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Structural and functional analysis of the protein network controlling centriole biogenesis

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This thesis is submitted for the degree of Doctor of Philosophy in Faculty of Science Department of Life, Health & Chemical Sciences at the Open University

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Abstract

Centrosomes function as microtubules organising centres in mitosis or as basal bodies in cilia and flagella formation. The duplication of centrioles, which are at the core of each centrosome, is tightly regulated and occurs only once per cell cycle, which allows for correct segregation of chromosomes. In *C. elegans*, only five proteins are essential for centriole duplication. How their *Drosophila* counterparts interact with each other on a molecular level still remains largely unknown.

To further our understanding of the protein interactions governing centriole duplication, I applied *in vivo* and *in vitro* methods to design a protein interaction network at the centriole. I analysed mass spectrometry data from purifications of ProteinA-tagged centriole duplication proteins to identify *in vivo* protein complexes; and performed direct *in vitro* and *in vivo* protein-protein interaction assays.

Additionally, I studied the *Drosophila* proteins Ana2 and Sas6; showing that Plk4 phosphorylates S318, S365, S370, and S373 of the Ana2-STAN motif; which identifies a direct substrate of Plk4. By *in vitro* interaction studies I show that Sas6 aa276-432 and Ana2-STAN interact directly, if the latter is phosphorylated by Plk4. The depletion of Ana2 or expression of Ana2-4A causes loss of centrosomes in *Drosophila* cell culture, which was not observed when expressing Ana2-4D. This supports the importance of Plk4-mediated phosphorylation of Ana2-STAN in centrile duplication.

Mass spectrometry analysis of Sas6 purifications from cultured *Drosophila* cells identified the uncharacterised protein CG33052 (Dragon) and reciprocal purifications of tagged Dragon from *Drosophila* cell culture and syncytial embryos identified Sas6. By *in vitro* interaction studies I confirm that Dragon aa191-318/GoRab and Sas6 aa351-462/HsSas6 interact directly. The deletion mutant Dragon∆aa260-286 does not interact with Sas6 *in vitro* or *in vivo*, and fails to rescue centriole duplication after Dragon depletion. Dragon localises to the *trans*-Golgi and co-localises with Sas6 at the centriole throughout the cell cycle.

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List of Abbreviations

AD	Activation Domain		
AKAP450	A-kinase anchor proteins, Drosophila homologue Plp		
AL	Activation Loop		
Ana1, 2, 3	anastral spindle 1, 2, 3		
Asl	Asterless		
BD	Binding Domain		
Cdk1	cyclin-dependent kinase 1		
CLASPs	cytoplasmic linker-associated proteins		
Cnn	centrosomin		
CtBP	C-terminal binding protein		
D-Plp	Drosophila pericentrin-like protein		
DRE	downstream regulatory element		
ER	endoplasmic reticulum		
GMAP210	Golgi microtubules associated protein of 210kDa		
IFT	intraflagellar transport		
IM	interaction motif		
IVTT	in vitro transcription translation		
KDEL	Lysine-Aspartic acid-Glutamic acid-Leucine		
KLP10A	kinesin-like protein 10A		
LC8	dynein light chain		
MDM2	mouse double minute gene number 2		
МТОС	microtubules organising centre		
Nap1	Nucleosome assembly protein 1		
РВ	polo box		
PCM	pericentriolar material		
PISA	present in Sas6		
Plk	Polo like kinase		
Poly-Ub/ pUb	poly-Ubiquitin		
PP2A	protein phosphatase 2A		

PPH4	protein phosphatase 4
Rcd4	Reduction in Cnn dots 4
RNAi	ribonucleic acid interferance
Sas4, 6	spindle assembly abnormal 4, 6
Spd2	spindle defective 2
STAN	STIL Ana2
TGN	trans-Golgi-network
ТІМ	truncated in microcephaly
Zyg-1	zygote defective-1

Chapter 1 Introduction

1 Introduction

1.1 The cell cycle

The cell cycle is a series of events that are categorised into interphase and mitosis; with interphase being separated into G_1 -, S-, G_2 - and M-phases (Figure 1-1). During each cell cycle the cell's DNA is replicated in S-phase and the duplicated chromatids are segregated to the opposite poles of the mitotic spindle during M-phase followed by the division of the cell into two identical daughters at cytokinesis.



Figure 1-1 Cell cycle phases. The cell division cycle is divided into interphase and mitosis. Interphase composes of G_1 -phase where cell growth occurs and centriole duplication begins, S-phase in which the DNA replicates and G_2 -phase which is characterised by final cell growth and the completion of centriole duplication. During mitosis the duplicated DNA copies are separated into daughter cells. G_0 -phase is a dormancy phase of the cell when conditions do not favour to progress through G_1 -phase and into S-phase. M phase initiates with prophase, when the chromatin fibres condense to chromosomes, followed by the beginning of nuclear envelope breakdown at the end of prophase; and the migration of the two centrosomes to opposite sides of the nucleus. Centrosomes are the major MTOCs (microtubules organising centres) