cluster by monitoring cluster properties of a neighbour with respect to a cluster, i.e., the program runs with two parameters; “the network density” and “the cluster property”. To evaluate optimal values of these two parameters to predict protein complexes, I used a set of experimentally determined protein complexes (reference complex set). 89 protein complexes were manually collected from scientific literature and 55 complexes were got from three-dimensional structures of human protein complexes recorded in the PDB (Sussman et al.

1998). Parameter optimization was performed to select the two best parameters on the basis of which the predicted set could be best matched with the reference complex set. DPClus was run using all possible combinations of the two parameters (network density, cluster property, 0.0–1.0 in 0.1 increments). In the parameter optimization process, DPClus was limited to find complex sizes of three or more. In this case, a predicted complex needs at least two proteins in common with a known complex to be considered a match. I found two scores; the sum of recalls, which is a ratio of the number of matched proteins of a known complex to those of a predicted complex, and the sum of precisions, which is a ratio of the number of matched proteins of a predicted complex to those of a known complex, for each parameter set. When proteins of a known complex matched fewer than two proteins of a predicted complex, recall and precision would be zero. When proteins of a known complex matched perfectly to proteins of a predicted complex, recall and precision would be one. To avoid over prediction of duplicated complexes, which shared several proteins and matched an identical known complex, the best recall and precision scores were divided by their number. The best parameter choice for DPClus for the reference complex set is to find those parameters that generate a good combination of the two scores (the sum of recalls and the sum of precisions) that predicts a complex set matching with the largest protein members of the reference complex set. Precision-Recall curve (Wicker et al. 2010; Sankararaman et al. 2010; Kastrin et al. 2010; Qiu et al. 2010) of the sum of recalls versus the sum of precisions for each of the 100 parameter combinations tested during parameter optimization was examined (**Figure 2.1**). A parameter combination closest to the upper right portion of the curve maximizes overlaps of predicted complexes and known complexes. A parameter combination with network density 0.6 and cluster property 0.5 optimizes DPClus on this data set. This parameter combination led DPClus to predict 1,264 complexes, which matched 92 of the 144 known complexes. The average recall and precision of these 92 matched complexes were 0.54 and 0.66, respectively. I also calculated average number of complexes that share a common protein. A protein was found out in 1.24 complexes on an average from the reference complex set. So according to the optimized parameters, the result was the same as that by the predicted set.

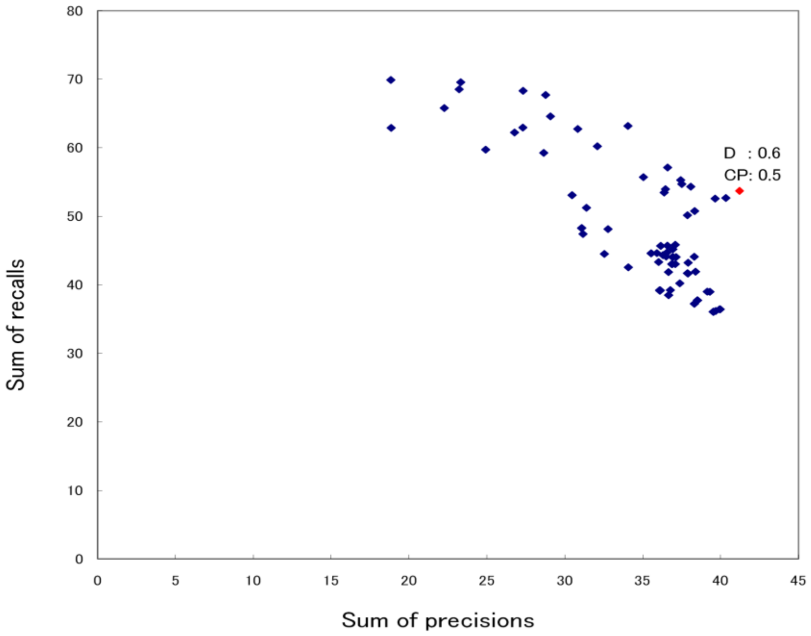


Figure 2.1 Precision-Recall curve for each of the 100 parameter combinations tested during parameter optimization.

The y-axis indicates the sum of recalls, which is a ratio of the number of matched proteins of a known complex to those of a predicted complex, the x-axis indicates and the sum of precisions, which is a ratio of the number of matched proteins of a predicted complex to those of a known complex.

2.3.3. Manual annotation of the predicted protein complexes

We annotated the predicted complexes according to our defined procedures, and curators confirmed the supporting evidence regarding proteins of the predicted complexes to be the experimentally defined complex members or subunits from the literature in advance and then integrated data entities such as complex names, descriptions, localizations, complex-complex interactions (CCIs), and their subunits' functions, structures, expression profiles, gene loci, and PPIs among protein subunits. I defined three categories of proteins in a predicted complex; category I: a protein of a known complex reported in the literature, category II: a protein which has a related function to a complex, and category III: a protein which has not been reported in the literature but is predicted as a complex member from the PPI network. I defined a reliability index "CQI" for a whole annotated complex based on this protein categorization. CQI is written as [Number of category I proteins].[category II proteins].[category III proteins] /[Total number of proteins in a predicted complex].

I gave names to the predicted complexes in which I used scientific names from the literature, if the majority of proteins in a complex are common to a known complex and a name is available for it (e.g., exosome, spliceosome); otherwise, I used artificial descriptions using concatenated gene symbols [e.g., GLI1-STK36-SUFU complex, DBNL-ITK-PLCG1-SH3BP2 containing complex (using "containing complex" when all symbols of proteins were not available)]. Descriptions of complexes were quoted from references with their PubMed IDs. Functional categories and subcellular localizations were added if the descriptions were available from the literature.

2.3.4. Consistency of GO terms assigned to the members in a complex

All GO terms of “biological process”, “cellular component” and “molecular function” assigned to the H-InvDB 5.0 transcripts were used for this study. The depth of GO terms from the root in the GO hierarchy was set to five. Hence, the GO terms representing nodes with depth less than five were ignored in the analysis. If the GO term assigned to the transcript had depth greater than five, the corresponding parental node with depth five was re-assigned and redundancy was removed. As a control set representing an entire proteome, GO terms assigned to all 36,073 representative transcripts in H-InvDB 5.0 were collected. All protein members in 1,264 complexes are used as one set of protein complexes (PCset1) for the assessment. To construct the manually curated set of protein complexes (PCset2), I collected only category I proteins from perfectly matched and partially matched complexes and discarded those category II or III proteins which have not been described as members of a complex in the literature. PCset2 contains 541 complexes.

Significance of enrichment of a given GO term in a complex was tested by one-sided Fisher’s exact test using 2×2 contingency table (A, B, C, D). “A” represents the number of members expressing the given GO term, and “B” is the number of members not having the GO term in the protein complex. “C” and “D” represent the corresponding numbers estimated for the entire proteome.

To estimate the quality of protein complex annotation, another quality index, “GO consistency index”, was defined. The GO consistency index for the given protein complex is estimated by the following equation; GO consistency index = $N_{cons}/N_{all,}$ where N_{cons} is the number of edges that connect two proteins sharing the same GO term, and N_{all} is the number of possible combinations (edges) for all members of the complex.

2.3.5. Similarity of gene expression profiles among proteins in the same complex

In the downloaded file of H-ANGEL (Tanino et al. 2005) (“H-ANGEL_matrix.txt”, December, 2007 version), I used gene expression data measured by the iAFLP method (Kawamoto et al. 1999) for 10 tissue categories. As large number of iAFLP tags were used, for some loci, multiple iAFLP-tags correspond to the same locus; then, the different expression profiles for a single locus were averaged over the tags. Expression profile of a gene was expressed by a vector of 10 elements. The similarity of gene expression profiles between two loci was calculated using the cosine of the two vectors. The similarity of multiple gene expression profiles for members of a protein complex were defined by the averaged cosines of all combinations of all the different members. The cosines of a complex were evaluated by simulation described below. For every number (k) of members in the complex, k-genes from genes that have expression profiles were randomly picked up. Then, the averages of the cosines of the expression profiles were calculated. The procedure was repeated 100,000 times for every number of members (k), and used them for p-value estimation.

2.3.6. Judgement of the duplicated gene pair in a given protein complex

For all combination of members in a protein complex, it was judged whether the genes were paralogous, i.e., the two genes were copied by segmental duplication, using the method established by Gu et al (2002). The gene models, which were mapped onto the "random" or "haplotype" contigs, were not used in the analysis. FASTA package version 34t25 (Lipman et al. 1985) was used for the analysis. In addition, I also conducted another paralog analysis with BLASTP calculation using less stringent criteria for the judgment of duplicated genes. BLAST version 2.2.17 was used. If the gene pair has a similarity with E-value less than 1E-05, I judged the gene pair as paralogous.

2.4. List of abbreviations used

BIND (Biomolecular Interaction Network Database), BLAST (Basic Local Alignment Search Tool), CAGE (Cap Analysis of Gene Expression), CCI (Complex-Complex Interaction), cDNA (Complementary DNA), CQI (Complex annotation Quality check Index), DIP (Database of Interacting Proteins), EST (Expressed Sequence Tag), FDR (False Discovery Rate), GNP (Genome Network Project), GO (Gene Ontology), H-ANGEL (Human Anatomic Gene Expression Library), H-InvDB (H-Invitational Database), HPRD (Human Protein Reference Database), iAFLP (introduced Amplified Fragment Length Polymorphism), MINT (Molecular INTeraction database), ORF (Open Reading Frame), PDB (Protein Data Bank), PPI (Protein-Protein Interaction), PSI-MI (Proteomics Standards Initiative Molecular Interaction

Standard), RFC (Replication Factor C), ROC (Receiver Operating Characteristic), XML (Extensible Markup Language).

2.5. Results

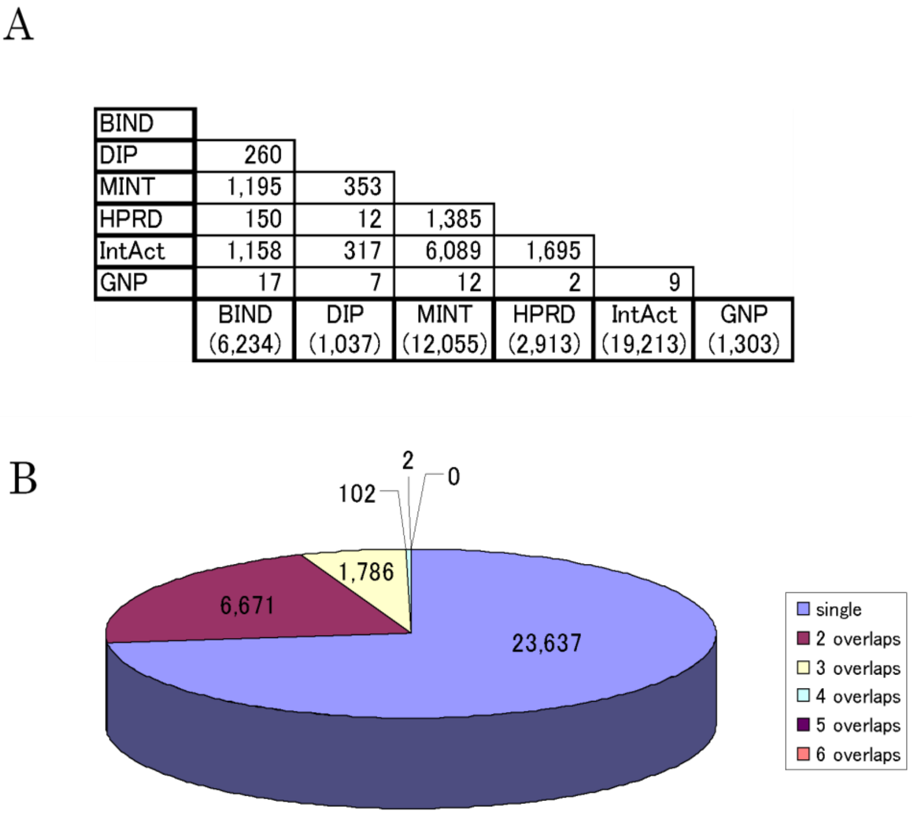
2.5.1. Integration of PPI data onto the H-InvDB proteins

Imanishi et al. and Yamasaki et al. developed a comprehensive database of human genes and transcripts, called H-InvDB (http://www.h-invitational.jp/) (Imanishi et al. 2004; Yamasaki et al. 2008). It is a unique database that integrates annotation of sequences, structure, function, expression, subcellular localization, evolution, and the diversity of the human genes and the encoded proteins into a single entity. It is useful as a platform for conducting in silico data mining. International collaboration for analysis of high-quality full-length cDNA clones, in addition to the EST assemblies and CAGE tags, now provides integrative annotation of 187,156 transcripts placed on 36,073 loci (Release 5.0). Based on the open reading frame (ORF) prediction of H-InvDB 5.0 transcript sequences, followed by the functional annotation of experienced annotators, 108,530 non-redundant human protein candidates (H-InvDB proteins) were determined. To survey human PPIs from the landscape of the human interactome, the PPI information was mapped onto the H-InvDB proteins.

A number of public PPI databases are currently available. I selected BIND (Bader et al. 2000; 2003), DIP (Xenarios et al. 2002), MINT (Zanzoni et al. 2002; Chatr-aryamontri et al. 2007), HPRD (Peri et al. 2003), IntAct (Hermjakob et al. 2004) and GNP as major resources for

PPI integration. I removed PPI data redundancies by sequence similarity and then integrated human PPIs with the H-InvDB proteins (see also **2.3.1**). As a result, I obtained 32,198 human PPIs composed of 9,268 proteins.

Figure 2.2 shows the overlap of human PPIs across the six databases. There are 6,234 non-redundant human PPIs in BIND, while DIP, MINT, HPRD, IntAct, and GNP have 1,037, 12,055, 2,913, 19,213, and 1,303 PPIs, respectively. **Figure 2.2A** shows pairwise overlaps of integrated PPIs across the databases; MINT and IntAct share 6,089 PPIs, which is the highest overlap among these databases. As shown in **Figure 2.2B**, 6,671, 1,786, 102, and 2 PPIs are shared in 2, 3, 4, and 5 databases, respectively, but there are no PPI in common among all the 6 databases. There are 23,637 unique PPIs in the databases, occupying 73% of the PPI dataset. The overlap across these databases was relatively small, which reflects the fact that the actual size of the human interactome will probably be much larger than that of the currently known PPIs (von Mering et al. 2002; Bader and Hogue 2002; Kumar and Snyder 2002). Thus, it is essential to integrate the PPI data to achieve a complete view of the human interactome.



BIND						
DIP	260					
MINT	1,195	353				
HPRD	150	12	1,385			
IntAct	1,158	317	6,089	1,695		
GNP	17	7	12	2	9	
	BIND (6,234)	DIP (1,037)	MINT (12,055)	HPRD (2,913)	IntAct (19,213)	GNP (1,303)

Figure 2.2 Overlap of human PPIs in six PPI databases.

A) Pairwise overlaps of integrated PPIs across databases are shown in cells. The number of integrated PPIs is shown in parentheses for each database. B) Overlaps of PPIs sharing in common in single, two, three, four, five, and six databases are shown.

2.5.2. Prediction of protein complexes

View of integrated PPI network composed of 32,198 human PPIs was represented in **Figure 2.3**. The next important issue for the elucidation of the functional organization of the proteome is the extraction of information about protein complex formation and function from the PPI network.

In the past, the algorithm called “DPClus” was developed by Altaf-Ul-Amin et al. (2006), which extracts the densely connected regions in a network and demonstrated that many of these densely connected regions correspond to known protein complexes or protein functional units (Bader and Hogue 2003; Altaf-Ul-Amin et al. 2006). DPClus is a robust algorithm not affected by a high rate of false positives in data from high-throughput interaction-detection techniques (Altaf-Ul-Amin et al. 2006).

On prediction of protein complexes by DPClus, I adopted the “overlapping clustering mode”, which allows identical proteins to be classified into different clusters, because it is biologically well established that proteins can be present in multiple complexes at different times and locations. For example, POLR2E/RPB5 (HIP000039507), POLR2F/RPB6 (HIP000096671), POLR2H/RPB8 (HIP000027404), POLR2K/RPB12 (HIP000043404), and POLR2L/RPB10 (HIP000064404) are conserved throughout RNA polymerases I, II, and III (Werner et al. 2007). Before complex prediction, I evaluated the optimal values of DPClus parameters by comparing the predicted complex set with the experimentally determined 144 reference complex set (see also **2.3.2**).

As the result, 1,264 protein complexes were predicted in the PPI network composed of 32,198 human PPIs using DPClus with the best parameter set (network density 0.6, cluster property 0.5) determined on the basis of the reference complex set.

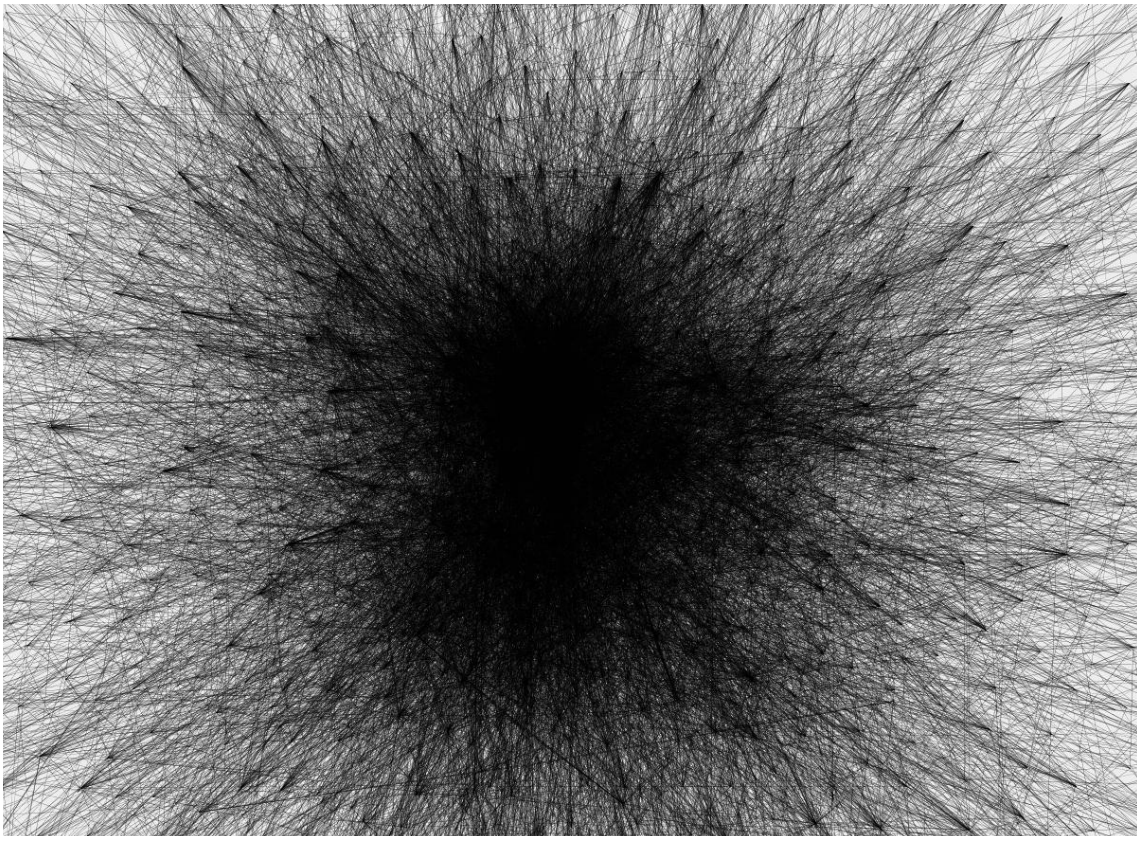


Figure 2.3 View of Integrated PPI network.

Nodes and edges represent proteins and interactions respectively. How do we understand PPI network and biological process? The next important issue for the elucidation of the functional organization of the proteome is the extraction of information about protein complex formation and function from the PPI network.

2.5.3. Manual annotation of the predicted protein complexes

An annotation of the predicted complexes was performed with the following procedures; 1) curators searched for supporting evidence in the scientific literature, which could confirm that the proteins of the predicted complexes are experimentally defined complex members or subunits, 2) missing proteins were manually added to the predicted complexes if there was evidence in the literature that they were members of complexes but had been dropped in the complex prediction, 3) I integrated data such as complex names, descriptions, localizations, complex-complex interactions (CCIs), and their subunits' functions, structures, expression profiles, gene loci, and PPIs among protein subunits. I did not remove proteins that were predicted to be complex subunits but for which no evidence was found, because they are complex subunit candidates.

The protein members of the predicted complexes were categorized into three categories based on their annotation level: category I, proteins that are confirmed as subunits of a known complex in the literature or as ternary structures in the PDB (Sussman et al. 1998); category II, proteins for which no evidence of a complex membership exists in the literature, but have functions related to those of other category I members in the predicted complex according to their protein definitions or Gene Ontology (GO) terms (Ashburner et al. 2000); and category III, proteins that are predicted as a complex subunits by DPClus and do not overlap with functions of the other two categories, i.e., do not have functions related to those of other category I members in a predicted complex according to their protein definitions or Gene Ontology (GO) terms. Our protein complex prediction allowed the same proteins to be subunits of different complexes; therefore, such shared proteins could be classified into the other categories as members of different complexes (see also **2.3.3**).

In total, 1,264 protein complexes were predicted and annotated. A list of the all annotated complexes is available at http://h-invitational.jp/hinv/ppi/. As the result of annotation, 2,106 proteins, 299 proteins and 3,273 proteins were respectively classified into category I, category II, category III when protein subunit sharing in complexes was allowed (**Table 2.1A**). The average numbers of protein subunits per complex were 3.9 (category I proteins only), 4.3 (category I and II proteins), and 4.5 (all categories) respectively, and a large number of smaller complexes than average size (i.e., numbers of protein subunits per complex) and a small number of larger complexes than average size were observed in that the relationship between the size of a complex and its frequency follows an inverse power law (**Figure 2.4A**).

In this annotation, 136 predicted complexes matched perfectly with known complexes (all subunits are in category I) and 405 complexes had at least two subunits that matched with a known complex (at least two subunits are in category I), while 723 complexes had only predictive support (all subunits are in category III) (**Table 2.1B**). I defined three types of predicted complexes: perfectly matched complex, partially matched complex, and hypothetical complex; these correspond, respectively, to a complex with all subunits in category I, a complex with at least two proteins in category I, and a complex with all subunits in category III.

From information in the scientific literature, functional categories and subcellular localization were assigned to the annotated complexes (**Figure 2.4 C, D**). The major functional categories were signal transduction (90 complexes, 19%), transcription (61, 14%), cell cycle (52, 12%), and immune response (49, 11%); over 70% of the complexes are localized in the cell nucleus (160, 33%), membranes (111, 22%), and cytoplasm (81, 16%).

Table 2.1 Protein and the complex annotation summary.

A) Number of proteins in H-InvDB, the integrated PPI data set, the predicted complexes. The categorized proteins in the predicted complexes are described in the text. Since, complex sharing proteins could be classified into the other categories as members of different complexes, total number of the categorized proteins is more than number of proteins in the predicted complexes. B) Type of the predicted complexes. Three types of predicted complexes were defined by matching degree to known complexes (details are in the text). Total number of the predicted complexes in this study is 1,264.

A

	Number of proteins
H-InvDB proteins	108,530
Proteins in the PPI data set	9,268
Proteins in the predicted complexes	4,513
Category I proteins in the predicted complexes	2,106
Category II proteins in the predicted complexes	299
Category III proteins in the predicted complexes	3,273

B

Type of the predicted complexes	Number of complexes
Perfectly matched complex	136
Partially matched complex	405
Hypothetical complex	723
Total	1,264

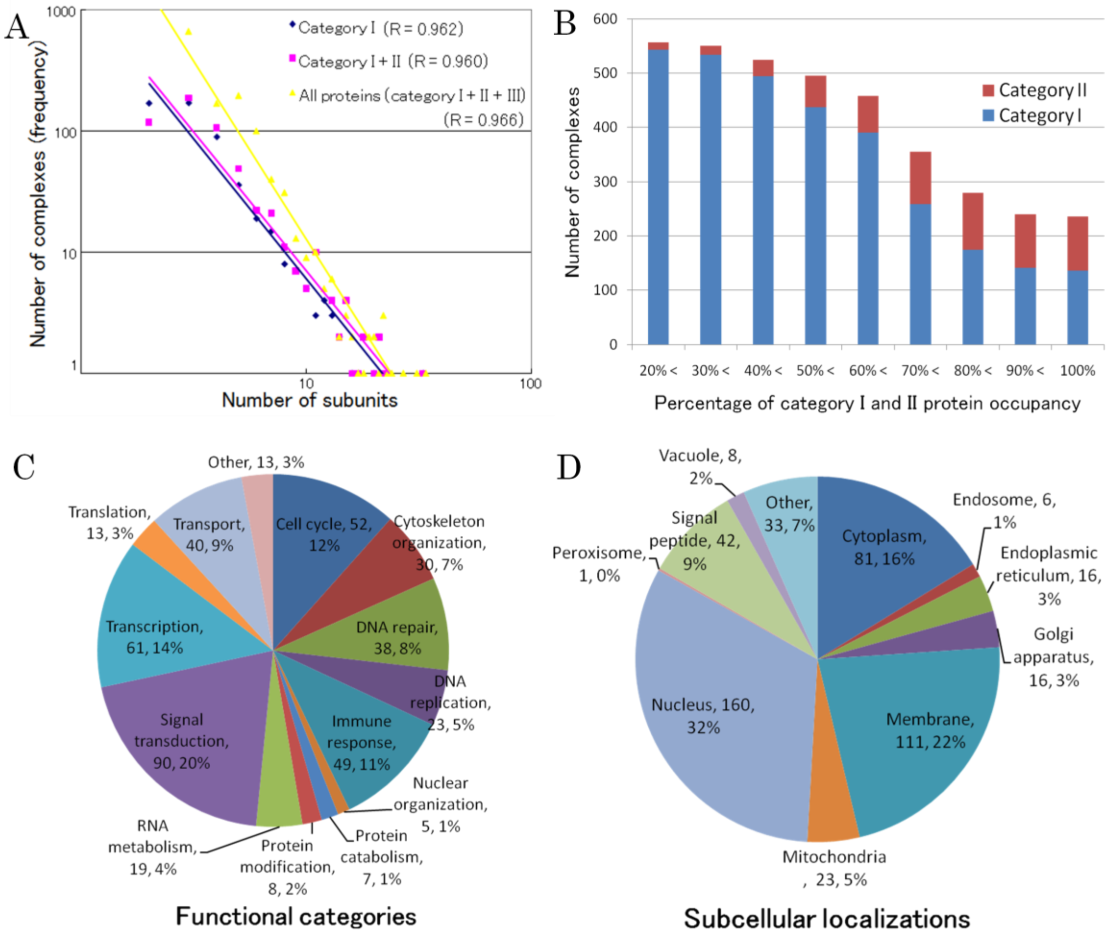


Figure 2.4 Properties of annotated complexes

A) The relationship between complex size (number of different protein subunits of each category) and frequency. B) Percentage of category I and II protein occupancy of the annotated complexes. C) Distributions of functional categories. D) Distributions of subcellular localizations.

2.5.4. Consistency of GO terms assigned to members in a complex

Since proteins in a complex cooperatively exert a biological role, it is expected that they exist in the same location at a particular time and that they are players in the same biological process or pathway. To assess the quality of our protein complex annotation, the enrichment and the ratio of consistency of GO terms among members of a complex were estimated. This assessment is based on the assumption that the same GO terms are assigned to proteins in a single protein complex.

First, the enrichment of some GO terms in a complex compared to GO terms assigned to the proteome were estimated. The proteome set comprised 36,073 representative transcripts in H-InvDB 5.0. The enrichment of GO terms was estimated against two sets of protein complexes: PCset1 represents all 1,264 protein complexes comprising of all member proteins including category III proteins which is unknown for the complex-related function but predicted as complex subunits by DPClus based on PPI interconnectivity, and PCset2 represents 541 complexes whose subunits are limited to contain manually curated category I proteins obtained from perfectly matched and partially matched complexes. As a result, 450 protein complexes out of 1,264 PCset1 (35.6%) complexes have at least one significantly enriched GO term (Fisher's exact test, p-value ≤ 0.01). On the other hand, 254 protein complexes out of the 541 PCset2 complexes (47%) have at least one significantly enriched GO term. The ratio of protein complexes having enriched GO terms is greater in PCset2 than in PCset1, suggesting that the reliability of protein complex annotation was significantly refined by manual check.

Second, the degree of consistency of GO terms among members in a complex; i.e., homogeneity of GO terms assigned for complex members were estimated. A consistency index (see **2.3.4**) was used as an indicator of homogeneity. In order to estimate the degree of GO term consistency expected by chance, 100 sets of randomly selected genes from H-InvDB 5.0, all representative transcripts with complex sizes matched to our annotation of PCset1, were created and used as a control. Average consistency indexes were estimated to be 0.23, 0.41, and 0.04 for protein complexes of PCset1, PCset2, and the random set, respectively. The value is significantly higher in PCset1 (Student's t test, p-value 2.9E-111) than in the random set, and in PCset2 than in PCset1 (Student's t test, p-value 1.6E-25). These results are still statistically significant after Bonferoni multiple test, which is relatively conservative. The histogram of consistency indexes for the three sets is shown in **Figure 2.5**. In particular, cases in which the consistency index equals 1.0 (i.e., all members share common GO terms with other members), increased dramatically after manual curation, indicating the relatively high quality of manual annotation and the advantage of protein complex prediction followed by manual annotation as opposed to only single computational prediction.

Intriguingly, 28 PCset1 unique complexes with consistency index equal to 1.0 were found. Although the existence of the protein complexes has not yet been validated experimentally, the compatibility between the prediction of protein complexes by our clustering method and the consistency of GO terms offers us reliable candidates as novel functional protein complexes to be validated by future experiments.

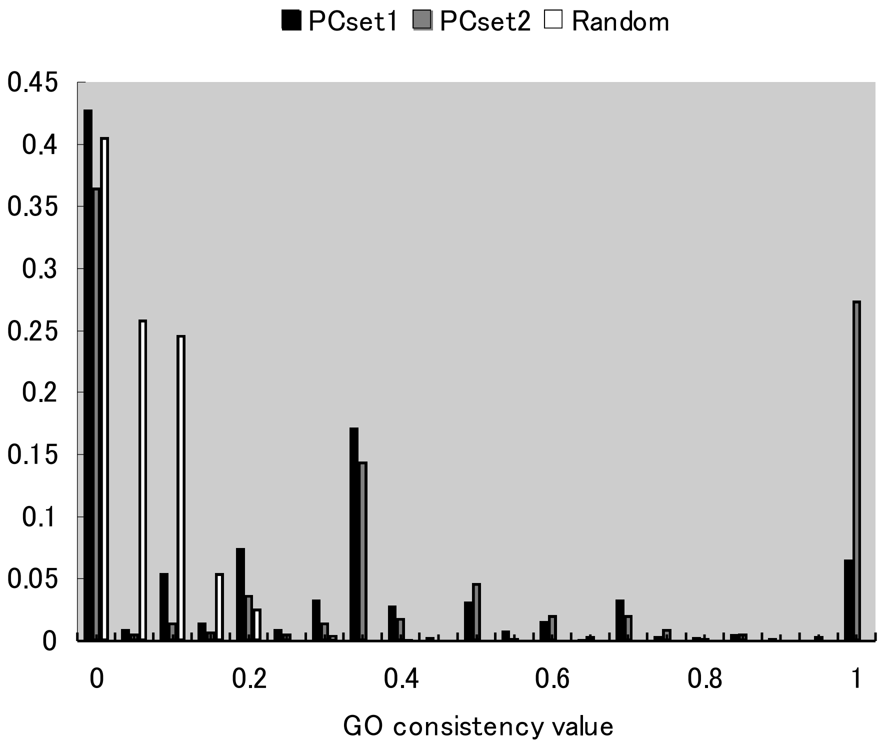


Figure 2.5 Distributions of GO consistency index in PCset1, PCset2, and random set.

Histogram of GO consistency index for protein complexes in PCset1, PCset2, and random set, shows a shift toward larger values in PCset1 and PCset2 than those in the random set.

2.5.5. Similarity of gene expression profiles among proteins in the same complexes

Based on the idea that co-expressed genes are more likely to have similar functions, cluster analysis of gene expression data have been utilized to predict the functions of non-annotated proteins (Devos et al. 2000; Rost 2002). In reverse, I examined as to whether proteins in the same complex (involved in the same functions) have similar expression profiles. For each complex, the expression profiles of protein members in the complex were compared. If the members of a complex are similar in their expression profiles, the profile should indicate some functional information about the complex whose function is unknown.

Expression profiles of 729 complexes were obtained from the Human Anatomic Gene Expression Library (H-ANGEL) (Tanino et al. 2005), the satellite database of H-InvDB. Among 729 complexes, six complexes were found to have significant gene expression similarlity by a false discovery rate (FDR) criterion of 0.05. FDR, the expected proportion of incorrectly rejected null hypotheses, is a widely used statistic for multiple tests (Kim and van de Wiel 2008). The six complexes are shown in **Table 2.2**. Some of the most interesting complexes in which the expression of the protein members was similar and tissue specific were found. The fibrinogen complex (Complex No. 130) was one of complexes in such a case, and in which the expression of the protein members was liver specific. Other examples were the AK5-CPNE6-TRIM46 complex (Complex No. 540) and the troponin complex (Complex No. 258). Though FDR of the two complexes was not significant, 0.22 and 0.68, respectively, the gene expression profiles were very similar (the cosines were 0.99 and 0.95). For troponin, the gene expression of the members is specific to muscle/heart tissue (average entropy, 1.12). The expression profiles of the troponin complex are shown in **Figure 2.6**. The similarity of their expression profiles suggests that they may function as a complex.

As shown above, the gene expression of the protein members was not significantly similar in most of the predicted protein complexes. However, instead I found that, for large complexes, the gene expression of complex members is more likely to be similar. For each complex, I calculated p-values of gene expression similarities (see also **2.3.5**), then plotted the distribution of p-values for different number of proteins in a complex (**Figure 2.7**). The figure illustrates that gene expression of proteins in the same complex is more similar as the number of protein members (complex size) increases. This would be the first report of a relationship between expression similarity and complex size in human PPI and is consistent with the results for *Yeast* (Liu et al. 2009).

Table 2.2 The protein complexes consisting of members with significantly similar gene expression profiles.

Complex No.	CQI	Complex name	cosine	FDR	# of genes
30	21.1.0/22	19S proteasome of the 26S proteasome	0.92	0.001	13
12	18.0.4/22	20S proteasome of the 26S proteasome	0.88	0.006	17
41	12.1.0/13	RNA polymerase II complex	0.92	0.008	10
68	0.0.11/11	COP9 signalosome (CSN)	0.92	0.014	9
130	3.0.8/11	Fibrinogen	0.96	0.037	4
77	4.0.8/12	18S U11/U12 complex	0.89	0.041	14

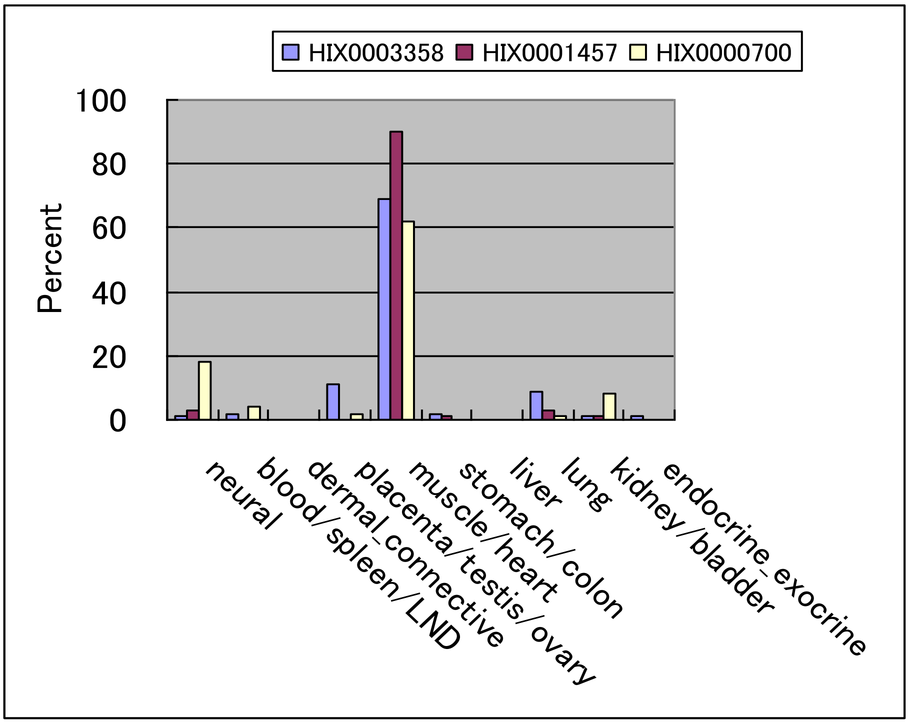


Figure 2.6 Relative percentage of gene expression levels of troponin complex.

The three gene loci of the troponin complex (Complex No. 258) member proteins are expressed specifically in muscle/heart tissue.

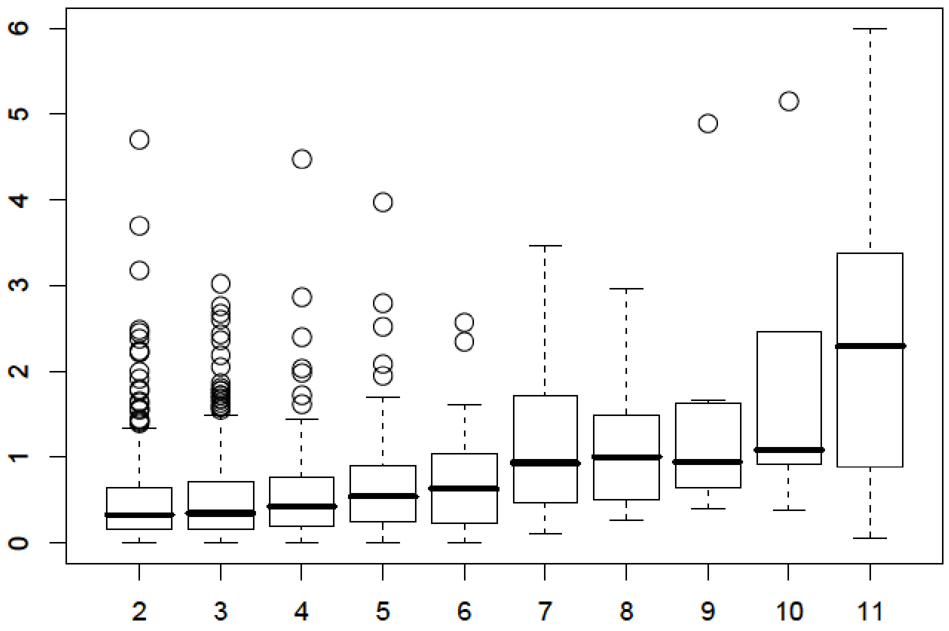


Figure 2.7 Boxplot of gene expression profile similarity and the number of protein members in a complex.

The y-axis indicates gene expression similarity (negative logarithm of p-value of average cosine of gene expression profiles) in a complex; a higher y-value means that the members of the complex have similar gene expression profiles. The x-axis indicates the number of protein members with expression data in the complex. The gene expression profiles are more similar as the number of proteins increases.

2.5.6. Relationship between the formation of protein complexes and gene duplication

To reveal how gene duplication contributes to the formation of protein complexes, the ratio of duplicated genes in a complex were examined.

The paralog judgment established by Gu et al. (2002) yielded 2,353 duplicated genes in a total of 4,191 genes that were the components of 1,264 complexes (see **2.3.6**). Of the 1,264 complexes, 336 (26.5%) were judged to have at least one paralog pair. Moreover, 218 complexes (17.2%) were obtained in which more than half of the components were judged to be paralogous to another gene in the same complex. By using a less stringent method with BLASTP (E-value ≤1e-05), these percentages were estimated to be 38.5% and 27.3%, respectively.

The replication factor C (RFC) complex (Complex No. 105) is a good example of the formation of a protein complex induced by gene duplication. This complex consists of five RFC subunits and one binding partner, PCNA (Cai et al. 1996). The complex is known to be related to DNA synthesis (Cai et al. 1996), and the function and machinery are conserved between yeast and human (O'Donnell et al. 1993), indicating that this is an ancient protein complex. Paralog judgment by the Gu method suggested that three (RFC 36, 37, 40) out of five RFC subunits are paralogous, i.e., they originated from a common ancestor, whereas the result obtained by the less stringent BLASTP method suggested that all five subunits are mutually paralogous. The existence of the “RFC box” motif in all five proteins and the consistency of exon-intron boundaries also support the homologous relationships of these five subunits. These results indicate that the enlargement of a protein complex is mainly mediated by homologous interactions, and gene duplication events greatly contribute to the establishment of protein complexes.

2.5.7. Functional assignments for hypothetical proteins in the annotated complexes

An important goal of proteomics is a functional assignment for proteins that cannot be annotated by homology alone. Several approaches for functional assignment from PPIs have been developed (Hishigaki et al. 2001; Kemmeren et al. 2002; Titz et al. 2004).

H-InvDB proteins were analyzed with standardized functional annotation by curators who classified the proteins into several categories; i) identical to known human proteins, ii) similar to known proteins (having 50% sequence similarity), iii) InterPro domain containing proteins, and iv) hypothetical proteins (no biological functions were inferred).

We found 78 hypothetical proteins in the 82 predicted complexes. Although the majority of hypothetical proteins (61 proteins, 78.2%) were subunits of 67 hypothetical complexes (none of their subunits were reported as complexes in the literature), 13 hypothetical proteins were subunits of 12 complexes whose functions were strongly deduced because at least half of their subunits were annotated as common to known complexes. A protein complex is thought to be a functional unit where proteins get together and perform biological functions; therefore, a hypothetical protein can be assigned a function related to that of the complex it joins. For example, two hypothetical proteins HIP000013164 and HIP000053526 were in the

“DREAM complex (Complex No. 24)”, which is tightly bound to E2F-regulated promoters in G0 and dissociates from these promoters in S phase of the cell cycle. In addition, some subunits of the complex can also interact specifically with MYB and may be involved in expression of MYB-dependent genes important in G2/M progression (Litovchick et al. 2007). I expected that these two hypothetical proteins would then join the DREAM complex and might play roles in the cell cycle. Moreover, I found that annotated complexes such as “Fanconi anemia (FA) core complex (Complex No. 61)”, “INO80 complex (Complex No. 75)”, and “Lamins complex (Complex No. 101)” include hypothetical proteins (HIP000177716 for the FA core complex, HIP000079962 for the INO80 complex, and HIP000024165 for the Lamins complex). These complexes have DNA repair, DNA repair and transcription, and nuclear organization functions, respectively. Therefore, these hypothetical proteins might also have functions associated with those complexes. **Table 2.1** summarizes the 12 complexes and their CQIs, which include hypothetical proteins as subunits and at least half of whose subunits are common to known complexes.

Table 2.3 The hypothetical proteins in the annotated complexes.

12 complexes which had hypothetical proteins as the subunits and in which at least half of subunits were common to known complexes are shown.

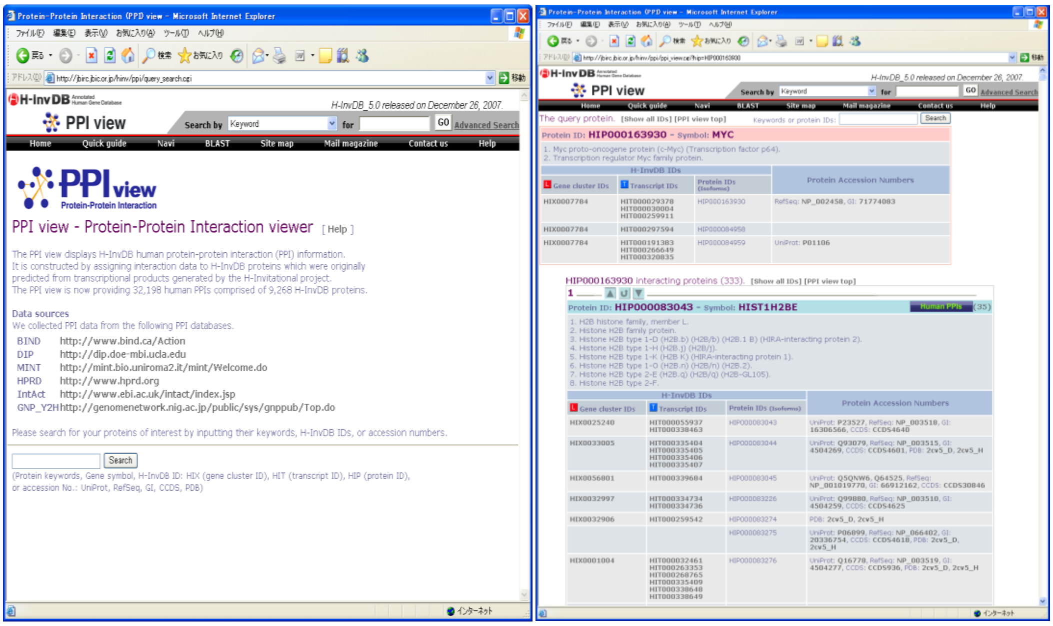
Complex No.	CQI	Hypothetical proteins	Name
24	10.1.2/13	HIP000013164 HIP000053526	dREAM complex
61	8.0.1/9	HIP000177716	Fanconi anemia (FA) core complex
75	11.0.2/13	HIP000079962	INO80 complex
101	4.0.1/5	HIP000024165	Lamins complex
200	3.0.2/5	HIP000046613	C8orf32-EFCBP2-RUNX1T1-ZNF652 containing complex
673	3.0.2/5	HIP000038372	BCL2A1-BCL2L1-BCL2L2-HRK-PMAIP1 complex
922	4.0.3/7	HIP000089800	HIF-1alpha-pVHL-ElonginB-ElonginC complex
940	2.0.1/3	HIP000027799	SRGAP3-WASF1 containing complex
960	3.0.1/4	HIP000060581	C19orf25-KNTC1-ZW10 containing complex
967	3.0.2/5	HIP000015491	NONO-PSPC1-WBP4-ZNRD1 containing complex
1156	2.0.2/4	HIP000114159	NUTF2-RAN complex
1310	4.0.3/7	HIP000091971	SCF (Skp1, cullin 1, F-box) ubiquitin E3 ligase complex

2.5.8. Development of "PPI view" and "PPI map"

Database of PPIs and protein complexes called “PPI view (http://hinvitational.jp/hinv/ppi/)” and visualization tool of protein complexes “PPI map” were developed. PPI view provides detailed information of PPIs and predicted and annotated protein complexes (**Figure 2.8**). As PPIs information, we can obtain interacting proteins with a target protein, in addition we can check 1) the experimental methods that detected the PPI, 2) the experimental scale (large scale or small scale) detecting the PPI 3) the number of papers which report the PPI. This information would be important and useful to judge the reliability of PPIs. In information of predicted and annotated protein complexes, detailed complex annotations (complex name, functions, localization, etc.) and CQIs (Complex annotation Quality check Index) are provided. CQI is a reliability index for a whole annotated complex based on the protein category. For example, CQI is a simple index of 5.2.1/8 which means that the complex has eight subunits in which five, two, and one proteins are classified into categories I, II, and III, respectively.

The visualization tool “PPI map” in PPI view can show protein interconnectivity of a complex, complex-outside protein interactions: interactions among proteins in a complex and an outside protein, and complex-complex interactions: interactions among proteins in a complex and proteins in the other complex, and has two kinds of window, “detailed network” window and “whole network” window as shown in **Figure 2.9**. Detailed network window shows member proteins of a target complex in the center and directly interacting proteins or protein complexes in the neighborhood. Other hand, whole network window displays whole of proteins and protein complexes network. On PPI map, each node (circle) represents an individual complex and edges represent their interactions. A node size represents number of proteins in a complex and thicknesses of edges connecting complexes, which is exponential to the number of PPIs between connected nodes. On using PPI map, a user can change scale of visualization by slide bar in the upper right of windows, and move displaying part of proteins and complexes interaction network by pressing-and-holding the mouse button and dragging. On scale down of visualization or moving displaying part of network, to avoid over-traffic on internet and reduce the time of visualization, PPI map request just information of new nodes and new edges to visualize to the WWW server and get the information by XML through the internet (**Figure 2.10**). Thus, PPI map can be used to show CCIs of interest, with the ability to seamlessly scale, move, and change the represented thicknesses of edges connecting complexes. Using the "PPI map" I had drawn an overhead view of CCIs with the subcellar localizations of the annotated complexes (**Figure 2.11**). Node colors indicate subcellular localization of the annotated complexes. To avoid a CCI network to be too complicated to understand, 541 complexes (perfectly matched and partially matched complexes) and the complex-complex interactions or the protein-complex interactions comprising more than 10 PPIs are here shown. From this "map", we can understand the relationship of known and partially-known protein complexes.

As far as I know, PPI view is the first database that can show CCIs in the human interactome with detailed annotation.



PPI view - Protein-Protein Interaction viewer [Help]

The PPI view displays H-InvDB human protein-protein interaction (PPI) information.
It is constructed by assigning interaction data to H-InvDB proteins which were originally predicted from transcriptional products generated by the H-Invitational project.
The PPI view is now providing 32,198 human PPIs comprised of 9,268 H-InvDB proteins.

Data sources
We collected PPI data from the following PPI databases.

BIND	http://www.bind.ca/Action
DIP	http://dip.doe-mbi.ucla.edu
MINT	http://mint.bio.uniroma2.it/mint/Welcome.do
HPRD	http://www.hprd.org
IntAct	http://www.ebi.ac.uk/intact/index.jsp
GNP_Y2H	http://genomenetwork.nig.ac.jp/public/sys/gnppub/Top.do

Please search for your proteins of interest by inputting their keywords, H-InvDB IDs, or accession numbers.

Search
(Protein keywords, Gene symbol, H-InvDB ID: HIX (gene cluster ID), HIT (transcript ID), HIP (protein ID), or accession No.: UniProt, RefSeq, GI, CCDS, PDB)

http://jbirc.jbic.or.jp/hinv/ppi/ppi_view.cgi?hip=HIP000163930

The query protein. [Show all IDs] [PPI view top] Keywords or protein IDs: Search

Protein ID: HIP000163930 - Symbol: MYC

1. Myc proto-oncogene protein (c-Myc) (Transcription factor p64).
2. Transcription regulator Myc family protein.

H-InvDB IDs			Protein Accession Numbers
Gene cluster IDs	Transcript IDs	Protein IDs (Isoforms)	
HIX0007784	HIT000029378 HIT000030004 HIT000259911	HIP000163930	RefSeq: NP_002458, GI: 71774083
HIX0007784	HIT000297594	HIP000084958	
HIX0007784	HIT000191383 HIT000266649 HIT000320835	HIP000084959	UniProt: P01106

HIP000163930 interacting proteins (333). [Show all IDs] [PPI view top]

1

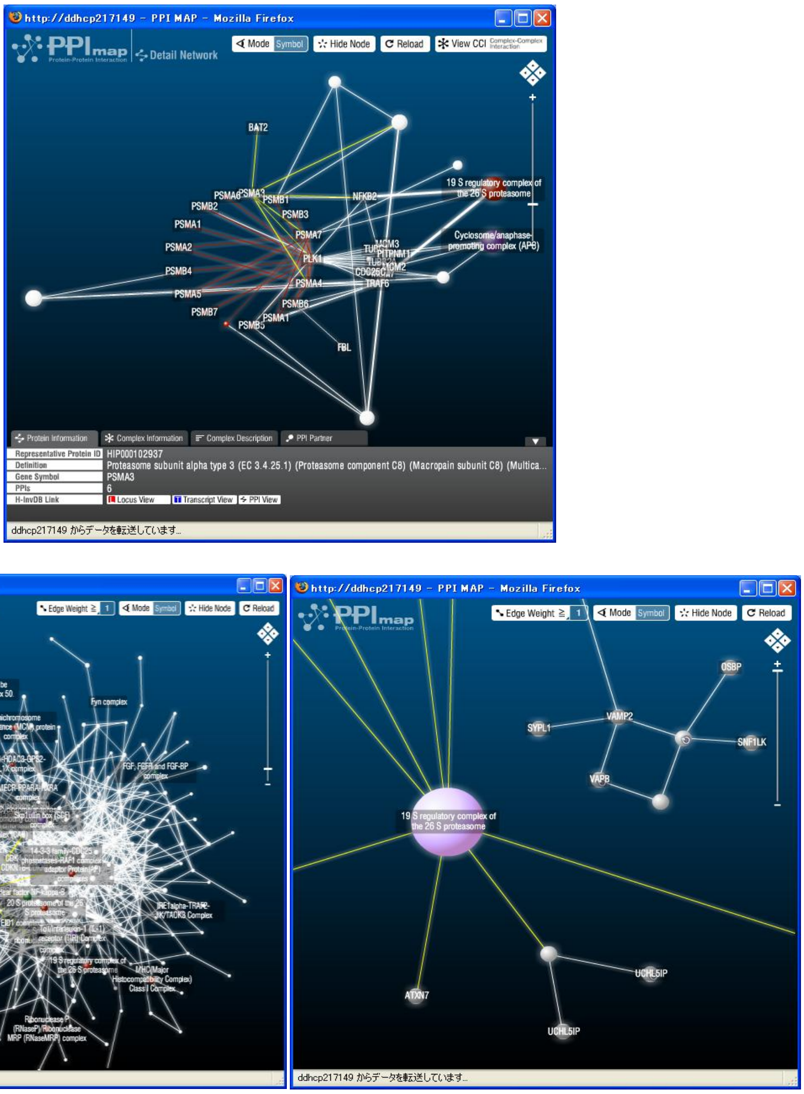
Protein ID: HIP000083043 - Symbol: HIST1H2BE Human PPIs (35)

1. H2B histone family, member L.
2. Histone H2B family protein.
3. Histone H2B type 1-D (H2B.b) (H2B/b) (H2B.1 B) (HIRA-interacting protein 2).
4. Histone H2B type 1-H (H2B.j) (H2B/j).
5. Histone H2B type 1-K (H2B K) (HIRA-interacting protein 1).
6. Histone H2B type 1-O (H2B.n) (H2B/n) (H2B.2).
7. Histone H2B type 2-E (H2B.q) (H2B/q) (H2B-GL105).
8. Histone H2B type 2-F.

H-InvDB IDs			Protein Accession Numbers
Gene cluster IDs	Transcript IDs	Protein IDs (Isoforms)	
HIX0025240	HIT000055937 HIT000338463	HIP000083043	UniProt: P23527, RefSeq: NP_003518, GI: 16306566, CCDS: CCDS4640
HIX0033005	HIT000335404 HIT000335405 HIT000335406 HIT000335407	HIP000083044	UniProt: Q93079, RefSeq: NP_003515, GI: 4504269, CCDS: CCDS4601, PDB: 2cv5_D, 2cv5_H
HIX0056801	HIT000339684	HIP000083045	UniProt: Q5QNW6, Q64525, RefSeq: NP_001019770, GI: 66912162, CCDS: CCDS30846
HIX0032997	HIT000334734 HIT000334736	HIP000083226	UniProt: Q99880, RefSeq: NP_003510, GI: 4504259, CCDS: CCDS4625
HIX0032906	HIT000259542	HIP000083274	PDB: 2cv5_D, 2cv5_H
		HIP000083275	UniProt: P06899, RefSeq: NP_066402, GI: 20336754, CCDS: CCDS4618, PDB: 2cv5_D, 2cv5_H
HIX0001004	HIT000032461 HIT000263353 HIT000268765 HIT000335409 HIT000338648 HIT000338649	HIP000083276	UniProt: Q16778, RefSeq: NP_003519, GI: 4504277, CCDS: CCDS936, PDB: 2cv5_D, 2cv5_H

Figure 2.8 Database of PPIs and predicted and annotated protein complexes, “PPI view”

We can search an interesting protein from “top search page (left part)” and know information of interacting proteins with the target protein in the “results page (right part)”. In addition to information of interacting proteins, we can check 1) an experimental methods to detect the PPI, 2) the experiment al scale (large scale or small scale) detecting the PPI 3) the number of papers which report the PPI.



Representative Protein ID	HIP000102937
Definition	Proteasome subunit alpha type 3 (EC 3.4.25.1) (Proteasome component C8) (Macropain subunit C8) (Multica...
Gene Symbol	PSMA3
PPIs	6
H-InvDB Link	Locus View Transcript View PPI View

ddhcp217149 からデータを転送しています...

Figure 2.9 Visualization tool of protein and protein complex network, “PPI map”

“Detailed network” window (upper part) shows member proteins of a target complex in the center and directly interacting proteins or protein complexes in the neighborhood. “Whole network” window (lower part) displays whole of proteins and protein complexes interaction network. Scale of visualization can be changed by slide bar in the upper right of windows (left and right in the lower part).

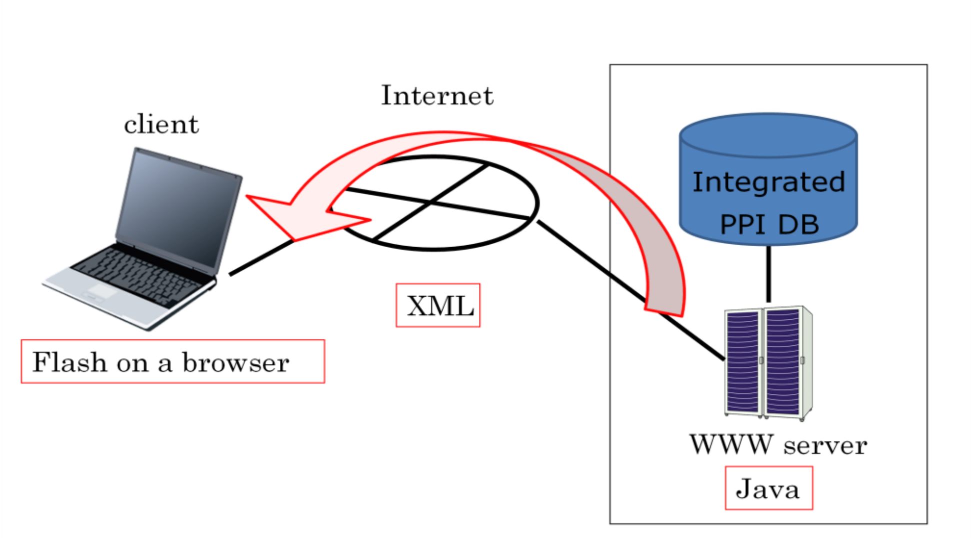


Figure 2.10 System architecture of PPI map

On scale down of visualization or moving displaying part of network, to avoid over-traffic on internet and reduce the time of visualization, PPI map request just information of new nodes and new edges to visualize to the WWW server and get the information by XML through the internet.

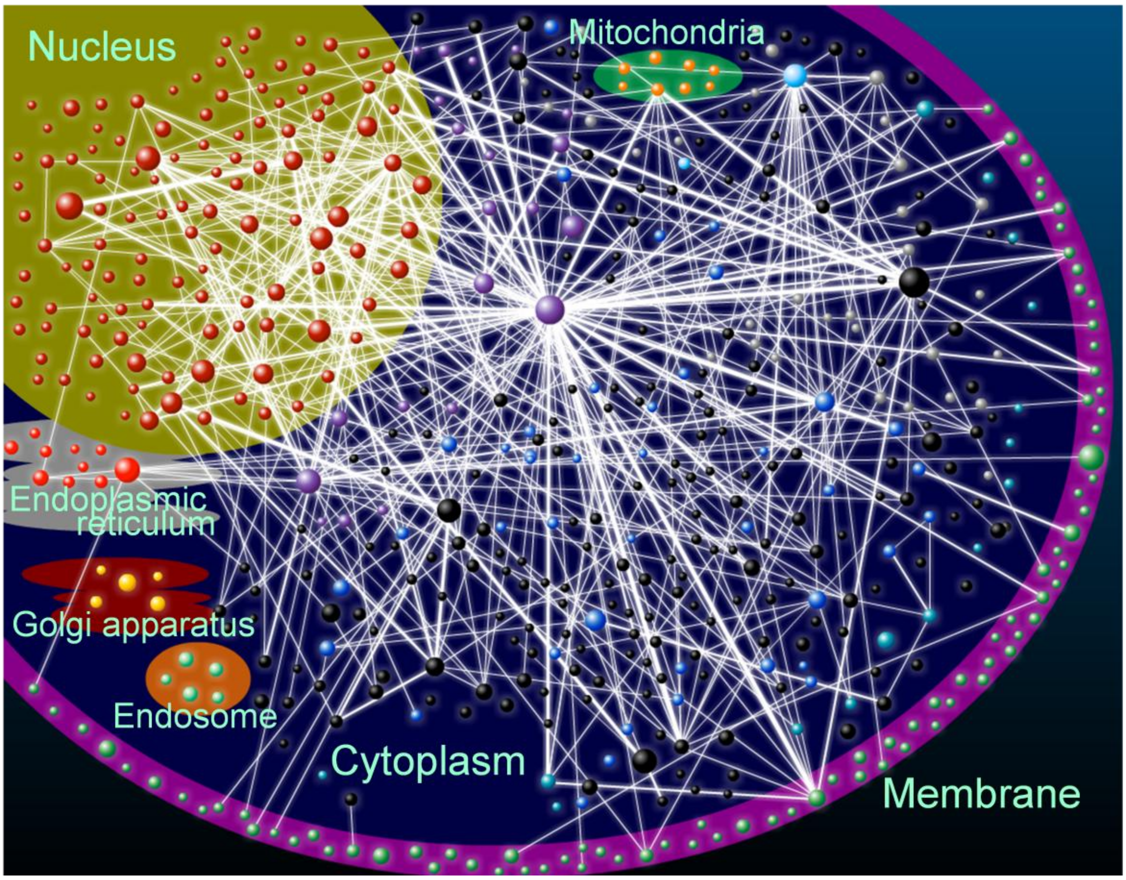


Figure 2.11 An overhead view of complex-complex interactions (CCIs) with the subcellar localizations of the annotated complexes.

Node colors indicate subcellular localization of the annotated complexes; dark red: nucleus, blue: cytoplasm, green: membrane, purple: nucleus and cytoplasm, yellow: Golgi apparatus, blue-green: cytoplasm and membrane, light blue: cytoplasm, membrane and nucleus, orange: mitochondria, light red: endoplasmic reticulum, light green: endosome, grey: other subcellular localization, black: NA/unknown.

2.6. **Discussion**

Here, I report the first attempt of comprehensive annotation of human protein complexes identified from the network of integrated PPIs of six well-organized databases. I predicted 1,264 human protein complexes from 32,198 PPIs comprising 9,268 proteins by finding densely connected regions with their cluster properties in the PPI network. After evaluating the predicted complexes and comparing with the manually collected 144 reference complex set, the annotation of the predicted complexes was carried out according to our original procedures. In this annotation, 136 complexes were perfect matches to the experimentally defined complexes; 405 complexes included at least two proteins common to the experimentally defined complexes; and 723 hypothetical complexes with no supporting evidence of complexes in the literature were predicted as protein complexes.

To assess the quality of protein complex annotation, I estimated the enrichment and the ratio of consistency of GO terms among members of a complex. This assessment is based on the assumption that the same GO terms are assigned to the proteins in a single protein complex. The ratios of protein complexes having enriched GO terms and the degree of GO term consistency were greater in the manually curated set of protein complexes (PCset2) than in all the predicted complexes (PCset1) or the random set, indicating the relatively high quality of manual annotation and the advantage of protein complex prediction followed by manual annotation as opposed to only single computational prediction.

Next, for each complex, I compared the expression profiles of the protein members in the complex based on the idea that proteins in the same complex would have similar functions and that co-expressed genes are more likely to have similar functions. Members of large complexes tend to express similarly. Furthermore, the ratio of duplicated genes in a complex was evaluated. The results indicated that the enlargement of a protein complex is considerably mediated by homologous interactions, and that gene duplication events greatly contribute to the establishment of protein complexes.

Recent statistics of manually curated H-InvDB proteins showed that 43% of H-InvDB representative transcripts were hypothetical proteins (Yamasaki et al. 2008). Hence, assigning functions to hypothetical proteins of unknown function is one of the most important problems in proteome analysis. Since subunits of a complex generally tend to have the same biological function, prediction of a protein complex allows increased confidence in the annotation of hypothetical proteins. Protein complex prediction and the following annotation found that 78 hypothetical proteins were in the 82 predicted complexes. Although the majority of hypothetical proteins tended to be subunits of hypothetical complexes that I defined and whose subunits had not been reported in the literature as parts of a complex but were just predicted as complexes by DPClus, 13 hypothetical proteins were subunits of 12 function annotatable complexes (**Table 2.3**). These hypothetical proteins are probably involved in biological processes related to other subunits of the complexes they joined. Thus, I could expect that hypothetical proteins HIP000013164 and HIP000053526 in the DREAM complex might function in the cell cycle, and HIP000177716 (FA core complex), HIP000079962 (INO80 complex), and HIP000024165 (Lamins complex) might function in DNA repair, DNA repair and transcription, and nuclear organization, respectively. The number of hypothetical proteins to whom functions were assigned in this study was very small compared to the total number of proteins in the proteome; however, information about protein complex prediction and annotation will offer annotation clues for hypothetical proteins.

Therefore, protein complexes determined solely on the basis of interaction data can help us predict the functions of proteins, and can also be useful in understanding and explaining certain biological processes. In this study, I could assign protein complex data for about 10% of the total human locus stored in H-InvDB (34,700 gene clusters [HIX]). Thus, as a rough approximation, I estimated that the total number of human protein complexes will be 10,000–20,000.

The new database “PPI view” was constructed to provide this large annotation of human protein complexes, URL; http://h-invitational.jp/hinv/ppi/. PPI view includes a new visualization tool “PPI map”, which allows users to show not only PPIs among the protein subunits, but also complex-complex interactions (CCIs) through a seamless and detailed annotation of each protein complex and its subunits. PPI view will be a useful platform for understanding protein function from the viewpoint of a complex as another level of functional unit, and will provide annotation clues for proteins of unknown function.

2.7. Conclusion

1,264 human protein complexes were predicted and annotated from the integrated PPI data. GO analysis increased the reliability of both complex prediction and manual annotation. The analysis of expression profiles and duplicated genes made it clear that protein members tend to express similarly and are mutually paralogous in a complex. Comprehensive protein complex prediction and annotation will provide strong functional annotation clues about hypothetical proteins. The new database "PPI view" was constructed to provide this large annotation of human protein complexes. PPI view is available at http://h-invitational.jp/hinv/ppi/

Chapter 3

Predicting topological structure of protein complexes by determining statistically significant domain-domain interactions

3.1. Abstract

Background: More or less over the past 10 years, vast amount of protein-protein interaction data have been generated by high-throughput methods for detecting protein interactions, such as the affinity purification- mass spectrometry (affinity purification-MS) and the yeast two-hybrid (Y2H) system (Uetz et al. 2000; Ito et al. 2001; Ho et al. 2002; Gavin et al. 2002). However, high-throughput methods for detecting protein interactions generate a significant number of false-positives, and that is serious problem because they cause erroneous results and misleading conclusions. Additionally, the affinity purification-MS detects non-direct interactions: “prey-prey” interactions, it implies that the topological structure of the protein complexes cannot be determined from the individual experiments only.

Results: The present study proposes a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs). As the first step, I extracted 312 statistically significant DDIs out of 1,162 DDIs underlying 3,118 protein-protein interactions (PPIs). Significant DDIs were determined based on statistical analysis of 2 x 2

contingency tables, estimated using pairs of domains reported to interact in determined structures of protein complexes in iPfam (Finn et al. 2005) as true positive DDIs. Next, 67 protein complexes were obtained by finding densely connected regions with their cluster properties in the PPI network. Finally, I discussed the topological structure of protein complexes based on DDI information extracted in the first step.

Conclusion: This work has proposed a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs). Significant DDIs were determined based on statistical analysis of 2 x 2 contingency tables, 312 significant DDIs underlying 3,118 protein-protein interactions (PPIs) were obtained. In the present study, 1,629 out of 3,118 PPIs were supported by statistically significant domain-domain pairs. Furthermore, I validated 67 protein complexes detected in the protein interaction network composed of 1,302 proteins in view of significant DDIs. The present study makes it possible to interpret the topological structure of protein complexes by configuring interactions supported by DDIs.

3.2. Introduction

Experimental methods to detect protein-protein interactions (PPIs), such as Yeast two-hybrid method (Y2H) and affinity purification-mass spectrometry method (affinity purification-MS), generates a significant number of false-negatives and false-positives (Titz et al. 2004), and false-positives are especially a more serious problem in that they cause erroneous results and misleading conclusions. In addition to that, on affinity purification-MS, all of the “prey” proteins in complexes containing a “bait” protein are identified as interacting proteins. It implies PPIs detected by affinity purification-MS include “bait-prey” and “prey-prey” interactions, and topological structure of the protein complexes cannot be determined from the individual experiments only. In case that proteins A, B and C are identified in isolation as a protein complex using protein A with a tag as a “bait”, it is difficult to conclude what is the true topological structure of the complex out of the four possible cases as shown in i)～iv) in **Figure 3.1**. Though understanding the topological structure of protein complexes is necessary in order to obtain useful information about them, little attention has been given by the bioinformatics researchers to decipher the true topological structure of the protein complexes. Also the experimental technologies used to detect PPIs do not focus on this matter.

The bioinformatics analysis of PPIs has mainly followed two different approaches after the high throughput experiments started to produce huge amount of data. One of the approaches is the analysis of protein interaction networks based on graph theory, aiming to detection of protein complexes from PPIs networks (Bader and Hogue 2003; Altaf-Ul-Amin et al. 2006). These studies have reported that the densely connected regions in a network correspond to known protein complexes or protein functional units. The other approach is the analysis of DDIs coming out from PPIs data by statistics or machine learning intended to predict unknown PPIs (Sprinzak and Margalit 2001; Riley et al. 2005; Singhal and Resat 2007; Liu et al. 2009). These studies have shown that the concept of DDIs statistically extracted from large-scale PPI data can explain the makeup of PPIs to some extent.

Taking these two recent approaches into account, the present study focuses on statistically significant DDIs i.e. the direct interactions to predict the topological structure of protein complexes by avoiding the effects of false-positives or non-direct interactions. Corresponding to **Figure 3.1**, if DDI analysis supports that protein B and C directly interacts with different domains of protein A then I would predict the topological structure of ii), and on the other hand, if protein B and C directly interacts with an identical domain of protein A competitively then I would predict the topological structure of iv). Further detail prediction of interactions in protein complexes were performed based on DDIs.

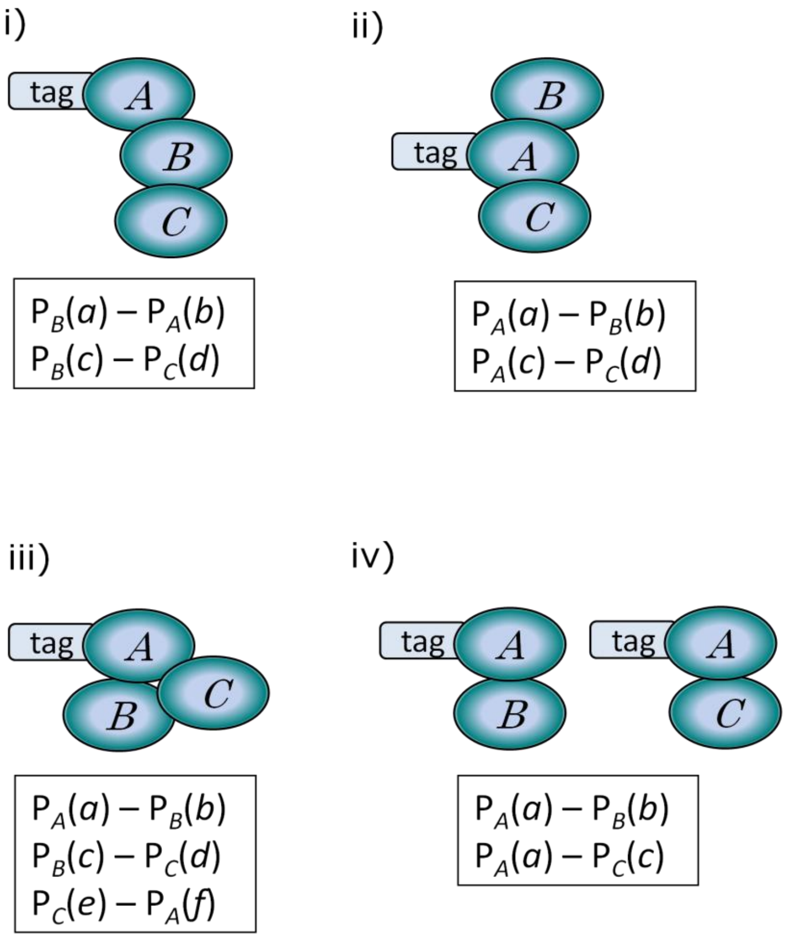
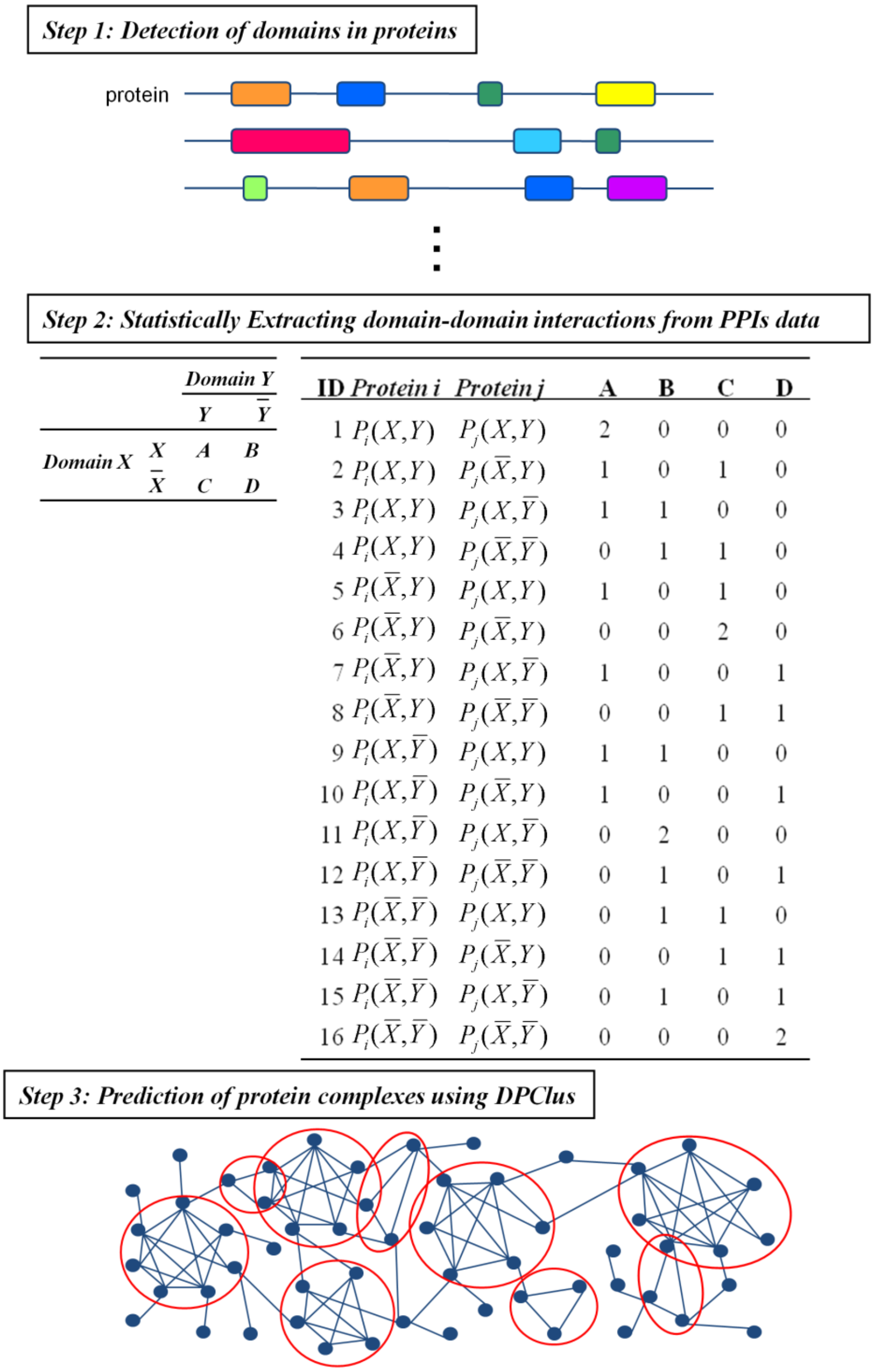


Figure 3.1 Topological structure diversity of protein complexes in case that proteins A, B and C are identified by MS.

Notations in boxes indicate example of direct protein interactions by domains, i.e., $P_A(a) - P_B(b)$ represents that the domain *a* of protein A directly interacts the domain *b* of protein *B*.

3.3. **Methods**

In the present study, I propose a procedure for inferring topological structure of protein complexes with reliable PPIs by using information of DDIs (**Figure 3.2**), which comprises three steps, (Step 1) Detection of domains in proteins, (Step 2) Extraction of statistically significant DDIs, and (Step 3) validation of protein complexes based on extracted DDIs.



		Domain Y	
		Y	$\bar{Y}$
Domain X	*X*	*A*	*B*
	$\bar{X}$	*C*	*D*

ID	Protein i	Protein j	A	B	C	D
1	$P_i(X,Y)$	$P_j(X,Y)$	2	0	0	0
2	$P_i(X,Y)$	$P_j(\bar{X},Y)$	1	0	1	0
3	$P_i(X,Y)$	$P_j(X,\bar{Y})$	1	1	0	0
4	$P_i(X,Y)$	$P_j(\bar{X},\bar{Y})$	0	1	1	0
5	$P_i(\bar{X},Y)$	$P_j(X,Y)$	1	0	1	0
6	$P_i(\bar{X},Y)$	$P_j(\bar{X},Y)$	0	0	2	0
7	$P_i(\bar{X},Y)$	$P_j(X,\bar{Y})$	1	0	0	1
8	$P_i(\bar{X},Y)$	$P_j(\bar{X},\bar{Y})$	0	0	1	1
9	$P_i(X,\bar{Y})$	$P_j(X,Y)$	1	1	0	0
10	$P_i(X,\bar{Y})$	$P_j(\bar{X},Y)$	1	0	0	1
11	$P_i(X,\bar{Y})$	$P_j(X,\bar{Y})$	0	2	0	0
12	$P_i(X,\bar{Y})$	$P_j(\bar{X},\bar{Y})$	0	1	0	1
13	$P_i(\bar{X},\bar{Y})$	$P_j(X,Y)$	0	1	1	0
14	$P_i(\bar{X},\bar{Y})$	$P_j(\bar{X},Y)$	0	0	1	1
15	$P_i(\bar{X},\bar{Y})$	$P_j(X,\bar{Y})$	0	1	0	1
16	$P_i(\bar{X},\bar{Y})$	$P_j(\bar{X},\bar{Y})$	0	0	0	2

Figure 3.2 Procedure of validation of protein complexes based on extracted DDIs.

Firstly, domains were extracted by InterProScan (Step 1), then statistically co-occurred domain-domain pairs were extracted by Fisher's exact test for 2 x 2 contingency table (Step 2), and, in Step 3, validation of protein complexes were carried out using the domain-domain pairs determined in Step 2.

3.3.1. Step 1: Detection of domains in proteins

The InterProScan, which is a tool that combines different protein signature recognition methods into one resource, can detect protein families, domains, repeats and functional sites containing post-translational modification sites (Zdobnov and Apweiler 2001). In the present study the domains of all proteins were detected by InterProScan. The protein signature by InterProScan has the hierarchical structure, that is, a parent/child relationship between two signatures is defined in the output of InterProScan, and the parent is the entry containing a more general signature, while the children are more specific to certain members of the signature. In the context of protein interaction, domains or smaller peptide motifs act as recognition elements, therefore domains, repeats and functional sites of second depth in hierarchy but not families by InterProScan were simply used as domains in this DDI analysis.

3.3.2. Step 2: Statistically extracting domain-domain interactions from PPI data

Statistical analysis based on 2 x 2 contingency table was applied to detect significant relation between a domain pair by judging their presence and absence in a set of interacting protein pairs (**Figure 3.2**). Concerning the presence and absence of two domains say, X and Y in two interacting proteins say, i and j there could be 16 combinations and **Figure 3.2** shows how I counted A, B, C and D of the contingency table corresponding to each combination. The null hypothesis is that the occurrence of domain X in a protein and the occurrence of domain Y in the other protein in a PPI are independent of each other. So, the test of independence between domain X and domain Y was performed using Fisher's exact test with significance level α=0.01, taking multiple hypotheses into consideration, that is, Bonferroni's correction was adopted in order to avoid statistical significance that might occur by chance. To determine significant DDIs, I statistically tested potential DDIs, containing self-DDIs, for which a protein has a domain and the other protein has another domain in at least one PPI, i.e., the count *A* on the contingency table in **Figure 3.2** is not lower than one.

3.3.3. Step 3: Validation of protein complexes generated using DPClus

Firstly, protein complexes were predicted by applying DPClus (Altaf-Ul-Amin et al. 2006) to the whole PPI network by setting three parameters as 0.7 for network density, 0.5 for cluster property and 3 for least number of members in a cluster. DPClus detects densely connected regions of a graph comprising nodes and edges as clusters which correspond to protein complexes in case of a PPI network. Prediction of protein complexes based on network density demonstrates a tendency that protein complexes with fewer number of members are more detected in a protein interaction network: by setting 3 as the parameter for least number of members in a cluster, complexes composed of 3 protein members are most found out. A protein complex of 3 members with network density 0.7 and over indicates complete graph among 3 members, whereas the density between 0.6 ~ 0.7 density indicates just single-linkage chain of 3 members. Here, to discuss the topological structure of protein complexes using DDIs as evidence of true-positive PPIs, I applied 0.7 for network density in this study. After prediction of protein complexes with these parameter set, the PPIs in the complexes are validated by significant domain-domain pairs obtained in Step 2 which in turn helps to cast insight into probable topological structure of the complexes.

3.4. Results and Discussion

3.4.1. Collection and integration of PPIs data

The PPIs of the *Arabidopsis* interactome were collected by following two procedures: collecting from public PPI databases and manual collecting from research papers. Any computationally predicted PPI was excluded from this study. In the first procedure, the PPI data was assembled from BIND (Bader et al. 2000; 2003), DIP (Xenarios et al. 2002), MINT (Zanzoni et al. 2002; Chatr-aryamontri et al. 2007), HPRD (Peri et al. 2003) and IntAct (Hermjakob et al. 2004) which are major PPIs data resources accepting experimentally determined PPIs from research papers. In the second procedure, 946 PPIs were manually gathered by reading experimental research papers. PPI data redundancies were removed by mapping PPI information onto the *Arabidopsis* genes (AGI codes), and, as a result an integrated PPI data, 3,118 PPIs composed of 1,302 *Arabidopsis* proteins was obtained.

3.4.2. Significant domain-domain interactions extracted from PPI data

Proteins must physically bind to other proteins, either stably or transiently, to perform their functions. Interaction specificity results from the binding of a modular domain to another domain or smaller peptide motif in the target protein (Pawson and Nash 2003). For example, some cytoskeletal proteins bind to actin through their modular gelsolin repeat domains

(McGough et al. 2003), and Src-homology 3 domains (SH3) bind to proline rich peptides that have a PxxP consensus sequence (Lim et al. 1994). In the context of protein interaction, such domains and peptides act as recognition elements; I refer to these binding domains or recognized peptides simply as 'domains' in this study. Over the past few years with developments of high-throughput PPI detection technologies, many researchers have shown an interest in extracting domain-domain interactions (DDIs) from large-scale PPI data by statistical methods, demonstrating that the idea of DDIs explain the cause of PPIs in some measure (Sprinzak and Margalit 2001; Riley et al. 2005; Singhal and Resat 2007; Liu et al. 2009). Here, I statistically extracted DDIs from integrated PPI data of *Arabidopsis* by original procedure described in the ‘Method’ section. Total 312 significant DDIs were obtained (Fisher’s exact test, α=0.01 with Bonferroni correction) out of 1,162 potential DDIs for which a protein has a domain and the other protein has another domain in at least one PPI.

PPI detection technologies experimentally provide the information about existence of interaction, but usually no direct information about the domains and peptides which act as recognition elements or binding sites, and determining binding domains and peptides in proteins require further analysis. Therefore, as a benchmark for true-positive DDIs, I used pairs of domains reported to interact in determined structures of protein complexes in iPfam (Finn et al. 2005). In iPfam, two domains are defined as interacting if they are close enough to form at least one interaction based on available PDB structures. It should be noted that known set of interacting domain pairs determined from structures are only a small fraction of all DDIs that may exist, i.e. though these are the gold standard DDIs, it is certainly possible that predicted

DDIs are also true and structures which contains predicted DDIs have not been determined yet. According to a recent study (Itzhaki et al. 2006), DDIs in iPfam and 3DID (Stein et al. 2005) databases could explain no more than 20% of the PPIs for any of the *E. coli*, *S. cerevisiae*, *C. elegans*, *D.melanogaster*, and *H. sapience,* suggesting that the number of known DDIs is rather small. So I used iPfam to assess true-positive rate with respect to P-value after Bonferroni's correction for DDIs and 70% of the known DDIs have been recognized within the threshold of 0.01 (**Figure 3.3**). Using this threshold, 312 statistically significant pairs of interacting domains were obtained (**Figure 3.3B**). So I used iPfam to assess true-positive rate with respect to P-value after Bonferroni's correction for DDIs and 70% of the known DDIs have been recognized within the threshold of 0.01 showing the effectiveness of our method (**Figure 3.3A**). Using this threshold, 312 statistically significant pairs of interacting domains were obtained (**Figure 3.3B**) and if I add 20 other gold DDIs not detected by our method then the number of total significant DDIs is 332. Now 20% of the PPIs can be explained by 66 DDIs and if I consider a linear relation then 330 DDIs are required to explain 100% PPIs which almost matches with the number 332 implying that the proposed DDI prediction method is a good one.

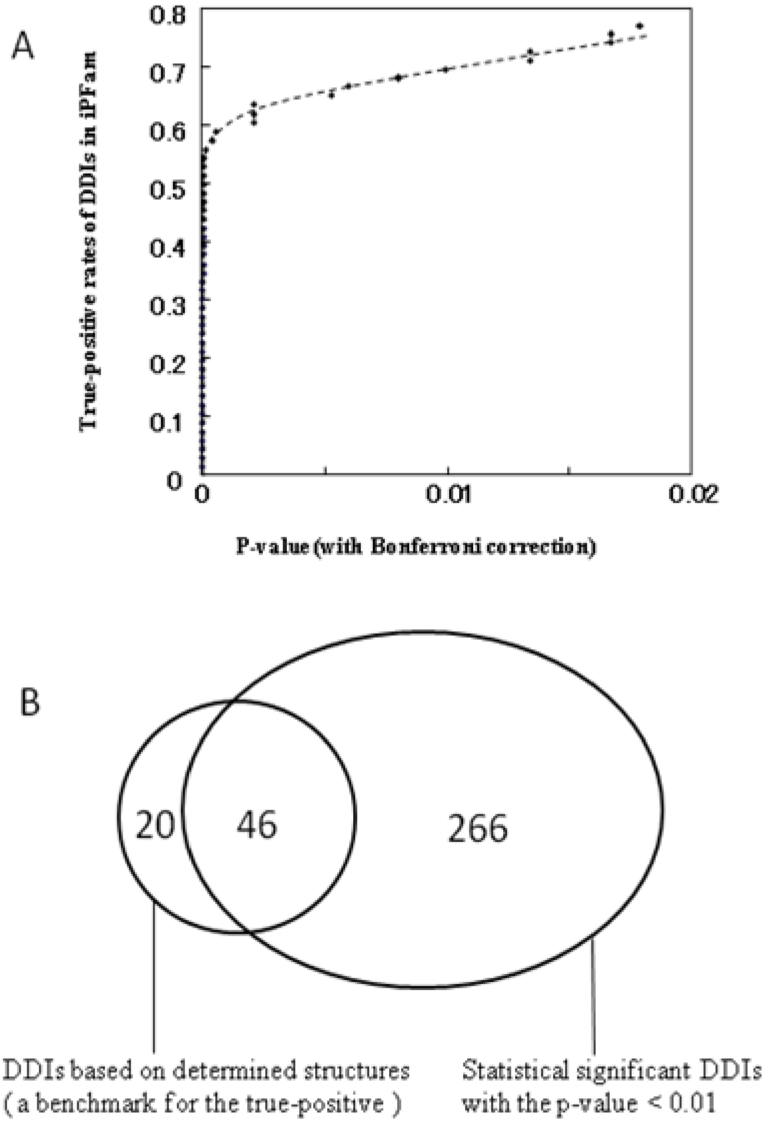


Figure 3.3 Validation of statistically extracted DDIs using iPfam.

(A) True-positive DDIs with the p-value; (B) true-positive DDIs out of statistically significant DDIs. By iPfam, 66 reported DDIs were obtained out of 1,162 potential domains. Of them, 46 DDIs were included in statistically significant cooccured domain-domain pairs in Step 2 in Figure 2. So the true-positive rate is estimated to be as 0.70.

3.4.3. Prediction of protein complexes

In the past, the algorithm called "DPClus" was developed by Altaf-Ul-Amin et al. (2006), which extracts the densely connected regions in a network and demonstrated that many of these densely connected regions correspond to known protein complexes or protein functional units. DPClus is a robust algorithm not affected by high rate of false positives in data from high-throughput interaction-detection techniques. While predicting the protein complexes by DPClus, I adopted the "overlapping clustering mode", which allows identical proteins to be classified into different clusters, because it is biologically well established that proteins can be present in multiple complexes at different times and locations. By setting three parameters as 0.7 for network density, 0.5 for cluster property and 3 for least number of members in a cluster, 67 protein complexes were obtained from 3,118 PPIs (**Figure 3.4**). In the present study, 1,629 out 3,118 PPIs were supported by statistically significant domain-domain pairs (**Appendix Table 1**), suggesting that high-potential PPIs of true-positives in that DDIs can explain mechanisms of protein recognition and interaction. Additionally, using significant DDIs information, I provided considerable information for deducing the topological structure of all protein complexes detected by DPClus (**Appendix Table 2**). **Appendix Table 2** shows protein members of complexes with domains detected by InterProScan and the locations of domains in proteins, PPIs and DDIs supporting the PPIs in the complexes. The (*) notation with a PPI indicates that the PPI is supported by statistically significant DDIs. In this method predicting topological structure of complexes using DDIs, multiple existences of identical domains in disparate locations of proteins were taken account.

Out of the all predicted 67 complexes, 16 complexes (cluster ID: 9, 20, 27, 33, 37, 39, 40, 43, 45, 46, 47, 55, 57, 60, 61, 65) had no PPIs supported by statically significant DDIs. The proteins of these complexes have very few domains detected by InterProScan. For examples, in case of cluster 9, only two kinds of domains (IPR001932: Protein phosphatase 2C-related and IPR003124: Actin-binding WH2) were detected in 9 proteins, and in case of cluster 27 which has 4 protein members, only one domain was detected. In these cases, it seems wrong to interpret that all PPIs in predicted complexes are false-positives because these proteins in predicted complexes densely (density $\geq$ 0.7) interact among them. It should be interpreted that DDIs explaining PPIs could not be detected by present study. On prediction of DDIs, relations of pairwise domains detected by InterProScan in interacting proteins were statistically tested, therefore, DDIs cannot be predicted if proteins do not have domains or InterProScan cannot detects domains in proteins. These results and consideration leads us to presume that there can be unknown mechanisms of protein recognition and interaction.

Other hand, in 19 complexes (cluster ID: 5, 11, 12, 16, 17, 21, 22, 24, 25, 28, 34, 42, 44, 49, 50, 54, 59, 64, 66), all PPIs composing the complex were supported by significant DDIs. Interpretation of complex topological structure demands a lot of attention though these all PPIs seem like apparent true-positives. Large number of these complexes in which all PPIs were supported by significant DDIs are complexes of DNA- or RNA- binding proteins such as transcription factor complex (cluster ID: 5, 12, 17, 21, 24, 25, 42, 44, 49, 50, 54, 64). These complexes are mixture of protein and DNA or RNA and proteins interacts other proteins in the complex through DNA or RNA, inferring high possibility that ever predicted DDIs from these DNA- or RNA- binding proteins are false-positives. In other protein complexes in which all PPIs were supported by significant DDIs, there is a tendency that most protein members have some identical domains with that of other protein members and PPIs among these proteins are explainable by a few DDIs. This tendency can be explained by considering competition of interacting domain: for instance of cluster 28, all 4 proteins have one IPR008271 (Serine/threonine protein kinase, active site) and one IPR000719 (Protein kinase, core), and according to DDIs prediction IPR000719 interacts with IPR008271, i.e., in the complex IPR000719 of 3 proteins competitively contact with IPR008271 of another protein.

In other 32 complexes (cluster ID: 1, 2, 3, 4, 6, 7, 8, 10, 13, 14, 15, 18, 19, 23, 26, 29, 30, 31, 32, 35, 36, 38, 41, 48, 51, 52, 53, 56, 58, 62, 63, 67), some PPIs have evidence of DDIs, but other PPIs did not have that. **Figure 3.5** shows some examples, in which each node and each edge represent a protein and an interaction respectively: blue and red edges represent interactions determined by PPI experiments and interactions supported by statistically significant domain-domain pairs (suggesting direct interaction) respectively. The complex represented by cluster 41 in **Figure 3.5** is composed of At1g16970, At1g4805 and At4g13870, and according to the present DDIs analysis, domain IPR005160 (Ku70/Ku80 C-terminal arm) and IPR006164 (DNA helicase, ATP-dependent, Ku type) of At1g16970 and At1g4805 contact with identical domain IPR002562 (3’-5’ exonuclease) of At4g13870 respectively. Thus this complex is explainable by the competitive interactions of two proteins, At1g16970 and At1g4805, with domain IPR002562 of At4g13870. The cluster 23 consists of 5 proteins and 3 of its 7 PPIs are supported by significant DDIs. At1g16240 has two domains (IPR000727:

Target SNARE coiled-coil region and IPR010989: t-SNARE) to interact with At1g28490 and At5g46860, respectively, and At1g28490 also has two domains (IPR000727 and IPR010989) to interact with At1g16240 and At5g26980. This can be explained by the consecutively ordered interaction of four proteins At5g46860, At1g16240, At1g28490 and At5g26980. In the complex 35, it is presumed from the graph that At1g74740 and At3g19290 play a vital role. In fact, At1g74740 and At3g19290 have characteristic domains respectively: At1g74740 has IPR008271 (serine/threonine protein kinase active site in protein kinase core) and At3g19290 has IPR004827 (Basic-leucine zipper (bZIP) transcription factor), whereas other all proteins in the complex has only common domains (IPR002048: Calcium-binding EF-hand and IPR011992: EF-Hand type). Based on DDIs analysis, At1g74740 and At3g19290 play a central part of complex by directly interacting with other each protein (At3g43810, At3g51920, At3g56800, At4g14640, At5g21274) and these each 5 proteins interact each other directly.

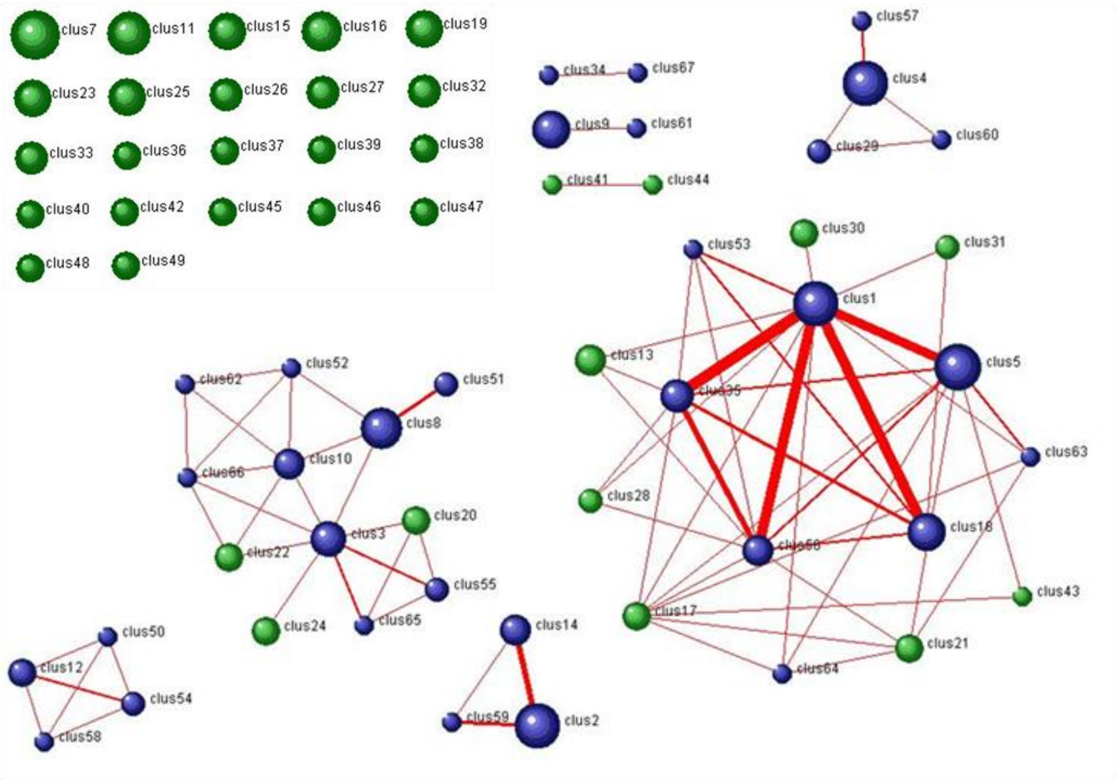


Figure 3.4 Complex-complex interaction network emerged from PPI network by adopting DPClus.

Nodes represent complexes and edges represent their interactions. Size of nodes shows the number of proteins in complexes and thickness of edges suggests the number of PPIs between complexes. Protein complex prediction allowed identical proteins to be classified into different clusters. Blue nodes represent to be clusters containing such shared proteins and Green nodes represent not to be.

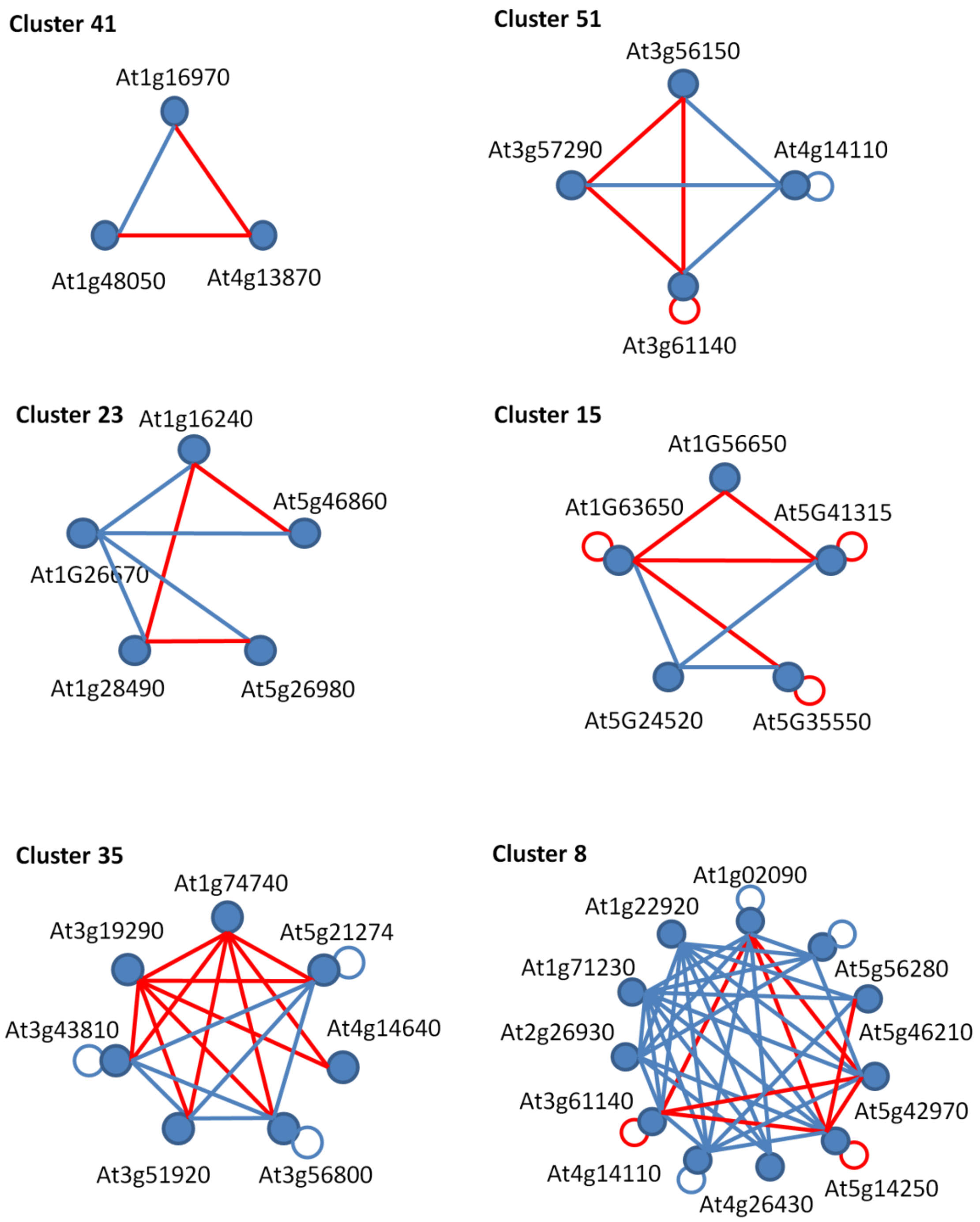


Figure 3.5 Prediction of the topological structure of protein complexes using significant DDIs information.

Each node and edge represents protein and interaction respectively. Blue edges show original interaction, and red edges show confidential interactions supported by significant DDIs. Blue and red circles represent self-interactions.

3.5. Conclusion and Remarks

This work has originally proposed a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs). Significant DDIs were determined based on statistical analysis of 2 x 2 contingency tables, 312 significant DDIs underlying 3,118 protein-protein interactions (PPIs) were obtained. In the present study, 1,629 out of 3,118 PPIs were supported by statistically significant DDIs. Furthermore, I validated 67 protein complexes detected in the protein interaction network composed of 1,302 proteins in view of significant DDIs. The present study makes it possible to interpret the topological structure of protein complexes by configuring interactions supported by DDIs. A further study of topological structure of protein complexes from PPI data should be conducted, which can also help computer simulations of protein complexes to develop new drugs. The more understanding of conformation of protein complexes would give new clues to development of drugs.

Chapter 4 Conclusion and Remarks

Introduction (Chapter 1) of this dissertation explained the background of protein-protein interaction (PPI) analysis and two representative PPI detection methods (Y2H and affinity purification-MS). Then, I elucidated problems of high-throughput methods for detecting protein interactions: each detection method generates a significant number of false-positives, and that is serious problem because they cause erroneous results and misleading conclusions. Additionally, affinity purification-MS detects non-direct interactions: “prey-prey” interactions. It implies that the topological structure of the protein complexes cannot be determined from the individual experiments only. Moreover, detecting “prey-prey” interactions makes determining certain members of protein complexes complicated and difficult. Therefore, based on above background, I aimed to predict and evaluate certain protein complexes, more specifically i) to predict members of protein complexes and to evaluate that by annotation (in Chapter 2) and ii) to propose a method to predict the topological structure of protein complexes (in Chapter 3). Aiming to the goal of this dissertation, I tried two kinds of studies respectively.

Analysis on human PPI network is presented in Chapter 2, which predicts 1,264 protein complexes from 32,198 PPIs comprising 9,268 proteins by finding densely connected regions with their cluster properties in the network. These predicted complexes were annotated and evaluated using integrated data such as literatures and research papers, ternary structures, descriptions of protein, localizations, expression profiles, gene loci, and PPIs among protein subunits. In this annotation of predicted 1,264 protein complexes, I found that 136 complexes were well-known complexes; 405 complexes were partially-known complexes; and 723 were unknown complexes with no supporting evidence of complexes in the literature.

In addition, I found 78 hypothetical proteins that were annotated as members of 82 complexes that included several well-known complexes. Recent statistics of manually curated H-InvDB proteins showed that 43% of H-InvDB representative transcripts were hypothetical proteins (Yamasaki et al. 2008). Hence, assigning functions to hypothetical proteins of unknown function is one of the most important problems in proteome analysis. Since subunits of a complex generally tend to have the same biological function, prediction of a protein complex allows increased confidence in the annotation of hypothetical proteins. The number of hypothetical proteins to whom functions were assigned in this study was very small compared to the total number of proteins in the proteome; however, comprehensive protein complex prediction and annotation will provide strong functional clues about hypothetical proteins.

To provide this large annotation of human protein complexes, the new database “PPI view” was constructed, URL; http://h-invitational.jp/hinv/ppi/. PPI view includes a new visualization tool “PPI map”, which allows users to show not only PPIs among the protein subunits, but also complex-complex interactions (CCIs) through a seamless and detailed annotation of each protein complex and its subunits. PPI view will be a useful platform for understanding protein function from the viewpoint of a complex as another level of functional unit.

The study on *Arabidopsis* PPI network of Chapter 3 originally proposed a method to predict the topological structure of protein complexes by using domain-domain interactions (DDIs). As the first step, I extracted 312 statistically significant DDIs out of 1,162 DDIs underlying 3,118 protein-protein interactions (PPIs). Significant DDIs were determined based on statistical analysis of 2 x 2 contingency tables, estimated using pairs of domains reported to interact in determined structures of protein complexes in iPfam (Finn et al. 2005) as true positive DDIs. And, 1,629 out of 3,118 PPIs were supported by statistically significant domain-domain pairs. Next, 67 protein complexes were obtained by finding densely connected regions with their cluster properties in the PPI network. Finally, I validated 67 protein complexes and discussed the topological structure based on DDI information extracted in the first step. The present study makes it possible to interpret the topological structure of protein complexes by configuring interactions supported by DDIs.

In present study, using *Arabidopsis* PPI network composed of 1,302 proteins and 3,118 PPIs, I tried to predict the topological structure of protein complexes based on DDIs and proposed the method. Here, human PPI network is composed of 9,268 proteins and 32,198 PPIs, so proteins and PPIs of human are respectively 7.12 times and 10.33 times as much as that of *Arabidopsis*. On human PPI network of about 10 times the large of *Arabidopsis* one, analysis of the topological structure of protein complexes will require a lot of machine power: especially, calculation of statistical analysis of DDIs grows at a rate of second power of number of domains in interacting proteins, because all potential domain pairs are tested by Fisher’s exact test. Therefore, progress of machine power or contrivance of computation is required in order to analyze the topological structure of protein complexes on human.

In this dissertation, I discussed prediction of protein complex based on protein interaction network and topological structure of protein complexes, taking into account the fact that experimental methods to detect PPIs generates a significant number of false-positives and affinity purification- MS equally detect direct and non-direct interactions. To understand the protein functions required for various biological processes in cells, comprehensive analysis of PPIs and protein complexes as fundamental functional units of macromolecular systems would provide a valuable framework. And, in order to elucidate PPIs, it is important to unravel the mechanisms of protein recognition at the molecular level. The understanding of mechanisms of protein recognition and interaction would release us from problems of false-negative and false-positive. Concurrently a further study of topological structure of protein complexes from PPI data should be conducted, which can also help computer simulation of protein complexes to develop new drugs. The more understanding of conformation of protein complexes and mechanisms of protein recognition and interaction would give new clues to development of drugs.

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Achievements

Reviewed publications and manuscripts in preparation

1. **Kensaku Nishikata**, Masayoshi Wada, Hiroki Takahashi, Kensuke Nakamura, Shigehiko KanAya, Md Altaf-Ul-Amin, Predicting conformation of protein complexes by determining statistically significant Domain-Domain interactions, *Plant Biotechnology* 26: 495-501
2. Chisato Yamasaki, Katsuhiko Murakami, Yasuyuki Fujii, Yoshiharu Sato, Erimi Harada, Jun-ichi Takeda, Takayuki Taniya, Ryuichi Sakate, Shingo Kikugawa, Makoto Shimada, Motohiko Tanino, Kanako O. Koyanagi, Roberto A. Barrero, Craig Gough, Hong-Woo Chun, Takuya Habara, Hideki Hanaoka, Yosuke Hayakawa, Phillip B. Hilton, Yayoi Kaneko, Masako Kanno, Yoshihiro Kawahara, Toshiyuki Kawamura, Akihiro Matsuya, Naoki Nagata, **Kensaku Nishikata**, Akiko Ogura Noda, Shin Nurimoto, Naomi Saichi, Hiroaki Sakai, Ryoko Sanbonmatsu, Rie Shiba, Mami Suzuki, Kazuhiko Takabayashi, Aiko Takahashi, Takuro Tamura, Masayuki Tanaka, Susumu Tanaka, Fusano Todokoro, Kaori Yamaguchi, Naoyuki Yamamoto, Toshihisa Okido, Jun Mashima, Aki Hashizume, Lihua Jin, Kyung-Bum Lee, Yi-Chueh Lin, Asami Nozaki, Katsunaga Sakai, Masahito Tada, Satoru Miyazaki, Takashi Makino, Hajime Ohyanagi, Naoki Osato, Nobuhiko Tanaka, Yoshiyuki Suzuki, Kazuho Ikeo, Naruya Saitou, Hideaki Sugawara, Claire O'Donovan, Tamara Kulikova, Eleanor Whitfield, Brian Halligan, Mary Shimoyama, Simon Twigger, Kei Yura, Kouichi Kimura, Tomohiro Yasuda, Tetsuo Nishikawa, Yutaka Akiyama, Chie Motono, Yuri Mukai, Hideki Nagasaki, Makiko Suwa, Paul Horton, Reiko Kikuno, Osamu Ohara, Doron Lancet, Eric Eveno, Esther Graudens, Sandrine Imbeaud, Marie Anne Debily, Yoshihide Hayashizaki, Clara Amid, Michael Han, Andreas Osanger, Toshinori Endo, Michael A. Thomas, Mika Hirakawa, Wojciech Makalowski, Mitsuteru Nakao, Nam-Soon Kim, Hyang-Sook Yoo, Sandro J. De Souza, Maria de Fatima Bonaldo, Yoshihito Niimura, Vladimir Kuryshev, Ingo Schupp, Stefan Wiemann, Matthew Bellgard, Masafumi Shionyu, Libin Jia, Danielle Thierry-Mieg, Jean Thierry-Mieg, Lukas Wagner, Qinghua Zhang, Mitiko Go, Shinsei Minoshima, Masafumi Ohtsubo, Kousuke Hanada, Peter Tonellato, Takao Isogai, Ji Zhang, Boris Lenhard, Sangsoo Kim, Zhu Chen, Ursula Hinz, Anne Estreicher, Kenta Nakai, Izabela

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3. Arifuzzaman M., Maeda M., Itoh A., **Nishikata K.**, Takita C., Saito R., Ara T., Nakahigashi K., Huang, H.C., Hirai A., Tsuzuki K., Nakamura S., Altaf-Ul-Amin M., Oshima T., Baba T., Yamamoto N., Kawamura T., Ioka-Nakamichi T., Kitagawa M., Tomita M., Kanaya S., Wada C. and Mori H. (2006) "Large-scale identification of protein-protein interaction of Escherichia coli K-12", Genome Research 16: 686 - 691
4. **Kensaku Nishikata**, Shingo Kikugawa, Yoshiharu Sato, Katsuhiko Murakami, Mami Suzuki, Md Altaf-Ul-Amin, Shigehiko Kanaya, and Tadashi Imanishi, Integrative Annotation of Predicted Protein Complexes in the Network of Human Protein-Protein Interactions in H-Invitational Human Transcriptome Database, *in preparation.*

Other publications

Japanese journal

1. Md. Altaf-Ul-Amin、和田眞昌、**西潟憲策**、旭弘子、黒川顕、金谷重彦、生体ネットワークにおけるタンパク質間相互作用の研究法、生体の科学、58(5):391-394(2007)

Public DB and tool

2. “PPI view” and “PPI map” http://www.h-invitational.jp/hinv/ppi/

International Conferences

1. Shingo Kikugawa, **Kensaku Nishikata**, Md. Altaf-Ul-Amin, Shigehiko Kanaya, and Tadashi Imanishi, "Integration and Analysis of Human Protein-Protein Interaction Data on the Human Transcriptome Database, H-InvDB", HUPO 6th Annual World Congress, October 6-10, 2007, Seoul, Korea.
2. Md. Altaf-Ul-Amin, **Kensaku Nishikata**, Toshihiro Koma, Teppei Miyasato, Yoko Shinbo, Md. Arifuzzaman, Chieko Wada, Maki Maeda, Taku Oshima, Hirotada Mori,

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Local Conferences

1. **西濶 憲策**、喜久川 真悟、渡辺 賢、金谷 重彦、今西 規「タンパク質間相互作用に関わるドメインの統計的抽出」ＢＭＢ2007 第 30 回日本分子生物学会年会・第 80 回日本生化学会大会 合同大会、2007 年 12 月 11 日-15 日、横浜

Appendix

Appendix Table 1

List of PPIs supported by statistically significant domain-domain interactions.

A) PPIs supported by statistically significant domain-domain interactions.

(Example)	Protein 1	list of domains in the protein 1('|'delimited)
	Protein 2	list of domains in the protein 2('|'delimited)
	List of supporting DDIs('|'delimited)	
No.0001	At1g01040	IPR003100|IPR001159|IPR005034|IPR011545|IPR001650|IPR000999
	At1g09700	IPR001159
	IPR000999-IPR001159|IPR001159-IPR001159|IPR001159-IPR001650|IPR001159-IPR003100|IPR001159-IPR005034|IPR001159-IPR011545	
No.0002	At1g01040	IPR003100|IPR001159|IPR005034|IPR011545|IPR001650|IPR000999
	At2g28380	IPR001159
	IPR000999-IPR001159|IPR001159-IPR001159|IPR001159-IPR001650|IPR001159-IPR003100|IPR001159-IPR005034|IPR001159-IPR011545	
No.0003	At1g01040	IPR003100|IPR001159|IPR005034|IPR011545|IPR001650|IPR000999
	At5g41070	IPR001159
	IPR000999-IPR001159|IPR001159-IPR001159|IPR001159-IPR001650|IPR001159-IPR003100|IPR001159-IPR005034|IPR001159-IPR011545	
No.0004	At1g01140	IPR004041|IPR008271|IPR011009|IPR000719
	At4g17615	IPR011992|IPR002048
	IPR000719-IPR002048|IPR000719-IPR011992|IPR002048-IPR004041|IPR002048-IPR008271|IPR002048-IPR011009|IPR004041-IPR011992|IPR008271-IPR011992|IPR011009-IPR011992	
No.0005	At1g01140	IPR004041|IPR008271|IPR011009|IPR000719
	At5g55990	IPR011992|IPR002048
	IPR000719-IPR002048|IPR000719-IPR011992|IPR002048-IPR004041|IPR002048-IPR008271|IPR002048-IPR011009|IPR004041-IPR011992|IPR008271-IPR011992|IPR011009-IPR011992	
No.0006	At1g01380	IPR001005|IPR009057
	At1g63650	IPR001092
	IPR001005-IPR001092|IPR001092-IPR009057	
No.0007	At1g01480	IPR004839|IPR004838
	At1g01480	IPR004839|IPR004838
	IPR004838-IPR004838|IPR004838-IPR004839|IPR004839-IPR004839	
No.0008	At1g01480	IPR004839|IPR004838
	At4g11280	IPR004839|IPR004838
	IPR004838-IPR004838|IPR004838-IPR004839|IPR004839-IPR004839	
No.0009	At1g01530	IPR002100
	At1g31630	IPR002100
	IPR002100-IPR002100	
No.0010	At1g01530	IPR002100
	At1g65300	IPR002100
	IPR002100-IPR002100	
No.0011	At1g01530	IPR002100
	At1g65330	IPR002100
	IPR002100-IPR002100	
No.0012	At1g01640	IPR000210
	At1g26830	IPR011991
	IPR000210-IPR011991	
No.0013	At1g01640	IPR000210
	At4g02570	IPR011991
	IPR000210-IPR011991	
No.0014	At1g01700	IPR005512
	At1g75840	IPR005225
	IPR005225-IPR005512	
No.0015	At1g02090	IPR000717
	At3g57290	IPR000717
	IPR000717-IPR000717	
No.0016	At1g02090	IPR000717
	At3g61140	IPR000717
	IPR000717-IPR000717	
No.0017	At1g02090	IPR000717
	At5g14250	IPR000717|IPR011991

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	IPR008207-IPR011006	
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B) Descriptions of IPRs (InterPro ID)

IPR(InterPro ID)	**Description**
IPR000014	PAS
IPR000048	IQ calmodulin-binding region
IPR000061	SWAP/Surp
IPR000073	Alpha/beta hydrolase fold-1
IPR000095	PAK-box/P21-Rho-binding
IPR000127	Ubiquitin-activating enzyme repeat
IPR000152	EGF-type aspartate/asparagine hydroxylation conserved site
IPR000157	Toll-Interleukin receptor
IPR000182	GCN5-related N-acetyltransferase
IPR000194	ATPase, F1/V1/A1 complex, alpha/beta subunit, nucleotide-binding
IPR000197	Zinc finger, TAZ-type
IPR000210	BTB/POZ-like
IPR000225	Armadillo
IPR000283	NADH dehydrogenase 75 kDa subunit, conserved site
IPR000299	FERM domain
IPR000315	Zinc finger, B-box
IPR000330	SNF2-related
IPR000342	Regulator of G protein signalling
IPR000357	HEAT
IPR000375	Dynamin central region
IPR000403	Phosphatidylinositol 3- and 4-kinase, catalytic
IPR000408	Regulator of chromosome condensation, RCC1
IPR000433	Zinc finger, ZZ-type
IPR000477	RNA-directed DNA polymerase (reverse transcriptase)
IPR000504	RNA recognition motif, RNP-1
IPR000534	Semialdehyde dehydrogenase, NAD-binding
IPR000571	Zinc finger, CCCH-type
IPR000572	Oxidoreductase, molybdopterin binding
IPR000573	Aconitase A/isopropylmalate dehydratase small subunit, swivel
IPR000594	UBA/THIF-type NAD/FAD binding fold
IPR000595	Cyclic nucleotide-binding
IPR000608	Ubiquitin-conjugating enzyme, E2
IPR000623	Shikimate kinase
IPR000626	Ubiquitin
IPR000629	RNA helicase, ATP-dependent, DEAD-box, conserved site
IPR000634	Serine/threonine dehydratase, pyridoxal-phosphate-binding site
IPR000674	Aldehyde oxidase and xanthine dehydrogenase, a/b hammerhead
IPR000683	Oxidoreductase, N-terminal
IPR000700	PAS-associated, C-terminal
IPR000717	Proteasome component region PCI
IPR000719	Protein kinase, core
IPR000727	Target SNARE coiled-coil region
IPR000756	Diacylglycerol kinase accessory region
IPR000793	ATPase, F1/V1/A1 complex, alpha/beta subunit, C-terminal
IPR000795	Protein synthesis factor, GTP-binding
IPR000836	Phosphoribosyltransferase
IPR000857	Unconventional myosin/plant kinesin-like protein/non-motor protein conserved region MyTH4
IPR000873	AMP-dependent synthetase and ligase
IPR000904	SEC7-like
IPR000928	SNAP-25
IPR000953	Chromo domain
IPR000961	AGC-kinase, C-terminal
IPR000999	Ribonuclease III
IPR001005	SANT, DNA-binding
IPR001025	Bromo adjacent region
IPR001026	Epsin, N-terminal
IPR001030	Aconitase/3-isopropylmalate dehydratase large subunit, alpha/beta/alpha
IPR001041	Ferredoxin
IPR001048	Aspartate/glutamate/uridylate kinase
IPR001092	Basic helix-loop-helix dimerisation region bHLH
IPR001159	Double-stranded RNA binding
IPR001179	Peptidyl-prolyl cis-trans isomerase, FKBP-type
IPR001206	Diacylglycerol kinase, catalytic region

IPR001214	SET
IPR001216	Cysteine synthase/cystathionine beta-synthase P-phosphate-binding site
IPR001220	Legume lectin, beta domain
IPR001229	Mannose-binding lectin
IPR001247	Exoribonuclease, phosphorolytic domain 1
IPR001252	Malate dehydrogenase, active site
IPR001279	Beta-lactamase-like
IPR001294	Phytochrome
IPR001296	Glycosyl transferase, group 1
IPR001327	Pyridine nucleotide-disulphide oxidoreductase, NAD-binding region
IPR001357	BRCT
IPR001431	Peptidase M16, zinc-binding site
IPR001440	Tetratricopeptide TPR-1
IPR001450	4Fe-4S ferredoxin, iron-sulphur binding, subgroup
IPR001451	Bacterial transferase hexapeptide repeat
IPR001453	Molybdopterin binding
IPR001471	Pathogenesis-related transcriptional factor and ERF, DNA-binding
IPR001487	Bromodomain
IPR001494	Importin-beta, N-terminal
IPR001589	Actinin-type, actin-binding, conserved site
IPR001594	Zinc finger, DHHC-type
IPR001610	PAC motif
IPR001611	Leucine-rich repeat
IPR001623	Heat shock protein DnaJ, N-terminal
IPR001646	Pentapeptide repeat
IPR001650	DNA/RNA helicase, C-terminal
IPR001680	WD40 repeat
IPR001683	Phox-like
IPR001715	Calponin-like actin-binding
IPR001736	Phospholipase D/Transphosphatidylase
IPR001752	Kinesin, motor region
IPR001765	Carbonic anhydrase
IPR001772	Kinase-associated KA1
IPR001810	Cyclin-like F-box
IPR001841	Zinc finger, RING-type
IPR001849	Pleckstrin homology
IPR001876	Zinc finger, RanBP2-type
IPR001878	Zinc finger, CCHC-type
IPR001926	Pyridoxal phosphate-dependent enzyme, beta subunit
IPR001932	Protein phosphatase 2C-related
IPR001969	Peptidase aspartic, active site
IPR002015	Proteasome/cyclosome, regulatory subunit
IPR002035	von Willebrand factor, type A
IPR002048	Calcium-binding EF-hand
IPR002068	Heat shock protein Hsp20
IPR002093	BRCA2 repeat
IPR002100	Transcription factor, MADS-box
IPR002109	Glutaredoxin
IPR002110	Ankyrin
IPR002121	Helicase and RNase D C-terminal, HRDC
IPR002130	Peptidyl-prolyl cis-trans isomerase, cyclophilin-type
IPR002182	NB-ARC
IPR002219	Protein kinase C, phorbol ester/diacylglycerol binding
IPR002346	Molybdopterin dehydrogenase, FAD-binding
IPR002482	Peptidoglycan-binding Lysin subgroup
IPR002487	Transcription factor, K-box
IPR002553	Clathrin/coatomer adaptor, adaptin-like, N-terminal
IPR002562	3'-5' exonuclease
IPR002569	Methionine sulphoxide reductase A
IPR002586	Cobyrinic acid a,c-diamide synthase
IPR002652	Importin-alpha-like, importin-beta-binding region
IPR002655	Acyl-CoA oxidase, C-terminal
IPR002719	Retinoblastoma-associated protein, B-box
IPR002720	Retinoblastoma-associated protein, A-box
IPR002735	Translation initiation factor IF2/IF5
IPR002885	Pentatricopeptide repeat
IPR002888	[2Fe-2S]-binding
IPR002893	Zinc finger, MYND-type
IPR002902	Protein of unknown function DUF26
IPR002913	Lipid-binding START
IPR002931	Transglutaminase-like
IPR002934	Nucleotidyltransferase
IPR003008	Tubulin/FtsZ, GTPase
IPR003016	2-oxo acid dehydrogenase, lipoyl-binding site
IPR003018	GAF
IPR003034	DNA-binding SAP
IPR003088	Cytochrome c, class I
IPR003100	Argonaute and Dicer protein, PAZ
IPR003106	Leucine zipper, homeobox-associated
IPR003124	Actin-binding WH2
IPR003126	Zinc finger, N-recognin
IPR003130	Dynamin GTPase effector
IPR003137	Protease-associated PA

IPR003151	PIK-related kinase, FAT
IPR003152	PIK-related kinase, FATC
IPR003169	GYF
IPR003395	RecF/RecN/SMC protein, N-terminal
IPR003409	MORN motif
IPR003441	No apical meristem (NAM) protein
IPR003583	Helix-hairpin-helix DNA-binding motif, class 1
IPR003593	ATPase, AAA+ type, core
IPR003594	ATP-binding region, ATPase-like
IPR003612	Plant lipid transfer protein/seed storage/trypsin-alpha amylase inhibitor
IPR003613	U box
IPR003657	DNA-binding WRKY
IPR003823	Protein of unknown function CP12
IPR003851	Zinc finger, Dof-type
IPR003903	Ubiquitin interacting motif
IPR003952	Fumarate reductase/succinate dehydrogenase, FAD-binding site
IPR003953	Fumarate reductase/succinate dehydrogenase flavoprotein, N-terminal
IPR004014	ATPase, P-type cation-transporter, N-terminal
IPR004041	NAF
IPR004045	Glutathione S-transferase, N-terminal
IPR004099	Pyridine nucleotide-disulphide oxidoreductase, dimerisation
IPR004100	ATPase, F1/V1/A1 complex, alpha/beta subunit, N-terminal
IPR004104	Oxidoreductase, C-terminal
IPR004112	Fumarate reductase/succinate dehydrogenase flavoprotein, C-terminal
IPR004125	Signal recognition particle, SRP54 subunit, M-domain
IPR004148	BAR
IPR004154	Anticodon-binding
IPR004176	Clp, N-terminal
IPR004192	Ubiquinol cytochrome reductase transmembrane region
IPR004201	Cell division protein 48, CDC48, domain 2
IPR004274	NLI interacting factor
IPR004330	Transcription factor, FAR1-related
IPR004367	Cyclin, C-terminal
IPR004827	Basic-leucine zipper (bZIP) transcription factor
IPR004837	Sodium/calcium exchanger membrane region
IPR004838	Aminotransferases, class-I, pyridoxal-phosphate-binding site
IPR004839	Aminotransferase, class I and II
IPR004843	Metallophosphoesterase
IPR004853	Protein of unknown function DUF250
IPR004871	Cleavage and polyadenylation specificity factor, A subunit, C-terminal
IPR004883	Lateral organ boundaries, LOB
IPR005034	Dicer double-stranded RNA-binding fold
IPR005066	Moybdenum cofactor oxidoreductase, dimerisation
IPR005101	DNA photolyase, FAD-binding/Cryptochrome, C-terminal
IPR005107	CO dehydrogenase flavoprotein, C-terminal
IPR005110	MoeA, N-terminal, domain I and II
IPR005111	MoeA, C-terminal, domain IV
IPR005123	2OG-Fe(II) oxygenase
IPR005160	Ku70/Ku80 C-terminal arm
IPR005172	Tesmin/TSO1-like, CXC
IPR005202	GRAS transcription factor
IPR005225	Small GTP-binding protein
IPR005467	Signal transduction histidine kinase, core
IPR005474	Transketolase, N-terminal
IPR005475	Transketolase, central region
IPR005512	Rop nucleotide exchanger, PRONE
IPR005539	ELK
IPR005540	KNOX1
IPR005541	KNOX2
IPR005559	CG-1
IPR005690	Chloroplast protein import component Toc86/159
IPR005735	Zinc finger, LSD1-type
IPR005806	Rieske [2Fe-2S] region
IPR005834	Haloacid dehalogenase-like hydrolase
IPR005843	Alpha-D-phosphohexomutase, C-terminal
IPR005844	Alpha-D-phosphohexomutase, alpha/beta/alpha domain I
IPR005845	Alpha-D-phosphohexomutase, alpha/beta/alpha domain II
IPR005846	Alpha-D-phosphohexomutase, alpha/beta/alpha domain III
IPR006016	UspA
IPR006050	DNA photolyase, N-terminal
IPR006058	2Fe-2S ferredoxin, iron-sulphur binding site
IPR006067	Nitrite and sulphite reductase 4Fe-4S region
IPR006091	Acyl-CoA dehydrogenase/oxidase, central region
IPR006094	FAD linked oxidase, N-terminal
IPR006121	Heavy metal transport/detoxification protein
IPR006137	NADH ubiquinone oxidoreductase, 20 kDa subunit
IPR006151	Quinate/shikimate 5-dehydrogenase/glutamyl-tRNA reductase
IPR006157	Dihydroneopterin aldolase
IPR006162	Phosphopantetheine attachment site
IPR006164	DNA helicase, ATP-dependent, Ku type
IPR006189	CHASE
IPR006195	Aminoacyl-tRNA synthetase, class II, conserved region
IPR006447	Myb-like DNA-binding region, SHAQKYF class

IPR006455	Homeobox domain, ZF-HD class
IPR006456	ZF-HD homeobox protein Cys/His-rich dimerisation region
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IPR006502	Protein of unknown function DUF506, plant
IPR006527	F-box associated
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IPR006563	POX
IPR006565	Bromodomain transcription factor
IPR006566	FBD-like
IPR006594	LisH dimerisation motif
IPR006597	Sel1-like
IPR006652	Kelch repeat type 1
IPR006656	Molybdopterin oxidoreductase
IPR006671	Cyclin, N-terminal
IPR006703	AIG1
IPR006751	TAFII55 protein conserved region
IPR006785	Peroxisome membrane anchor protein Pex14p, N-terminal
IPR006845	Pex, N-terminal
IPR007012	Poly(A) polymerase, central region
IPR007051	CHORD
IPR007087	Zinc finger, C2H2-type
IPR007192	Cdc23
IPR007201	RNA recognition motif 2
IPR007281	Mre11, DNA-binding
IPR007365	Transferrin receptor-like, dimerisation
IPR007484	Peptidase M28
IPR007517	Rad50 zinc hook
IPR007526	SWIRM
IPR007527	Zinc finger, SWIM-type
IPR007529	Zinc finger, HIT-type
IPR007582	WD40 associated region in TFIID subunit
IPR007699	SGS
IPR007854	Fip1
IPR007856	Saposin-like type B, 1
IPR007863	Peptidase M16, C-terminal
IPR007900	Transcription initiation factor TFIID component TAF4
IPR008138	Saposin-like type B, 2
IPR008139	Saposin B
IPR008146	Glutamine synthetase, catalytic region
IPR008147	Glutamine synthetase, beta-Grasp
IPR008152	Clathrin adaptor, alpha/beta/gamma-adaptin, appendage, Ig-like subdomain
IPR008207	Signal transduction histidine kinase, phosphotransfer (Hpt) region
IPR008210	Phosphoenolpyruvate carboxykinase, N-terminal
IPR008250	ATPase, P-type, ATPase-associated region
IPR008266	Tyrosine protein kinase, active site
IPR008271	Serine/threonine protein kinase, active site
IPR008274	Aldehyde oxidase and xanthine dehydrogenase, molybdopterin binding
IPR008280	Tubulin/FtsZ, C-terminal
IPR008284	Molybdenum cofactor biosynthesis, conserved site
IPR008778	Pirin, C-terminal
IPR008889	VQ
IPR008905	Eukaryotic translation initiation factor 3 subunit 8, N-terminal
IPR008928	Six-hairpin glycosidase-like
IPR008942	ENTH/VHS
IPR008973	C2 calcium/lipid-binding region, CaLB
IPR008974	TRAF-like
IPR008978	HSP20-like chaperone
IPR008984	SMAD/FHA domain
IPR008985	Concanavalin A-like lectin/glucanase
IPR008991	Translation protein SH3-like
IPR009000	Translation elongation and initiation factors/Ribosomal, beta-barrel
IPR009010	Aspartate decarboxylase-like fold
IPR009014	Transketolase, C-terminal/Pyruvate-ferredoxin oxidoreductase, domain II
IPR009025	DNA-directed RNA polymerase, RBP11-like
IPR009028	Clathrin/coatomer adaptor, adaptin-like, appendage, C-terminal subdomain
IPR009030	Growth factor, receptor
IPR009036	Molybdenum cofactor biosynthesis, MoeB
IPR009056	Cytochrome c, monohaem
IPR009057	Homeodomain-like
IPR009065	FERM, 3-helical bundle
IPR009067	TAFII-230 TBP-binding
IPR009071	High mobility group, superfamily
IPR009072	Histone-fold
IPR009075	Acyl-CoA dehydrogenase/oxidase C-terminal
IPR009076	FKBP12-rapamycin-associated protein, FKBP12-rapamycin-binding
IPR009082	Signal transduction histidine kinase, homodimeric
IPR009097	RNA ligase/cyclic nucleotide phosphodiesterase
IPR009100	Acyl-CoA dehydrogenase/oxidase, middle and N-terminal
IPR009743	Hs1pro-1, C-terminal
IPR009869	Hs1pro-1, N-terminal
IPR010399	Tify
IPR010402	CCT domain
IPR010493	Serine acetyltransferase, N-terminal

IPR010525	Auxin response factor
IPR010544	Kinesin-related
IPR010625	CHCH
IPR010827	Surface antigen variable number
IPR010916	TonB box, conserved site
IPR010987	Glutathione S-transferase, C-terminal-like
IPR010989	t-SNARE
IPR010995	DNA repair Rad51/transcription factor NusA, alpha-helical
IPR011001	Saposin-like
IPR011004	Trimeric LpxA-like
IPR011006	CheY-like
IPR011008	Dimeric alpha-beta barrel
IPR011009	Protein kinase-like
IPR011011	Zinc finger, FYVE/PHD-type
IPR011013	Glycoside hydrolase-type carbohydrate-binding
IPR011025	G protein alpha subunit, helical insertion
IPR011028	Cyclin-like
IPR011032	GroES-like
IPR011037	Pyruvate kinase, beta-barrel-like
IPR011039	Transcription Factor IIF, Rap30/Rap74, interaction
IPR011042	Six-bladed beta-propeller, TolB-like
IPR011043	Galactose oxidase/kelch, beta-propeller
IPR011046	WD40 repeat-like
IPR011053	Single hybrid motif
IPR011060	Ribulose-phosphate binding barrel
IPR011068	Nucleotidyltransferase, class I, C-terminal-like
IPR011108	RNA-metabolising metallo-beta-lactamase
IPR011124	Zinc finger, CW-type
IPR011261	DNA-directed RNA polymerase, dimerisation
IPR011262	DNA-directed RNA polymerase, insert
IPR011442	Protein of unknown function DUF1546
IPR011498	Kelch repeat type 2
IPR011525	Aux/IAA-ARF-dimerisation
IPR011527	ABC transporter, transmembrane region, type 1
IPR011538	NADH-ubiquinone oxidoreductase, 51 kDa subunit
IPR011545	DNA/RNA helicase, DEAD/DEAH box type, N-terminal
IPR011989	Armadillo-like helical
IPR011991	Winged helix repressor DNA-binding
IPR011992	EF-Hand type
IPR011993	Pleckstrin homology-type

Appendix Table 2

Predicted protein complexes with statistically significant domain-domain interaction information.

cluster number (number of members:)	
members	member proteins in the cluster. InterPro IDs in the protein (description of InterPro)[number of InterPro 'domains' in the protein: location of the 'domain'(',' delimited)]
PPIs	list of PPIs in the cluster: (*) indicate the PPI is supported by statistically extracted DDIs.
DDIs	list of DDIs, which support PPIs in the cluster.

cluster 1 (number of members: 14)	
members	At1g59530 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 48-97] At2g41090 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 82-110, 118-146] IPR011992(EF-Hand type)[1: 2-143] At3g43810 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g51920 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g56800 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g58780 IPR002100(Transcription factor, MADS-box)[1: 17-114] IPR002487(Transcription factor, K-box)[1: 102-192] At3g62420 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 23-86] At4g02640 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 221-276] At4g37940 IPR002100(Transcription factor, MADS-box)[1: 1-61]

	IPR002487(Transcription factor, K-box)[1: 86-176] At5g13790 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 80-170] At5g21274 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At5g24800 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 120-166] At5g37780 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At5g49450
PPIs	At1g59530-At2g41090 (*), At1g59530-At3g43810 (*), At1g59530-At3g51920 (*), At1g59530-At3g56800 (*), At1g59530-At5g21274 (*), At1g59530-At5g37780 (*), At1g59530-At5g49450, At2g41090-At3g58780, At2g41090-At3g62420 (*), At2g41090-At4g02640 (*), At2g41090-At4g37940, At2g41090-At5g13790, At2g41090-At5g24800 (*), At2g41090-At5g49450, At3g43810-At3g43810, At3g43810-At3g51920, At3g43810-At3g56800, At3g43810-At3g58780, At3g43810-At3g62420 (*), At3g43810-At4g02640 (*), At3g43810-At4g37940, At3g43810-At5g13790, At3g43810-At5g21274, At3g43810-At5g24800 (*), At3g43810-At5g49450, At3g51920-At3g56800, At3g51920-At3g58780, At3g51920-At3g62420 (*), At3g51920-At4g02640 (*), At3g51920-At4g37940, At3g51920-At5g13790, At3g51920-At5g21274, At3g51920-At5g24800 (*), At3g51920-At5g49450, At3g56800-At3g56800, At3g56800-At3g58780, At3g56800-At3g62420 (*), At3g56800-At4g02640 (*), At3g56800-At4g37940, At3g56800-At5g13790, At3g56800-At5g21274, At3g56800-At5g24800 (*), At3g56800-At5g49450, At3g58780-At3g58780 (*), At3g58780-At4g37940 (*), At3g58780-At5g13790 (*), At3g58780-At5g21274, At3g58780-At5g37780, At3g62420-At3g62420 (*), At3g62420-At4g02640 (*), At3g62420-At5g21274 (*), At3g62420-At5g24800 (*), At3g62420-At5g37780 (*), At3g62420-At5g49450, At4g02640-At4g02640 (*), At4g02640-At5g21274 (*), At4g02640-At5g24800 (*), At4g02640-At5g37780 (*), At4g02640-At5g49450, At4g37940-At4g37940 (*), At4g37940-At5g13790 (*), At4g37940-At5g21274, At4g37940-At5g37780, At5g13790-At5g13790 (*), At5g13790-At5g21274, At5g13790-At5g37780, At5g21274-At5g21274, At5g21274-At5g24800 (*), At5g21274-At5g49450, At5g24800-At5g24800 (*), At5g24800-At5g37780 (*), At5g24800-At5g49450, At5g37780-At5g49450, At5g49450-At5g49450
DDIs	IPR002048-IPR004827, IPR002100-IPR002100, IPR002100-IPR002487, IPR002487-IPR002487, IPR004827-IPR004827, IPR004827-IPR011992

cluster 2 (number of members: 14)

members	At1g06920 IPR006458(Protein of unknown function DUF623, plant)[1: 245-309] At1g19700 IPR006563(POX)[1: 164-300] IPR009057(Homeodomain-like)[1: 350-427] At1g23380 IPR005539(ELK)[1: 226-247] IPR005540(KNOX1)[1: 83-129] IPR005541(KNOX2)[1: 136-187] IPR009057(Homeodomain-like)[1: 247-324] At1g26260 IPR001092(Basic helix-loop-helix dimerisation region bHLH)[1: 223-280] At1g75410 IPR006563(POX)[1: 166-298] IPR009057(Homeodomain-like)[1: 345-422] At2g23760 IPR006563(POX)[1: 236-371] IPR009057(Homeodomain-like)[1: 423-500] At2g30400 IPR006458(Protein of unknown function DUF623, plant)[1: 260-319] At2g35940 IPR006563(POX)[1: 188-333] IPR009057(Homeodomain-like)[1: 384-461] At4g32040 IPR005539(ELK)[1: 281-302] IPR005540(KNOX1)[1: 116-160] IPR005541(KNOX2)[1: 167-222] IPR009057(Homeodomain-like)[1: 302-379] At4g34610 IPR006563(POX)[1: 139-269] IPR009057(Homeodomain-like)[1: 313-390] At4g36870 IPR006563(POX)[1: 311-445] IPR009057(Homeodomain-like)[1: 496-573] At5g01840 IPR006458(Protein of unknown function DUF623, plant)[1: 206-265] At5g25220 IPR005539(ELK)[1: 322-343] IPR005540(KNOX1)[1: 157-201] IPR005541(KNOX2)[1: 213-268] IPR009057(Homeodomain-like)[1: 343-420] At5g41410 IPR006563(POX)[1: 192-338] IPR009057(Homeodomain-like)[1: 390-467]
PPIs	At1g06920-At1g19700 (*), At1g06920-At1g23380 (*), At1g06920-At1g75410 (*), At1g06920-At2g35940 (*), At1g06920-At4g32040 (*), At1g06920-At4g34610 (*), At1g06920-At4g36870 (*), At1g06920-At5g25220 (*),

	At1g06920-At5g41410 (*), At1g19700-At1g23380 (*), At1g19700-At1g26260 (*), At1g19700-At1g75410 (*), At1g19700-At2g23760 (*), At1g19700-At2g30400 (*), At1g19700-At2g35940 (*), At1g19700-At4g32040 (*), At1g19700-At5g01840 (*), At1g23380-At1g75410 (*), At1g23380-At2g23760 (*), At1g23380-At2g30400 (*), At1g23380-At2g35940 (*), At1g23380-At4g32040 (*), At1g23380-At4g34610 (*), At1g23380-At4g36870 (*), At1g23380-At5g41410 (*), At1g26260-At1g75410 (*), At1g26260-At2g23760 (*), At1g26260-At2g35940 (*), At1g26260-At4g32040 (*), At1g26260-At4g36870 (*), At1g26260-At5g25220 (*), At1g26260-At5g41410 (*), At1g75410-At1g75410 (*), At1g75410-At2g23760 (*), At1g75410-At2g30400 (*), At1g75410-At2g35940 (*), At1g75410-At4g32040 (*), At1g75410-At5g01840 (*), At1g75410-At5g25220 (*), At1g75410-At5g41410 (*), At2g23760-At2g30400 (*), At2g23760-At2g35940 (*), At2g23760-At4g32040 (*), At2g23760-At5g01840 (*), At2g23760-At5g25220 (*), At2g23760-At5g41410 (*), At2g30400-At2g35940 (*), At2g30400-At4g32040 (*), At2g30400-At4g34610 (*), At2g30400-At4g36870 (*), At2g30400-At5g25220 (*), At2g35940-At2g35940 (*), At2g35940-At4g32040 (*), At2g35940-At4g34610 (*), At2g35940-At4g36870 (*), At2g35940-At5g01840 (*), At2g35940-At5g25220 (*), At2g35940-At5g41410 (*), At4g32040-At4g32040 (*), At4g32040-At4g34610 (*), At4g32040-At4g36870 (*), At4g32040-At5g01840 (*), At4g34610-At5g25220 (*), At4g36870-At5g01840 (*), At4g36870-At5g25220 (*), At5g01840-At5g01840, At5g01840-At5g25220 (*), At5g01840-At5g41410 (*)
DDIs	IPR001092-IPR009057, IPR005539-IPR005539, IPR005539-IPR005540, IPR005539-IPR005541, IPR005539-IPR006458, IPR005539-IPR006563, IPR005539-IPR009057, IPR005540-IPR005540, IPR005540-IPR005541, IPR005540-IPR006458, IPR005540-IPR006563, IPR005540-IPR009057, IPR005541-IPR005541, IPR005541-IPR006458, IPR005541-IPR006563, IPR005541-IPR009057, IPR006458-IPR006563, IPR006458-IPR009057, IPR006563-IPR006563, IPR006563-IPR009057, IPR009057-IPR009057

cluster 3 (number of members: 8)

members	At1g10940 IPR000719(Protein kinase, core)[1: 4-260] IPR008271(Serine/threonine protein kinase, active site)[1: 119-131] IPR011009(Protein kinase-like)[1: 2-291] At1g75950 At2g25490 IPR001810(Cyclin-like F-box)[2: 0-0, 67-106] At3g62980 IPR001810(Cyclin-like F-box)[2: 0-0, 9-50] At4g02570 IPR011991(Winged helix repressor DNA-binding)[1: 638-738] At5g20570 IPR001841(Zinc finger, RING-type)[1: 63-108] At5g42190 IPR001680(WD40 repeat)[1: 85-99] At5g57360 IPR000014(PAS)[1: 34-103] IPR000700(PAS-associated, C-terminal)[1: 0-0] IPR001610(PAC motif)[1: 118-161] IPR001810(Cyclin-like F-box)[1: 200-241] IPR006652(Kelch repeat type 1)[1: 292-342] IPR011043(Galactose oxidase/kelch, beta-propeller)[2: 218-505, 513-598] IPR011498(Kelch repeat type 2)[4: 345-392, 396-443, 450-501, 515-564]
PPIs	At1g10940-At1g75950, At1g10940-At2g25490, At1g10940-At3g62980, At1g10940-At4g02570, At1g10940-At5g57360, At1g75950-At2g25490, At1g75950-At3g62980, At1g75950-At4g02570, At1g75950-At5g57360, At2g25490-At4g02570, At2g25490-At5g42190 (*), At3g62980-At4g02570, At3g62980-At5g20570, At3g62980-At5g42190 (*), At4g02570-At5g20570, At4g02570-At5g42190, At4g02570-At5g57360, At5g20570-At5g42190 (*), At5g20570-At5g57360, At5g42190-At5g57360 (*)
DDIs	IPR001680-IPR001810, IPR001680-IPR001841, IPR001680-IPR011043

cluster 4 (number of members: 14)

members	At1g27390 At1g51980 IPR001431(Peptidase M16, zinc-binding site)[1: 108-131] IPR007863(Peptidase M16, C-terminal)[1: 239-423] At2g21870 At2g27730 At3g02090 IPR001431(Peptidase M16, zinc-binding site)[1: 128-151] IPR007863(Peptidase M16, C-terminal)[1: 260-446] At3g20000 At3g52300 At5g08670 IPR000194(ATPase, F1/V1/A1 complex, alpha/beta subunit, nucleotide-binding)[1: 423-432] IPR000793(ATPase, F1/V1/A1 complex, alpha/beta subunit, C-terminal)[1: 435-552] IPR003593(ATPase, AAA+ type, core)[1: 223-495] IPR004100(ATPase, F1/V1/A1 complex, alpha/beta subunit, N-terminal)[1: 86-154] At5g08690 IPR000194(ATPase, F1/V1/A1 complex, alpha/beta subunit, nucleotide-binding)[1: 423-432] IPR000793(ATPase, F1/V1/A1 complex, alpha/beta subunit, C-terminal)[1: 435-552] IPR003593(ATPase, AAA+ type, core)[1: 223-495] IPR004100(ATPase, F1/V1/A1 complex, alpha/beta subunit, N-terminal)[1: 86-154] At5g13440 IPR004192(Ubiquinol cytochrome reductase transmembrane region)[1: 79-147] IPR005806(Rieske [2Fe-2S] region)[1: 174-270] At5g13450 At5g47030 ATMG00220 ATMG01190

PPIs	At1g27390-At1g51980, At1g27390-At2g21870, At1g27390-At2g27730, At1g27390-At3g02090, At1g27390-At3g20000, At1g27390-At3g52300, At1g27390-At5g08670, At1g27390-At5g08690, At1g27390-At5g13440, At1g27390-At5g13450, At1g27390-At5g47030, At1g27390-ATMG00220, At1g27390-ATMG01190, At1g51980-At2g21870, At1g51980-At2g27730, At1g51980-At3g02090, At1g51980-At3g20000, At1g51980-At3g52300, At1g51980-At5g08670 (*), At1g51980-At5g08690 (*), At1g51980-At5g13440, At1g51980-At5g13450, At1g51980-At5g47030, At1g51980-ATMG00220, At1g51980-ATMG01190, At2g21870-At2g27730, At2g21870-At3g02090, At2g21870-At3g20000, At2g21870-At3g52300, At2g21870-At5g08670, At2g21870-At5g08690, At2g21870-At5g13440, At2g21870-At5g13450, At2g21870-At5g47030, At2g21870-ATMG00220, At2g21870-ATMG01190, At2g27730-At3g02090, At2g27730-At3g20000, At2g27730-At3g52300, At2g27730-At5g08670, At2g27730-At5g08690, At2g27730-At5g13440, At2g27730-At5g13450, At2g27730-At5g47030, At2g27730-ATMG00220, At2g27730-ATMG01190, At3g02090-At3g20000, At3g02090-At3g52300, At3g02090-At5g08670 (*), At3g02090-At5g08690 (*), At3g02090-At5g13440, At3g02090-At5g13450, At3g02090-At5g47030, At3g02090-ATMG00220, At3g02090-ATMG01190, At3g20000-At3g52300, At3g20000-At5g08670, At3g20000-At5g08690, At3g20000-At5g13440, At3g20000-At5g13450, At3g20000-At5g47030, At3g20000-ATMG00220, At3g20000-ATMG01190, At3g52300-At5g08670, At3g52300-At5g08690, At3g52300-At5g13440, At3g52300-At5g13450, At3g52300-At5g47030, At3g52300-ATMG00220, At3g52300-ATMG01190, At5g08670-At5g13440, At5g08670-At5g13450, At5g08670-At5g47030, At5g08670-ATMG00220, At5g08670-ATMG01190, At5g08690-At5g13440, At5g08690-At5g13450, At5g08690-At5g47030, At5g08690-ATMG00220, At5g08690-ATMG01190, At5g13440-At5g13450, At5g13440-At5g47030, At5g13440-ATMG00220, At5g13440-ATMG01190, At5g13450-At5g47030, At5g13450-ATMG00220, At5g13450-ATMG01190, At5g47030-ATMG00220, At5g47030-ATMG01190, ATMG00220-ATMG01190
DDIs	IPR000194-IPR001431, IPR000194-IPR007863, IPR000793-IPR001431, IPR000793-IPR007863, IPR001431-IPR004100, IPR004100-IPR007863

cluster 5 (number of members: 15)

members	At1g24260 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 75-177] At1g69120 IPR002100(Transcription factor, MADS-box)[1: 1-61] IPR002487(Transcription factor, K-box)[1: 75-174] At2g42830 IPR002100(Transcription factor, MADS-box)[1: 16-75] IPR002487(Transcription factor, K-box)[1: 102-194] At2g45650 IPR002100(Transcription factor, MADS-box)[1: 3-57] IPR002487(Transcription factor, K-box)[1: 86-176] At2g45660 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 87-177] At3g57230 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 86-176] At3g58780 IPR002100(Transcription factor, MADS-box)[1: 17-114] IPR002487(Transcription factor, K-box)[1: 102-192] At4g09960 IPR002100(Transcription factor, MADS-box)[1: 27-86] IPR002487(Transcription factor, K-box)[1: 113-203] At4g11880 IPR002100(Transcription factor, MADS-box)[1: 9-59] IPR002487(Transcription factor, K-box)[1: 100-173] At4g18960 IPR002100(Transcription factor, MADS-box)[1: 19-73] IPR002487(Transcription factor, K-box)[1: 103-193] At4g24540 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 87-177] At4g37940 IPR002100(Transcription factor, MADS-box)[1: 1-61] IPR002487(Transcription factor, K-box)[1: 86-176] At5g15800 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 88-178] At5g23260 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 74-172] At5g60910 IPR002100(Transcription factor, MADS-box)[1: 1-61] IPR002487(Transcription factor, K-box)[1: 88-178]
PPIs	At1g24260-At1g69120 (*), At1g24260-At2g42830 (*), At1g24260-At2g45650 (*), At1g24260-At2g45660 (*), At1g24260-At3g57230 (*), At1g24260-At3g58780 (*), At1g24260-At4g09960 (*), At1g24260-At4g18960 (*), At1g24260-At4g24540 (*), At1g24260-At5g23260 (*), At1g24260-At5g60910 (*), At1g69120-At1g69120 (*), At1g69120-At2g45650 (*), At1g69120-At2g45660 (*), At1g69120-At3g57230 (*), At1g69120-At4g11880 (*), At1g69120-At4g24540 (*), At1g69120-At4g37940 (*), At1g69120-At5g15800 (*), At1g69120-At5g23260 (*), At2g42830-At2g45650 (*), At2g42830-At2g45660 (*), At2g42830-At3g57230 (*), At2g42830-At3g58780 (*), At2g42830-At4g09960 (*), At2g42830-At4g11880 (*), At2g42830-At4g18960 (*), At2g42830-At4g37940 (*), At2g42830-At5g15800 (*), At2g42830-At5g23260 (*), At2g45650-At2g45660 (*), At2g45650-At3g57230 (*), At2g45650-At4g11880 (*), At2g45650-At4g18960 (*), At2g45650-At4g24540 (*), At2g45650-At4g37940 (*), At2g45650-At5g15800 (*), At2g45650-At5g60910 (*), At2g45660-At2g45660 (*), At2g45660-At3g57230 (*),

	At2g45660-At3g58780 (*), At2g45660-At4g11880 (*), At2g45660-At4g24540 (*), At2g45660-At4g37940 (*), At2g45660-At5g15800 (*), At2g45660-At5g60910 (*), At3g57230-At3g57230 (*), At3g57230-At3g58780 (*), At3g57230-At4g09960 (*), At3g57230-At4g11880 (*), At3g57230-At4g18960 (*), At3g57230-At4g24540 (*), At3g57230-At4g37940 (*), At3g57230-At5g15800 (*), At3g58780-At3g58780 (*), At3g58780-At4g09960 (*), At3g58780-At4g11880 (*), At3g58780-At4g18960 (*), At3g58780-At4g24540 (*), At3g58780-At4g37940 (*), At3g58780-At5g15800 (*), At3g58780-At5g23260 (*), At4g09960-At4g09960 (*), At4g09960-At4g11880 (*), At4g09960-At4g18960 (*), At4g09960-At4g37940 (*), At4g09960-At5g15800 (*), At4g09960-At5g23260 (*), At4g11880-At4g18960 (*), At4g11880-At4g24540 (*), At4g11880-At5g60910 (*), At4g18960-At4g18960 (*), At4g18960-At4g24540 (*), At4g18960-At4g37940 (*), At4g18960-At5g15800 (*), At4g18960-At5g23260 (*), At4g18960-At5g60910 (*), At4g24540-At4g24540 (*), At4g24540-At4g37940 (*), At4g24540-At5g15800 (*), At4g24540-At5g60910 (*), At4g37940-At4g37940 (*), At4g37940-At5g15800 (*), At4g37940-At5g60910 (*), At5g15800-At5g23260 (*), At5g15800-At5g60910 (*), At5g23260-At5g23260 (*)
DDIs	IPR002100-IPR002100, IPR002100-IPR002487, IPR002487-IPR002487

cluster 6 (number of members: 12)

members	At1g02680 IPR009072(Histone-fold)[1: 30-74] At1g17440 IPR009072(Histone-fold)[1: 525-598] At1g27720 IPR007900(Transcription initiation factor TFIID component TAF4)[1: 463-714] At2g18000 At3g10070 IPR009072(Histone-fold)[1: 397-470] At4g20280 IPR009072(Histone-fold)[1: 112-201] At4g31720 At4g34340 IPR006565(Bromodomain transcription factor)[1: 24-100] IPR009072(Histone-fold)[1: 29-96] At5g25150 IPR001680(WD40 repeat)[6: 341-380, 406-446, 449-488, 491-530, 533-572, 575-614] IPR007582(WD40 associated region in TFIID subunit)[1: 44-193] IPR011046(WD40 repeat-like)[1: 42-666] At5g43130 IPR007900(Transcription initiation factor TFIID component TAF4)[1: 537-823] At5g45600 At5g58470 IPR000504(RNA recognition motif, RNP-1)[1: 280-371] IPR001876(Zinc finger, RanBP2-type)[1: 84-115]
PPIs	At1g02680-At1g17440 (*), At1g02680-At1g27720 (*), At1g02680-At2g18000, At1g02680-At3g10070 (*), At1g02680-At4g20280 (*), At1g02680-At4g31720, At1g02680-At4g34340 (*), At1g02680-At5g43130 (*), At1g02680-At5g45600, At1g17440-At1g17440 (*), At1g17440-At1g27720 (*), At1g17440-At2g18000, At1g17440-At3g10070 (*), At1g17440-At4g20280 (*), At1g17440-At4g31720, At1g17440-At4g34340 (*), At1g17440-At5g25150 (*), At1g17440-At5g43130 (*), At1g17440-At5g45600, At1g17440-At5g58470, At1g27720-At2g18000, At1g27720-At3g10070 (*), At1g27720-At4g31720, At1g27720-At4g34340 (*), At1g27720-At5g25150, At1g27720-At5g43130 (*), At1g27720-At5g58470 (*), At2g18000-At2g18000, At2g18000-At3g10070, At2g18000-At4g34340, At2g18000-At5g25150, At2g18000-At5g43130, At2g18000-At5g45600, At2g18000-At5g58470, At3g10070-At4g20280 (*), At3g10070-At4g31720, At3g10070-At4g34340 (*), At3g10070-At5g25150 (*), At3g10070-At5g43130 (*), At4g20280-At4g31720, At4g20280-At5g43130 (*), At4g31720-At4g31720, At4g31720-At4g34340, At4g31720-At5g25150, At4g31720-At5g43130, At4g34340-At4g34340 (*), At4g34340-At5g25150 (*), At4g34340-At5g43130 (*), At5g25150-At5g25150 (*), At5g25150-At5g43130, At5g25150-At5g45600, At5g25150-At5g58470, At5g43130-At5g43130 (*), At5g43130-At5g45600, At5g43130-At5g58470 (*)
DDIs	IPR001680-IPR001680, IPR001680-IPR011046, IPR001876-IPR007900, IPR006565-IPR009072, IPR007582-IPR009072, IPR007900-IPR007900, IPR007900-IPR009072, IPR009072-IPR009072, IPR011046-IPR011046

cluster 7 (number of members: 10)

members	At1g14440 IPR006455(Homeobox domain, ZF-HD class)[1: 218-275] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 89-140] At1g26920 At1g69600 IPR006455(Homeobox domain, ZF-HD class)[1: 156-213] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 30-83] At1g75240 IPR006455(Homeobox domain, ZF-HD class)[1: 240-297] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 75-126] At2g18350 IPR006455(Homeobox domain, ZF-HD class)[1: 198-255] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 81-132] At2g36610 IPR009057(Homeodomain-like)[1: 56-140] At3g28920 IPR006455(Homeobox domain, ZF-HD class)[1: 192-249] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 51-104] At3g50890 IPR006455(Homeobox domain, ZF-HD class)[1: 181-238] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 59-110] At5g15210 IPR006455(Homeobox domain, ZF-HD class)[1: 179-236]

	IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 55-108] At5g65410 IPR006455(Homeobox domain, ZF-HD class)[1: 191-248] IPR006456(ZF-HD homeobox protein Cys/His-rich dimerisation region)[1: 74-125]
PPIs	At1g14440-At1g26920, At1g14440-At1g69600 (*), At1g14440-At1g75240 (*), At1g14440-At2g18350 (*), At1g14440-At2g36610, At1g14440-At3g28920 (*), At1g14440-At3g50890 (*), At1g14440-At5g15210 (*), At1g14440-At5g65410 (*), At1g26920-At1g69600, At1g26920-At1g75240, At1g26920-At2g18350, At1g26920-At3g50890, At1g26920-At5g15210, At1g26920-At5g65410, At1g69600-At1g69600 (*), At1g69600-At1g75240 (*), At1g69600-At2g18350 (*), At1g69600-At2g36610, At1g69600-At3g28920 (*), At1g69600-At3g50890 (*), At1g69600-At5g15210 (*), At1g69600-At5g65410 (*), At1g75240-At2g36610, At1g75240-At3g28920 (*), At1g75240-At3g50890 (*), At1g75240-At5g15210 (*), At1g75240-At5g65410 (*), At2g18350-At2g36610, At2g18350-At3g28920 (*), At2g18350-At5g15210 (*), At2g18350-At5g65410 (*), At2g36610-At2g36610 (*), At2g36610-At3g28920, At2g36610-At3g50890, At2g36610-At5g15210, At2g36610-At5g65410, At3g28920-At3g50890 (*), At3g28920-At5g15210 (*), At3g28920-At5g65410 (*), At3g50890-At5g15210 (*), At3g50890-At5g65410 (*), At5g15210-At5g15210 (*), At5g15210-At5g65410 (*), At5g65410-At5g65410 (*)
DDIs	IPR006455-IPR006455, IPR006455-IPR006456, IPR006456-IPR006456, IPR009057-IPR009057

cluster 8 (number of members: 11)

members	At1g02090 IPR000717(Proteasome component region PCI)[1: 86-177] At1g22920 At1g71230 At2g26930 At3g61140 IPR000717(Proteasome component region PCI)[1: 329-412] At4g14110 At4g26430 At5g14250 IPR000717(Proteasome component region PCI)[1: 293-383] IPR011991(Winged helix repressor DNA-binding)[1: 287-371] At5g42970 IPR000717(Proteasome component region PCI)[1: 263-362] IPR011991(Winged helix repressor DNA-binding)[1: 288-371] At5g46210 IPR011991(Winged helix repressor DNA-binding)[1: 690-792] At5g56280
PPIs	At1g02090-At1g22920, At1g02090-At1g71230, At1g02090-At2g26930, At1g02090-At3g61140 (*), At1g02090-At4g14110, At1g02090-At4g26430, At1g02090-At5g14250 (*), At1g02090-At5g42970 (*), At1g02090-At5g56280, At1g22920-At2g26930, At1g22920-At3g61140, At1g22920-At4g14110, At1g22920-At4g26430, At1g22920-At5g14250, At1g22920-At5g42970, At1g22920-At5g46210, At1g22920-At5g56280, At1g71230-At2g26930, At1g71230-At3g61140, At1g71230-At4g14110, At1g71230-At4g26430, At1g71230-At5g14250, At1g71230-At5g42970, At1g71230-At5g46210, At1g71230-At5g56280, At2g26930-At3g61140, At2g26930-At4g26430, At2g26930-At5g14250, At2g26930-At5g56280, At3g61140-At3g61140 (*), At3g61140-At4g14110, At3g61140-At5g14250 (*), At3g61140-At5g42970 (*), At4g14110-At4g14110, At4g14110-At5g14250, At4g14110-At5g42970, At4g14110-At5g46210, At5g14250-At5g14250 (*), At5g14250-At5g42970 (*), At5g14250-At5g46210 (*), At5g14250-At5g56280, At5g42970-At5g42970 (*), At5g42970-At5g46210 (*), At5g42970-At5g56280, At5g56280-At5g56280
DDIs	IPR000717-IPR000717, IPR000717-IPR011991, IPR011991-IPR011991

cluster 9 (number of members: 9)

members	At1g13180 At1g17550 IPR001932(Protein phosphatase 2C-related)[1: 222-501] At1g29170 At1g60430 At2g22640 At2g34150 At2g38440 IPR003124(Actin-binding WH2)[1: 1335-1353] At4g16340 At4g26080 IPR001932(Protein phosphatase 2C-related)[1: 143-422]
PPIs	At1g13180-At1g17550, At1g13180-At1g29170, At1g13180-At2g22640, At1g13180-At4g26080, At1g17550-At1g29170, At1g17550-At1g60430, At1g17550-At2g22640, At1g17550-At2g34150, At1g17550-At2g38440, At1g17550-At4g16340, At1g29170-At1g60430, At1g29170-At2g22640, At1g29170-At4g16340, At1g29170-At4g26080, At1g60430-At2g22640, At1g60430-At2g34150, At1g60430-At2g38440, At1g60430-At4g26080, At2g22640-At2g22640, At2g22640-At2g34150, At2g22640-At2g38440, At2g22640-At4g26080, At2g34150-At4g16340, At2g34150-At4g26080, At2g38440-At4g16340, At2g38440-At4g26080, At4g16340-At4g16340, At4g16340-At4g26080
DDIs	

cluster 10 (number of members: 6)

members	At1g02340 IPR001092(Basic helix-loop-helix dimerisation region bHLH)[1: 139-189] At1g09530 IPR001092(Basic helix-loop-helix dimerisation region bHLH)[1: 340-393] At1g09570 IPR000014(PAS)[2: 618-688, 748-803] IPR001680(WD40 repeat)[1: 633-647]

	IPR003018(GAF)[1: 218-412] IPR003594(ATP-binding region, ATPase-like)[1: 1007-1119] IPR005467(Signal transduction histidine kinase, core)[1: 902-1119] At2g18790 IPR000014(PAS)[2: 654-721, 785-855] IPR001294(Phytochrome)[10: 167-189, 267-286, 352-373, 463-483, 548-567, 581-599, 655-671, 674-689, 748-765, 768-788] IPR003018(GAF)[1: 252-433] IPR003594(ATP-binding region, ATPase-like)[1: 1039-1152] IPR005467(Signal transduction histidine kinase, core)[1: 934-1153] At2g32950 IPR001680(WD40 repeat)[6: 355-399, 410-449, 459-491, 493-534, 545-585, 633-672] IPR001841(Zinc finger, RING-type)[1: 52-90] IPR011046(WD40 repeat-like)[1: 1-670] At2g43010 IPR001092(Basic helix-loop-helix dimerisation region bHLH)[1: 263-312]
PPIs	At1g02340-At1g02340 (*), At1g02340-At1g09530 (*), At1g02340-At1g09570 (*), At1g02340-At2g18790 (*), At1g02340-At2g32950, At1g09530-At1g09530 (*), At1g09530-At1g09570 (*), At1g09530-At2g18790 (*), At1g09530-At2g43010 (*), At1g09570-At1g09570 (*), At1g09570-At2g18790 (*), At1g09570-At2g32950 (*), At1g09570-At2g43010 (*), At2g18790-At2g18790 (*), At2g18790-At2g32950, At2g18790-At2g43010 (*), At2g32950-At2g32950 (*)
DDIs	IPR000014-IPR000014, IPR000014-IPR001092, IPR000014-IPR001294, IPR000014-IPR003018, IPR000014-IPR003594, IPR000014-IPR005467, IPR001092-IPR001092, IPR001092-IPR001294, IPR001092-IPR003018, IPR001092-IPR003594, IPR001092-IPR005467, IPR001294-IPR001294, IPR001294-IPR003018, IPR001294-IPR003594, IPR001294-IPR005467, IPR001680-IPR001680, IPR001680-IPR001841, IPR001680-IPR011046, IPR001841-IPR001841, IPR003018-IPR003018, IPR003018-IPR003594, IPR003018-IPR005467, IPR003594-IPR003594, IPR003594-IPR005467, IPR005467-IPR005467, IPR011046-IPR011046

cluster 11 (number of members: 7)

members	At1g27320 IPR003594(ATP-binding region, ATPase-like)[1: 562-722] IPR005467(Signal transduction histidine kinase, core)[1: 457-723] IPR006189(CHASE)[1: 163-389] IPR009082(Signal transduction histidine kinase, homodimeric)[1: 440-511] IPR011006(CheY-like)[2: 738-872, 889-1029] At2g01760 IPR006447(Myb-like DNA-binding region, SHAQKYF class)[1: 200-255] IPR009057(Homeodomain-like)[1: 196-259] IPR011006(CheY-like)[1: 8-145] At3g21510 IPR008207(Signal transduction histidine kinase, phosphotransfer (Hpt) region)[1: 16-138] At3g29350 IPR008207(Signal transduction histidine kinase, phosphotransfer (Hpt) region)[1: 40-147] At4g16110 IPR009057(Homeodomain-like)[1: 217-276] IPR011006(CheY-like)[1: 25-153] At5g35750 IPR003594(ATP-binding region, ATPase-like)[1: 699-866] IPR005467(Signal transduction histidine kinase, core)[1: 594-862] IPR006189(CHASE)[1: 302-526] IPR009082(Signal transduction histidine kinase, homodimeric)[1: 577-648] IPR011006(CheY-like)[2: 883-1013, 1032-1174] At5g39340 IPR008207(Signal transduction histidine kinase, phosphotransfer (Hpt) region)[1: 18-141]
PPIs	At1g27320-At3g21510 (*), At1g27320-At3g29350 (*), At1g27320-At5g35750 (*), At1g27320-At5g39340 (*), At2g01760-At2g01760 (*), At2g01760-At3g21510 (*), At2g01760-At3g29350 (*), At2g01760-At4g16110 (*), At2g01760-At5g35750 (*), At2g01760-At5g39340 (*), At3g21510-At4g16110 (*), At3g21510-At5g35750 (*), At3g29350-At4g16110 (*), At3g29350-At5g35750 (*), At4g16110-At5g39340 (*), At5g35750-At5g35750 (*), At5g35750-At5g39340 (*)
DDIs	IPR003594-IPR003594, IPR003594-IPR005467, IPR003594-IPR006189, IPR003594-IPR008207, IPR003594-IPR009082, IPR005467-IPR005467, IPR005467-IPR006189, IPR005467-IPR008207, IPR005467-IPR009082, IPR005467-IPR011006, IPR006189-IPR006189, IPR006189-IPR008207, IPR006189-IPR009082, IPR006189-IPR011006, IPR006447-IPR006447, IPR006447-IPR008207, IPR006447-IPR011006, IPR008207-IPR009057, IPR008207-IPR009082, IPR008207-IPR011006, IPR009057-IPR009057, IPR009082-IPR009082, IPR009082-IPR011006, IPR011006-IPR011006

cluster 12 (number of members: 5)

members	At1g53720 IPR000504(RNA recognition motif, RNP-1)[1: 243-321] IPR001878(Zinc finger, CCHC-type)[1: 342-355] IPR002130(Peptidyl-prolyl cis-trans isomerase, cyclophilin-type)[1: 3-162] At1g55310 IPR000504(RNA recognition motif, RNP-1)[1: 37-110] At2g37340 IPR000504(RNA recognition motif, RNP-1)[1: 11-81] IPR001878(Zinc finger, CCHC-type)[2: 100-114, 122-138] At3g54460 IPR000330(SNF2-related)[1: 756-867] IPR001650(DNA/RNA helicase, C-terminal)[1: 1212-1289] IPR001810(Cyclin-like F-box)[1: 288-328] IPR001841(Zinc finger, RING-type)[1: 1048-1082]

IPR011124(Zinc finger, CW-type)[1: 575-621]
At5g18810
IPR000504(RNA recognition motif, RNP-1)[1: 47-125]

PPIs At1g53720-At1g55310 (*), At1g53720-At2g37340 (*), At1g53720-At3g54460 (*), At1g53720-At5g18810 (*), At1g55310-At1g55310 (*), At1g55310-At2g37340 (*), At1g55310-At5g18810 (*), At2g37340-At3g54460 (*), At2g37340-At5g18810 (*), At3g54460-At5g18810 (*)

DDIs IPR000504-IPR000504, IPR000504-IPR001878, IPR000504-IPR002130, IPR000504-IPR011124, IPR001878-IPR001878

cluster 13 (number of members: 6)

members At1g01040
IPR000999(Ribonuclease III)[2: 1357-1538, 1574-1730]
IPR001159(Double-stranded RNA binding)[2: 1734-1794, 1832-1904]
IPR001650(DNA/RNA helicase, C-terminal)[1: 651-812]
IPR003100(Argonaute and Dicer protein, PAZ)[1: 1180-1341]
IPR005034(Dicer double-stranded RNA-binding fold)[1: 840-935]
IPR011545(DNA/RNA helicase, DEAD/DEAH box type, N-terminal)[1: 250-421]
At1g09700
IPR001159(Double-stranded RNA binding)[2: 16-83, 102-169]
At2g28380
IPR001159(Double-stranded RNA binding)[2: 2-69, 88-154]
At3g03305
IPR004843(Metallophosphoesterase)[1: 59-278]
At3g43920
IPR000999(Ribonuclease III)[2: 955-1128, 1164-1314]
IPR001650(DNA/RNA helicase, C-terminal)[1: 345-513]
IPR003100(Argonaute and Dicer protein, PAZ)[1: 775-907]
At5g41070
IPR001159(Double-stranded RNA binding)[2: 2-69, 88-154]

PPIs At1g01040-At1g09700 (*), At1g01040-At2g28380 (*), At1g01040-At3g03305, At1g01040-At5g41070 (*), At1g09700-At1g09700 (*), At1g09700-At2g28380 (*), At1g09700-At3g03305, At1g09700-At3g43920 (*), At1g09700-At5g41070 (*), At2g28380-At2g28380 (*), At2g28380-At3g43920 (*), At2g28380-At5g41070 (*), At3g03305-At3g43920, At3g03305-At5g41070, At3g43920-At5g41070 (*), At5g41070-At5g41070 (*)

DDIs IPR000999-IPR001159, IPR001159-IPR001159, IPR001159-IPR001650, IPR001159-IPR003100, IPR001159-IPR005034, IPR001159-IPR011545

cluster 14 (number of members: 6)

members At1g11910
IPR001969(Peptidase aspartic, active site)[2: 97-108, 284-295]
IPR007856(Saposin-like type B, 1)[1: 377-415]
IPR008138(Saposin-like type B, 2)[1: 314-348]
IPR008139(Saposin B)[2: 312-352, 376-417]
IPR011001(Saposin-like)[1: 313-349]
At1g62990
IPR005539(ELK)[1: 194-215]
IPR005540(KNOX1)[1: 27-71]
IPR005541(KNOX2)[1: 80-135]
IPR009057(Homeodomain-like)[1: 215-291]
At4g08150
IPR005539(ELK)[1: 279-300]
IPR005540(KNOX1)[1: 132-176]
IPR005541(KNOX2)[1: 184-235]
IPR009057(Homeodomain-like)[1: 300-377]
At4g32980
IPR006563(POX)[1: 200-334]
IPR009057(Homeodomain-like)[1: 371-448]
At5g01840
IPR006458(Protein of unknown function DUF623, plant)[1: 206-265]
At5g11060
IPR005539(ELK)[1: 286-307]
IPR005540(KNOX1)[1: 121-165]
IPR005541(KNOX2)[1: 177-232]
IPR009057(Homeodomain-like)[1: 307-384]

PPIs At1g11910-At1g62990 (*), At1g11910-At4g08150 (*), At1g11910-At4g32980 (*), At1g11910-At5g11060 (*), At1g62990-At1g62990 (*), At1g62990-At4g08150 (*), At1g62990-At4g32980 (*), At1g62990-At5g01840 (*), At1g62990-At5g11060 (*), At4g08150-At5g01840 (*), At4g08150-At5g11060 (*), At4g32980-At5g01840 (*), At4g32980-At5g11060 (*), At5g01840-At5g01840, At5g01840-At5g11060 (*)

DDIs IPR001969-IPR005539, IPR001969-IPR005540, IPR001969-IPR005541, IPR001969-IPR006563, IPR001969-IPR009057, IPR005539-IPR005539, IPR005539-IPR005540, IPR005539-IPR005541, IPR005539-IPR006458, IPR005539-IPR006563, IPR005539-IPR007856, IPR005539-IPR008138, IPR005539-IPR008139, IPR005539-IPR009057, IPR005539-IPR011001, IPR005540-IPR005540, IPR005540-IPR005541, IPR005540-IPR006458, IPR005540-IPR006563, IPR005540-IPR007856, IPR005540-IPR008138, IPR005540-IPR008139, IPR005540-IPR009057, IPR005540-IPR011001, IPR005541-IPR005541, IPR005541-IPR006458, IPR005541-IPR006563, IPR005541-IPR007856, IPR005541-IPR008138, IPR005541-IPR008139, IPR005541-IPR009057, IPR005541-IPR011001, IPR006458-IPR006563, IPR006458-IPR009057, IPR006563-IPR007856, IPR006563-IPR008138, IPR006563-IPR008139, IPR006563-IPR009057, IPR006563-IPR011001, IPR007856-IPR009057, IPR008138-IPR009057, IPR008139-IPR009057, IPR009057-IPR009057, IPR009057-IPR011001

cluster 15 (number of members: 5)

members At1g56650

	IPR001005(SANT, DNA-binding)[2: 9-59, 62-110] IPR009057(Homeodomain-like)[2: 10-79, 82-125] At1g63650 IPR001092(Basic helix-loop-helix dimerisation region bHLH)[1: 407-456] At5g24520 IPR001680(WD40 repeat)[4: 64-109, 116-161, 164-202, 253-293] IPR011046(WD40 repeat-like)[1: 21-335] At5g35550 IPR001005(SANT, DNA-binding)[2: 15-65, 68-116] IPR009057(Homeodomain-like)[1: 16-85] At5g41315 IPR001092(Basic helix-loop-helix dimerisation region bHLH)[1: 443-492]
PPIs	At1g56650-At1g63650 (*), At1g56650-At5g41315 (*), At1g63650-At1g63650 (*), At1g63650-At5g24520, At1g63650-At5g35550 (*), At1g63650-At5g41315 (*), At5g24520-At5g35550, At5g24520-At5g41315, At5g35550-At5g35550 (*), At5g41315-At5g41315 (*)
DDIs	IPR001005-IPR001005, IPR001005-IPR001092, IPR001005-IPR009057, IPR001092-IPR001092, IPR001092-IPR009057, IPR009057-IPR009057

cluster 16 (number of members: 6)

members	At2g22810 IPR004838(Aminotransferases, class-I, pyridoxal-phosphate-binding site)[1: 270-283] IPR004839(Aminotransferase, class I and II)[1: 40-425] At3g49700 IPR004838(Aminotransferases, class-I, pyridoxal-phosphate-binding site)[1: 269-282] IPR004839(Aminotransferase, class I and II)[1: 40-424] At4g08040 IPR004838(Aminotransferases, class-I, pyridoxal-phosphate-binding site)[1: 264-277] IPR004839(Aminotransferase, class I and II)[1: 38-419] At4g26200 IPR004838(Aminotransferases, class-I, pyridoxal-phosphate-binding site)[1: 282-295] IPR004839(Aminotransferase, class I and II)[1: 54-437] At4g37770 IPR004838(Aminotransferases, class-I, pyridoxal-phosphate-binding site)[1: 269-282] IPR004839(Aminotransferase, class I and II)[1: 40-424] At5g65800 IPR004838(Aminotransferases, class-I, pyridoxal-phosphate-binding site)[1: 269-282] IPR004839(Aminotransferase, class I and II)[1: 40-424]
PPIs	At2g22810-At2g22810 (*), At2g22810-At3g49700 (*), At2g22810-At4g08040 (*), At2g22810-At4g26200 (*), At2g22810-At4g37770 (*), At2g22810-At5g65800 (*), At3g49700-At3g49700 (*), At3g49700-At4g08040 (*), At3g49700-At4g26200 (*), At3g49700-At4g37770 (*), At3g49700-At5g65800 (*), At4g08040-At4g08040 (*), At4g08040-At4g37770 (*), At4g08040-At5g65800 (*), At4g26200-At4g26200 (*), At4g26200-At4g37770 (*), At4g37770-At4g37770 (*), At4g37770-At5g65800 (*), At5g65800-At5g65800 (*)
DDIs	IPR004838-IPR004838, IPR004838-IPR004839, IPR004839-IPR004839

cluster 17 (number of members: 5)

members	At1g48150 IPR002100(Transcription factor, MADS-box)[1: 15-63] At1g60880 IPR002100(Transcription factor, MADS-box)[1: 3-51] At1g60920 IPR002100(Transcription factor, MADS-box)[1: 3-40] At5g38740 IPR002100(Transcription factor, MADS-box)[1: 27-69] At5g65330 IPR002100(Transcription factor, MADS-box)[1: 1-56]
PPIs	At1g48150-At1g60880 (*), At1g48150-At1g60920 (*), At1g48150-At5g38740 (*), At1g48150-At5g65330 (*), At1g60880-At5g65330 (*), At1g60920-At5g65330 (*), At5g38740-At5g65330 (*)
DDIs	IPR002100-IPR002100

cluster 18 (number of members: 9)

members	At1g75390 At2g18160 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 29-92] At3g54620 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 229-283] At3g62420 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 23-86] At4g02640 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 221-276] At4g34590 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 25-88] At5g24800 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 120-166] At5g28770 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 156-171] At5g49450
PPIs	At1g75390-At1g75390, At1g75390-At2g18160, At1g75390-At3g54620, At1g75390-At3g62420, At1g75390-At4g02640, At1g75390-At4g34590, At1g75390-At5g24800, At1g75390-At5g28770, At1g75390-At5g49450, At2g18160-At2g18160 (*), At2g18160-At3g54620 (*), At2g18160-At3g62420 (*), At2g18160-At4g02640 (*), At2g18160-At4g34590 (*), At2g18160-At5g24800 (*), At2g18160-At5g28770 (*), At2g18160-At5g49450, At3g54620-At3g54620 (*), At3g54620-At3g62420 (*), At3g54620-At4g02640 (*),

	At3g54620-At4g34590 (*), At3g54620-At5g24800 (*), At3g54620-At5g28770 (*), At3g54620-At5g49450, At3g62420-At3g62420 (*), At3g62420-At4g02640 (*), At3g62420-At4g34590 (*), At3g62420-At5g24800 (*), At3g62420-At5g28770 (*), At3g62420-At5g49450, At4g02640-At4g02640 (*), At4g02640-At4g34590 (*), At4g02640-At5g24800 (*), At4g02640-At5g28770 (*), At4g02640-At5g49450, At4g34590-At4g34590 (*), At4g34590-At5g24800 (*), At4g34590-At5g28770 (*), At4g34590-At5g49450, At5g24800-At5g24800 (*), At5g24800-At5g28770 (*), At5g24800-At5g49450, At5g28770-At5g28770 (*), At5g28770-At5g49450, At5g49450-At5g49450
DDIs	IPR004827-IPR004827

cluster 19 (number of members: 5)

members	At1g64750 At3g22880 IPR003593(ATPase, AAA+ type, core)[1: 125-311] IPR010995(DNA repair Rad51/transcription factor NusA, alpha-helical)[1: 22-91] At4g00020 IPR002093(BRCA2 repeat)[4: 63-97, 116-150, 163-197, 257-291] At5g01630 IPR002093(BRCA2 repeat)[4: 63-97, 116-150, 163-197, 257-291] At5g20850 IPR003583(Helix-hairpin-helix DNA-binding motif, class 1)[1: 61-80] IPR003593(ATPase, AAA+ type, core)[1: 122-309] IPR010995(DNA repair Rad51/transcription factor NusA, alpha-helical)[1: 19-88]
PPIs	At1g64750-At3g22880, At1g64750-At4g00020, At1g64750-At5g01630, At1g64750-At5g20850, At3g22880-At3g22880 (*), At3g22880-At4g00020 (*), At3g22880-At5g01630 (*), At3g22880-At5g20850 (*), At4g00020-At5g20850 (*), At5g01630-At5g20850 (*), At5g20850-At5g20850 (*)
DDIs	IPR002093-IPR003593, IPR002093-IPR010995, IPR003583-IPR010995, IPR003593-IPR003593, IPR003593-IPR010995, IPR010995-IPR010995

cluster 20 (number of members: 5)

members	At1g14920 IPR005202(GRAS transcription factor)[1: 143-508] At2g01570 IPR005202(GRAS transcription factor)[1: 195-560] At3g05120 At3g63010 At4g24210 IPR001810(Cyclin-like F-box)[2: 0-0, 30-77]
PPIs	At1g14920-At3g05120, At1g14920-At3g63010, At1g14920-At4g24210, At2g01570-At3g05120, At2g01570-At3g63010, At2g01570-At4g24210, At3g05120-At4g24210, At3g63010-At4g24210
DDIs	

cluster 21 (number of members: 5)

members	At1g31630 IPR002100(Transcription factor, MADS-box)[1: 1-48] At1g31640 IPR002100(Transcription factor, MADS-box)[1: 1-48] At1g46408 IPR002100(Transcription factor, MADS-box)[1: 3-48] At5g27960 IPR002100(Transcription factor, MADS-box)[1: 1-58] At5g60440 IPR002100(Transcription factor, MADS-box)[1: 6-66]
PPIs	At1g31630-At5g27960 (*), At1g31630-At5g60440 (*), At1g31640-At5g27960 (*), At1g31640-At5g60440 (*), At1g46408-At5g27960 (*), At1g46408-At5g60440 (*), At5g27960-At5g60440 (*)
DDIs	IPR002100-IPR002100

cluster 22 (number of members: 5)

members	At1g04240 IPR011525(Aux/IAA-ARF-dimerisation)[1: 93-180] At1g04250 IPR011525(Aux/IAA-ARF-dimerisation)[1: 111-212] At1g19850 IPR010525(Auxin response factor)[1: 284-367] IPR011525(Aux/IAA-ARF-dimerisation)[1: 794-876] At1g59750 IPR010525(Auxin response factor)[1: 250-332] IPR011525(Aux/IAA-ARF-dimerisation)[1: 543-625] At4g14560 IPR011525(Aux/IAA-ARF-dimerisation)[1: 75-162]
PPIs	At1g04240-At1g04240 (*), At1g04240-At1g19850 (*), At1g04240-At4g14560 (*), At1g04250-At1g19850 (*), At1g04250-At1g59750 (*), At1g04250-At4g14560 (*), At1g19850-At1g59750 (*), At1g19850-At4g14560 (*), At1g59750-At1g59750 (*), At4g14560-At4g14560 (*)
DDIs	IPR010525-IPR010525, IPR010525-IPR011525, IPR011525-IPR011525

cluster 23 (number of members: 5)

members	At1g16240 IPR000727(Target SNARE coiled-coil region)[1: 131-198] At1g26670 At1g28490 IPR000727(Target SNARE coiled-coil region)[1: 158-220]

	IPR010989(t-SNARE)[1: 5-102] At5g26980 IPR000727(Target SNARE coiled-coil region)[1: 221-288] IPR010989(t-SNARE)[1: 73-281] At5g46860 IPR000727(Target SNARE coiled-coil region)[1: 170-237] IPR010989(t-SNARE)[1: 15-230]
PPIs	At1g16240-At1g26670, At1g16240-At1g28490 (*), At1g16240-At5g46860 (*), At1g26670-At1g28490, At1g26670-At5g26980, At1g26670-At5g46860, At1g28490-At5g26980 (*)
DDIs	IPR000727-IPR000727, IPR000727-IPR010989, IPR010989-IPR010989

cluster 24 (number of members: 5)

members	At1g26830 IPR011991(Winged helix repressor DNA-binding)[2: 561-604, 627-732] At1g69670 IPR011991(Winged helix repressor DNA-binding)[2: 561-598, 627-732] At2g39760 IPR000210(BTB/POZ-like)[1: 194-303] IPR008974(TRAF-like)[1: 21-160] At3g43700 IPR000210(BTB/POZ-like)[1: 205-319] IPR008974(TRAF-like)[1: 32-171] At5g19000 IPR000210(BTB/POZ-like)[1: 203-312] IPR008974(TRAF-like)[1: 30-169]
PPIs	At1g26830-At2g39760 (*), At1g26830-At3g43700 (*), At1g26830-At5g19000 (*), At1g69670-At5g19000 (*), At2g39760-At2g39760 (*), At2g39760-At3g43700 (*), At2g39760-At5g19000 (*), At3g43700-At5g19000 (*), At5g19000-At5g19000 (*)
DDIs	IPR000210-IPR000210, IPR000210-IPR008974, IPR000210-IPR011991, IPR008974-IPR008974, IPR008974-IPR011991

cluster 25 (number of members: 5)

members	At1g17370 IPR000504(RNA recognition motif, RNP-1)[3: 54-128, 139-217, 260-335] At1g54080 IPR000504(RNA recognition motif, RNP-1)[3: 63-137, 148-230, 273-348] At2g22090 IPR000504(RNA recognition motif, RNP-1)[1: 106-175] At3g14100 IPR000504(RNA recognition motif, RNP-1)[3: 59-133, 144-222, 265-340] At3g56860 IPR000504(RNA recognition motif, RNP-1)[2: 140-217, 245-321]
PPIs	At1g17370-At2g22090 (*), At1g17370-At3g56860 (*), At1g54080-At2g22090 (*), At1g54080-At3g56860 (*), At2g22090-At2g22090 (*), At2g22090-At3g14100 (*), At2g22090-At3g56860 (*), At3g14100-At3g56860 (*), At3g56860-At3g56860 (*)
DDIs	IPR000504-IPR000504

cluster 26 (number of members: 4)

members	At2g27970 At3g19150 At3g48750 IPR000719(Protein kinase, core)[1: 4-287] IPR008271(Serine/threonine protein kinase, active site)[1: 123-135] IPR011009(Protein kinase-like)[1: 1-289] At4g34160 IPR004367(Cyclin, C-terminal)[1: 189-312] IPR006671(Cyclin, N-terminal)[1: 62-187] IPR011028(Cyclin-like)[1: 57-187]
PPIs	At2g27970-At3g48750, At2g27970-At4g34160, At3g19150-At3g48750, At3g19150-At4g34160, At3g48750-At4g34160 (*)
DDIs	IPR000719-IPR006671, IPR000719-IPR011028, IPR006671-IPR008271, IPR006671-IPR011009, IPR008271-IPR011028, IPR011009-IPR011028

cluster 27 (number of members: 4)

members	At3g53610 IPR005225(Small GTP-binding protein)[1: 13-175] At4g11220 At4g23630 At5g41600
PPIs	At3g53610-At4g11220, At3g53610-At4g23630, At3g53610-At5g41600, At4g11220-At4g11220, At4g11220-At4g23630, At4g11220-At5g41600, At4g23630-At4g23630, At4g23630-At5g41600, At5g41600-At5g41600
DDIs	

cluster 28 (number of members: 4)

members	At4g01370 IPR000719(Protein kinase, core)[1: 43-329] IPR008271(Serine/threonine protein kinase, active site)[1: 165-177] IPR011009(Protein kinase-like)[1: 34-376] At4g08500

	IPR000719(Protein kinase, core)[1: 333-587] IPR008271(Serine/threonine protein kinase, active site)[1: 452-464] IPR011009(Protein kinase-like)[1: 319-588] At4g26070 IPR000719(Protein kinase, core)[1: 68-328] IPR008271(Serine/threonine protein kinase, active site)[1: 186-198] IPR011009(Protein kinase-like)[1: 54-329] At4g29810 IPR000719(Protein kinase, core)[1: 79-339] IPR008271(Serine/threonine protein kinase, active site)[1: 197-209] IPR011009(Protein kinase-like)[1: 65-367]
PPIs	At4g01370-At4g08500 (*), At4g01370-At4g26070 (*), At4g01370-At4g29810 (*), At4g08500-At4g26070 (*), At4g08500-At4g29810 (*)
DDIs	IPR000719-IPR008271, IPR008271-IPR008271, IPR008271-IPR011009

cluster 29 (number of members: 4)

members	At1g47260 IPR001451(Bacterial transferase hexapeptide repeat)[5: 70-87, 91-108, 119-136, 142-159, 160-177] IPR011004(Trimeric LpxA-like)[1: 31-220] At3g48680 IPR001451(Bacterial transferase hexapeptide repeat)[2: 75-92, 153-170] IPR011004(Trimeric LpxA-like)[1: 48-233] At5g52840 At5g63510 IPR001451(Bacterial transferase hexapeptide repeat)[2: 71-88, 149-166] IPR011004(Trimeric LpxA-like)[1: 44-229]
PPIs	At1g47260-At1g47260 (*), At1g47260-At3g48680 (*), At1g47260-At5g52840, At1g47260-At5g63510 (*), At3g48680-At5g52840, At5g52840-At5g63510
DDIs	IPR001451-IPR001451, IPR001451-IPR011004, IPR011004-IPR011004

cluster 30 (number of members: 5)

members	At1g02450 At1g64280 IPR000210(BTB/POZ-like)[1: 65-194] IPR002110(Ankyrin)[3: 265-295, 328-357, 361-369] At1g74560 At3g12250 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 69-113] At5g06950 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 49-64]
PPIs	At1g02450-At1g64280, At1g02450-At3g12250, At1g02450-At5g06950, At1g64280-At3g12250 (*), At1g64280-At5g06950 (*), At1g74560-At3g12250, At1g74560-At5g06950
DDIs	IPR002110-IPR004827

cluster 31 (number of members: 4)

members	At1g65480 At2g17770 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 129-144] At4g35900 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 219-234] At5g03840
PPIs	At1g65480-At2g17770, At1g65480-At4g35900, At2g17770-At4g35900 (*), At2g17770-At5g03840, At4g35900-At4g35900 (*), At4g35900-At5g03840
DDIs	IPR004827-IPR004827

cluster 32 (number of members: 4)

members	At3g07740 IPR000433(Zinc finger, ZZ-type)[1: 53-94] IPR001005(SANT, DNA-binding)[1: 107-156] IPR007526(SWIRM)[1: 461-548] IPR009057(Homeodomain-like)[1: 102-156] At3g54610 IPR000182(GCN5-related N-acetyltransferase)[1: 222-371] IPR001487(Bromodomain)[1: 434-558] At4g16420 IPR000433(Zinc finger, ZZ-type)[1: 41-85] IPR001005(SANT, DNA-binding)[1: 101-150] IPR007526(SWIRM)[1: 401-487] IPR009057(Homeodomain-like)[1: 96-150] At4g25490 IPR001471(Pathogenesis-related transcriptional factor and ERF, DNA-binding)[1: 46-107]
PPIs	At3g07740-At3g54610 (*), At3g07740-At4g25490, At3g54610-At4g16420 (*), At3g54610-At4g25490, At4g16420-At4g25490
DDIs	IPR000182-IPR000433, IPR001487-IPR007526

cluster 33 (number of members: 4)

members	At3g51240 IPR005123(2OG-Fe(II) oxygenase)[1: 193-294] At3g55120 At5g13930

	At5g42800
PPIs	At3g51240-At3g55120, At3g51240-At5g13930, At3g55120-At5g13930, At3g55120-At5g42800, At5g13930-At5g42800
DDIs	

cluster 34 (number of members: 3)

members	At1g02280 IPR006703(AIG1)[1: 37-234] At4g02510 IPR005690(Chloroplast protein import component Toc86/159)[1: 739-1503] IPR006703(AIG1)[1: 856-1047] At5g19620 IPR010827(Surface antigen variable number)[1: 335-396]
PPIs	At1g02280-At4g02510 (*), At1g02280-At5g19620 (*), At4g02510-At5g19620 (*)
DDIs	IPR005690-IPR006703, IPR005690-IPR010827, IPR006703-IPR006703, IPR006703-IPR010827

cluster 35 (number of members: 7)

members	At1g74740 IPR000719(Protein kinase, core)[1: 59-317] IPR002048(Calcium-binding EF-hand)[4: 364-392, 400-428, 436-464, 472-500] IPR008271(Serine/threonine protein kinase, active site)[1: 179-191] IPR011009(Protein kinase-like)[1: 34-344] IPR011992(EF-Hand type)[1: 344-497] At3g19290 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 351-400] At3g43810 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g51920 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g56800 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At4g14640 IPR002048(Calcium-binding EF-hand)[4: 13-41, 49-77, 86-114, 122-150] IPR011992(EF-Hand type)[1: 3-147] At5g21274 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146]
PPIs	At1g74740-At3g19290 (*), At1g74740-At3g43810 (*), At1g74740-At3g51920 (*), At1g74740-At3g56800 (*), At1g74740-At4g14640 (*), At1g74740-At5g21274 (*), At3g19290-At3g43810 (*), At3g19290-At3g51920 (*), At3g19290-At3g56800 (*), At3g19290-At4g14640 (*), At3g19290-At5g21274 (*), At3g43810-At3g43810, At3g43810-At3g51920, At3g43810-At3g56800, At3g43810-At5g21274, At3g51920-At3g56800, At3g51920-At5g21274, At3g56800-At3g56800, At3g56800-At5g21274, At5g21274-At5g21274
DDIs	IPR000719-IPR002048, IPR000719-IPR011992, IPR002048-IPR004827, IPR002048-IPR008271, IPR002048-IPR011009, IPR004827-IPR011992, IPR008271-IPR011992, IPR011009-IPR011992

cluster 36 (number of members: 3)

members	At1g02580 IPR001005(SANT, DNA-binding)[1: 339-389] IPR001214(SET)[1: 543-663] At3g20740 IPR001680(WD40 repeat)[6: 82-114, 117-157, 160-203, 229-266, 278-319, 324-365] IPR011046(WD40 repeat-like)[1: 17-366] At5g58230 IPR001680(WD40 repeat)[6: 115-154, 167-207, 216-256, 262-302, 306-346, 363-403] IPR011046(WD40 repeat-like)[1: 3-404]
PPIs	At1g02580-At3g20740, At1g02580-At5g58230, At3g20740-At5g58230 (*)
DDIs	IPR001680-IPR001680, IPR001680-IPR011046, IPR011046-IPR011046

cluster 37 (number of members: 3)

members	At1g07310 IPR008973(C2 calcium/lipid-binding region, CaLB)[1: 2-137] At1g23820 At5g53120
PPIs	At1g07310-At1g23820, At1g07310-At5g53120, At1g23820-At5g53120
DDIs	

cluster 38 (number of members: 3)

members	At1g08480 At3g27380 IPR001041(Ferredoxin)[1: 52-141] IPR006058(2Fe-2S ferredoxin, iron-sulphur binding site)[1: 102-110] At5g66760 IPR003952(Fumarate reductase/succinate dehydrogenase, FAD-binding site)[1: 85-94] IPR003953(Fumarate reductase/succinate dehydrogenase flavoprotein, N-terminal)[1: 51-447] IPR004112(Fumarate reductase/succinate dehydrogenase flavoprotein, C-terminal)[1: 502-634]
PPIs	At1g08480-At3g27380, At1g08480-At5g66760, At3g27380-At5g66760 (*)
DDIs	IPR003952-IPR006058, IPR003953-IPR006058, IPR004112-IPR006058

cluster 39 (number of members: 3)

members	At1g09130 At4g25370 IPR004176(Clp, N-terminal)[2: 97-149, 184-226] ATCG00670
PPIs	At1g09130-At4g25370, At1g09130-ATCG00670, At4g25370-ATCG00670
DDIs	

cluster 40 (number of members: 3)

members	At1g09960 At1g22710 At2g02860
PPIs	At1g09960-At1g22710, At1g09960-At2g02860, At1g22710-At2g02860
DDIs	

cluster 41 (number of members: 3)

members	At1g16970 IPR003034(DNA-binding SAP)[1: 585-619] IPR005160(Ku70/Ku80 C-terminal arm)[1: 453-548] IPR006164(DNA helicase, ATP-dependent, Ku type)[1: 272-475] At1g48050 IPR005160(Ku70/Ku80 C-terminal arm)[1: 427-513] IPR006164(DNA helicase, ATP-dependent, Ku type)[1: 278-419] At4g13870 IPR002562(3'-5' exonuclease)[1: 105-283]
PPIs	At1g16970-At1g48050, At1g16970-At4g13870 (*), At1g48050-At4g13870 (*)
DDIs	IPR002562-IPR005160, IPR002562-IPR006164

cluster 42 (number of members: 3)

members	At1g21700 IPR001005(SANT, DNA-binding)[1: 399-447] IPR007526(SWIRM)[1: 176-274] IPR009057(Homeodomain-like)[1: 394-447] At2g33610 IPR001005(SANT, DNA-binding)[1: 224-272] IPR007526(SWIRM)[1: 48-145] IPR009057(Homeodomain-like)[1: 221-274] At2g46020 IPR000330(SNF2-related)[1: 984-1291] IPR001487(Bromodomain)[1: 1900-2007] IPR001650(DNA/RNA helicase, C-terminal)[1: 1338-1422]
PPIs	At1g21700-At2g33610 (*), At1g21700-At2g46020 (*), At2g33610-At2g33610 (*), At2g33610-At2g46020 (*)
DDIs	IPR001005-IPR001005, IPR001005-IPR007526, IPR001005-IPR009057, IPR001487-IPR007526, IPR007526-IPR007526, IPR009057-IPR009057

cluster 43 (number of members: 3)

members	At1g26310 IPR002100(Transcription factor, MADS-box)[1: 2-95] IPR002487(Transcription factor, K-box)[1: 90-180] At5g03790 IPR009057(Homeodomain-like)[1: 48-135] At5g61850
PPIs	At1g26310-At5g03790, At1g26310-At5g61850, At5g03790-At5g61850
DDIs	

cluster 44 (number of members: 3)

members	At1g49950 IPR001005(SANT, DNA-binding)[1: 4-59] IPR009057(Homeodomain-like)[1: 1-68] IPR011991(Winged helix repressor DNA-binding)[1: 110-196] At3g49850 IPR001005(SANT, DNA-binding)[1: 4-59] IPR009057(Homeodomain-like)[1: 2-62] IPR011991(Winged helix repressor DNA-binding)[1: 114-198] At5g67580 IPR001005(SANT, DNA-binding)[1: 4-59] IPR009057(Homeodomain-like)[1: 1-68] IPR011991(Winged helix repressor DNA-binding)[1: 116-200]
PPIs	At1g49950-At1g49950 (*), At1g49950-At3g49850 (*), At1g49950-At5g67580 (*), At3g49850-At3g49850 (*), At3g49850-At5g67580 (*), At5g67580-At5g67580 (*)
DDIs	IPR001005-IPR001005, IPR001005-IPR009057, IPR001005-IPR011991, IPR009057-IPR009057, IPR011991-IPR011991

cluster 45 (number of members: 3)

members	At1g50640 IPR001471(Pathogenesis-related transcriptional factor and ERF, DNA-binding)[1: 26-77] At2g45640 At4g38130

PPIs	At1g50640-At2g45640, At1g50640-At4g38130, At2g45640-At4g38130
DDIs	

cluster 46 (number of members: 3)

members	At2g06210 IPR001440(Tetratricopeptide TPR-1)[8: 128-161, 162-195, 278-311, 316-349, 422-449, 531-564, 686-714, 722-755] At4g29830 IPR001680(WD40 repeat)[7: 2-46, 49-88, 91-131, 134-186, 189-229, 232-271, 274-319] IPR011046(WD40 repeat-like)[1: 1-320] At5g61150
PPIs	At2g06210-At4g29830, At2g06210-At5g61150, At4g29830-At5g61150
DDIs	

cluster 47 (number of members: 3)

members	At3g12810 IPR000330(SNF2-related)[1: 539-825] IPR001005(SANT, DNA-binding)[1: 1670-1729] IPR001650(DNA/RNA helicase, C-terminal)[1: 1110-1188] IPR006562(HSA)[1: 36-107] At3g33520 At5g37055 IPR007529(Zinc finger, HIT-type)[1: 130-159]
PPIs	At3g12810-At3g33520, At3g12810-At5g37055, At3g33520-At5g37055
DDIs	

cluster 48 (number of members: 3)

members	At4g05420 IPR000408(Regulator of chromosome condensation, RCC1)[1: 503-513] IPR004871(Cleavage and polyadenylation specificity factor, A subunit, C-terminal)[1: 740-1027] IPR011046(WD40 repeat-like)[1: 287-922] At4g10180 IPR008928(Six-hairpin glycosidase-like)[1: 319-467] At5g58760 IPR001680(WD40 repeat)[5: 160-200, 203-244, 302-341, 344-386, 459-491] IPR001878(Zinc finger, CCHC-type)[3: 0-0, 76-99, 101-117] IPR011046(WD40 repeat-like)[1: 151-550]
PPIs	At4g05420-At4g10180, At4g05420-At5g58760 (*), At4g10180-At5g58760
DDIs	IPR001680-IPR011046, IPR011046-IPR011046

cluster 49 (number of members: 3)

members	At4g18290 IPR000595(Cyclic nucleotide-binding)[1: 395-484] At4g22200 IPR000595(Cyclic nucleotide-binding)[1: 394-513] IPR002110(Ankyrin)[1: 540-709] At5g46240 IPR000595(Cyclic nucleotide-binding)[1: 377-496]
PPIs	At4g18290-At4g22200 (*), At4g18290-At5g46240 (*), At4g22200-At5g46240 (*)
DDIs	IPR000595-IPR000595, IPR000595-IPR002110

cluster 50 (number of members: 3)

members	At1g23860 IPR000504(RNA recognition motif, RNP-1)[1: 2-73] IPR001878(Zinc finger, CCHC-type)[1: 90-106] At1g55310 IPR000504(RNA recognition motif, RNP-1)[1: 37-110] At3g50670 IPR000504(RNA recognition motif, RNP-1)[1: 138-216]
PPIs	At1g23860-At1g55310 (*), At1g23860-At3g50670 (*), At1g55310-At1g55310 (*), At1g55310-At3g50670 (*)
DDIs	IPR000504-IPR000504, IPR000504-IPR001878

cluster 51 (number of members: 4)

members	At3g56150 IPR000717(Proteasome component region PCI)[1: 705-793] IPR008905(Eukaryotic translation initiation factor 3 subunit 8, N-terminal)[1: 34-636] IPR011991(Winged helix repressor DNA-binding)[1: 699-782] At3g57290 IPR000717(Proteasome component region PCI)[1: 336-422] At3g61140 IPR000717(Proteasome component region PCI)[1: 329-412] At4g14110
PPIs	At3g56150-At3g57290 (*), At3g56150-At3g61140 (*), At3g56150-At4g14110, At3g57290-At3g61140 (*), At3g57290-At4g14110, At3g61140-At3g61140 (*), At3g61140-At4g14110, At4g14110-At4g14110
DDIs	IPR000717-IPR000717, IPR000717-IPR011991

cluster 52 (number of members: 3)

members	At2g32950 IPR001680(WD40 repeat)[6: 355-399, 410-449, 459-491, 493-534, 545-585, 633-672] IPR001841(Zinc finger, RING-type)[1: 52-90]

	IPR011046(WD40 repeat-like)[1: 1-670] At2g46340 IPR000719(Protein kinase, core)[1: 188-529] IPR001680(WD40 repeat)[6: 709-744, 781-795, 804-846, 890-930, 932-971, 982-1027] IPR011009(Protein kinase-like)[1: 274-525] IPR011046(WD40 repeat-like)[1: 554-1027] At5g11260 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 86-150]
PPIs	At2g32950-At2g32950 (*), At2g32950-At2g46340 (*), At2g32950-At5g11260, At2g46340-At5g11260
DDIs	IPR001680-IPR001680, IPR001680-IPR001841, IPR001680-IPR011046, IPR001841-IPR001841, IPR011046-IPR011046

cluster 53 (number of members: 3)

members	At1g13600 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 84-136] At3g30530 IPR004827(Basic-leucine zipper (bZIP) transcription factor)[1: 79-142] At5g49450
PPIs	At1g13600-At1g13600 (*), At1g13600-At3g30530 (*), At1g13600-At5g49450, At3g30530-At3g30530 (*), At3g30530-At5g49450, At5g49450-At5g49450
DDIs	IPR004827-IPR004827

cluster 54 (number of members: 4)

members	At1g53720 IPR000504(RNA recognition motif, RNP-1)[1: 243-321] IPR001878(Zinc finger, CCHC-type)[1: 342-355] IPR002130(Peptidyl-prolyl cis-trans isomerase, cyclophilin-type)[1: 3-162] At2g37340 IPR000504(RNA recognition motif, RNP-1)[1: 11-81] IPR001878(Zinc finger, CCHC-type)[2: 100-114, 122-138] At3g13570 IPR000504(RNA recognition motif, RNP-1)[1: 37-115] At5g64220 IPR000048(IQ calmodulin-binding region)[1: 871-899] IPR002110(Ankyrin)[2: 661-693, 694-726] IPR005559(CG-1)[1: 18-136]
PPIs	At1g53720-At2g37340 (*), At1g53720-At3g13570 (*), At1g53720-At5g64220 (*), At2g37340-At3g13570 (*), At2g37340-At5g64220 (*), At3g13570-At5g64220 (*)
DDIs	IPR000048-IPR000504, IPR000504-IPR000504, IPR000504-IPR001878, IPR000504-IPR002130, IPR000504-IPR005559, IPR001878-IPR001878

cluster 55 (number of members: 4)

members	At1g75950 At3g23050 IPR011525(Aux/IAA-ARF-dimerisation)[1: 125-225] At4g02570 IPR011991(Winged helix repressor DNA-binding)[1: 638-738] At4g03190 IPR001810(Cyclin-like F-box)[2: 0-0, 5-46]
PPIs	At1g75950-At3g23050, At1g75950-At4g02570, At1g75950-At4g03190, At3g23050-At4g02570, At3g23050-At4g03190, At4g02570-At4g03190
DDIs	

cluster 56 (number of members: 6)

members	At3g43810 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g51920 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At3g56800 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At5g21274 IPR002048(Calcium-binding EF-hand)[4: 12-40, 48-76, 85-113, 121-149] IPR011992(EF-Hand type)[1: 2-146] At5g27070 IPR002100(Transcription factor, MADS-box)[1: 30-78] At5g49490 IPR002100(Transcription factor, MADS-box)[1: 44-89]
PPIs	At3g43810-At3g43810, At3g43810-At3g51920, At3g43810-At3g56800, At3g43810-At5g21274, At3g43810-At5g27070, At3g43810-At5g49490, At3g51920-At3g56800, At3g51920-At5g21274, At3g51920-At5g27070, At3g51920-At5g49490, At3g56800-At3g56800, At3g56800-At5g21274, At3g56800-At5g27070, At3g56800-At5g49490, At5g21274-At5g21274, At5g21274-At5g27070, At5g21274-At5g49490, At5g27070-At5g49490 (*)
DDIs	IPR002100-IPR002100

cluster 57 (number of members: 3)

members	At5g47030 ATMG00480

	ATMG01080
PPIs	At5g47030-ATMG00480, At5g47030-ATMG01080, ATMG00480-ATMG01080
DDIs	

cluster 58 (number of members: 3)

members	At1g16610 IPR000504(RNA recognition motif, RNP-1)[1: 98-176] At1g55310 IPR000504(RNA recognition motif, RNP-1)[1: 37-110] At4g24740 IPR000719(Protein kinase, core)[1: 98-423] IPR008271(Serine/threonine protein kinase, active site)[1: 219-231] IPR011009(Protein kinase-like)[1: 84-424]
PPIs	At1g16610-At1g55310 (*), At1g16610-At4g24740, At1g55310-At1g55310 (*), At1g55310-At4g24740
DDIs	IPR000504-IPR000504

cluster 59 (number of members: 3)

members	At1g62360 IPR005539(ELK)[1: 262-283] IPR005540(KNOX1)[1: 119-163] IPR005541(KNOX2)[1: 170-221] IPR009057(Homeodomain-like)[1: 283-360] At1g75410 IPR006563(POX)[1: 166-298] IPR009057(Homeodomain-like)[1: 345-422] At5g02030 IPR006563(POX)[1: 169-292] IPR009057(Homeodomain-like)[1: 332-405]
PPIs	At1g62360-At1g75410 (*), At1g62360-At5g02030 (*), At1g75410-At1g75410 (*), At1g75410-At5g02030 (*), At5g02030-At5g02030 (*)
DDIs	IPR005539-IPR006563, IPR005539-IPR009057, IPR005540-IPR006563, IPR005540-IPR009057, IPR005541-IPR006563, IPR005541-IPR009057, IPR006563-IPR006563, IPR006563-IPR009057, IPR009057-IPR009057

cluster 60 (number of members: 3)

members	At2g20360 At5g37510 IPR000283(NADH dehydrogenase 75 kDa subunit, conserved site)[3: 103-120, 170-182, 217-227] IPR001041(Ferredoxin)[1: 72-150] IPR006656(Molybdopterin oxidoreductase)[1: 343-663] At5g52840
PPIs	At2g20360-At5g37510, At2g20360-At5g52840, At5g37510-At5g52840
DDIs	

cluster 61 (number of members: 3)

members	At2g22640 At2g35110 At5g18410
PPIs	At2g22640-At2g22640, At2g22640-At2g35110, At2g22640-At5g18410, At2g35110-At2g35110, At2g35110-At5g18410
DDIs	

cluster 62 (number of members: 3)

members	At1g09570 IPR000014(PAS)[2: 618-688, 748-803] IPR001680(WD40 repeat)[1: 633-647] IPR003018(GAF)[1: 218-412] IPR003594(ATP-binding region, ATPase-like)[1: 1007-1119] IPR005467(Signal transduction histidine kinase, core)[1: 902-1119] At2g37678 At5g02200
PPIs	At1g09570-At1g09570 (*), At1g09570-At2g37678, At1g09570-At5g02200, At2g37678-At5g02200
DDIs	IPR000014-IPR000014, IPR000014-IPR003018, IPR000014-IPR003594, IPR000014-IPR005467, IPR001680-IPR001680, IPR003018-IPR003018, IPR003018-IPR003594, IPR003018-IPR005467, IPR003594-IPR003594, IPR003594-IPR005467, IPR005467-IPR005467

cluster 63 (number of members: 3)

members	At3g12145 IPR001611(Leucine-rich repeat)[3: 3-25, 98-120, 121-144] At4g18960 IPR002100(Transcription factor, MADS-box)[1: 19-73] IPR002487(Transcription factor, K-box)[1: 103-193] At5g24780
PPIs	At3g12145-At4g18960, At3g12145-At5g24780, At4g18960-At4g18960 (*), At4g18960-At5g24780
DDIs	IPR002100-IPR002100, IPR002100-IPR002487, IPR002487-IPR002487

cluster 64 (number of members: 3)

members	At1g69120 IPR002100(Transcription factor, MADS-box)[1: 1-61]

	IPR002487(Transcription factor, K-box)[1: 75-174] At3g54340 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 84-174] At5g20240 IPR002100(Transcription factor, MADS-box)[1: 1-60] IPR002487(Transcription factor, K-box)[1: 84-170]
PPIs	At1g69120-At1g69120 (*), At1g69120-At3g54340 (*), At1g69120-At5g20240 (*), At3g54340-At3g54340 (*), At3g54340-At5g20240 (*), At5g20240-At5g20240 (*)
DDIs	IPR002100-IPR002100, IPR002100-IPR002487, IPR002487-IPR002487

cluster 65 (number of members: 3)

members	At4g02440 IPR001810(Cyclin-like F-box)[2: 0-0, 4-53] At4g02570 IPR011991(Winged helix repressor DNA-binding)[1: 638-738] At5g08590 IPR000719(Protein kinase, core)[1: 4-260] IPR008271(Serine/threonine protein kinase, active site)[1: 119-131] IPR011009(Protein kinase-like)[1: 2-287]
PPIs	At4g02440-At4g02570, At4g02440-At5g08590, At4g02570-At5g08590
DDIs	

cluster 66 (number of members: 3)

members	At2g18790 IPR000014(PAS)[2: 654-721, 785-855] IPR001294(Phytochrome)[10: 167-189, 267-286, 352-373, 463-483, 548-567, 581-599, 655-671, 674-689, 748-765, 768-788] IPR003018(GAF)[1: 252-433] IPR003594(ATP-binding region, ATPase-like)[1: 1039-1152] IPR005467(Signal transduction histidine kinase, core)[1: 934-1153] At4g16250 IPR000014(PAS)[2: 658-725, 789-859] IPR001294(Phytochrome)[10: 170-192, 270-289, 355-376, 467-487, 552-571, 585-603, 659-675, 678-693, 752-769, 772-792] IPR003018(GAF)[1: 255-437] IPR003594(ATP-binding region, ATPase-like)[1: 1043-1156] IPR005467(Signal transduction histidine kinase, core)[1: 938-1157] At4g18130 IPR000014(PAS)[2: 597-663, 734-801] IPR001294(Phytochrome)[10: 132-154, 232-251, 317-338, 417-437, 503-522, 536-554, 598-614, 617-632, 694-711, 714-734] IPR003018(GAF)[1: 217-387] IPR003594(ATP-binding region, ATPase-like)[1: 982-1095] IPR005467(Signal transduction histidine kinase, core)[1: 877-1096]
PPIs	At2g18790-At2g18790 (*), At2g18790-At4g16250 (*), At2g18790-At4g18130 (*), At4g16250-At4g16250 (*), At4g16250-At4g18130 (*), At4g18130-At4g18130 (*)
DDIs	IPR000014-IPR000014, IPR000014-IPR001294, IPR000014-IPR003018, IPR000014-IPR003594, IPR000014-IPR005467, IPR001294-IPR001294, IPR001294-IPR003018, IPR001294-IPR003594, IPR001294-IPR005467, IPR003018-IPR003018, IPR003018-IPR003594, IPR003018-IPR005467, IPR003594-IPR003594, IPR003594-IPR005467, IPR005467-IPR005467

cluster 67 (number of members: 3)

members	At4g02510 IPR005690(Chloroplast protein import component Toc86/159)[1: 739-1503] IPR006703(AIG1)[1: 856-1047] At5g05000 IPR006703(AIG1)[1: 39-236] At5g57180 IPR010402(CCT domain)[1: 383-425]
PPIs	At4g02510-At5g05000 (*), At4g02510-At5g57180, At5g05000-At5g57180
DDIs	IPR005690-IPR006703, IPR006703-IPR006703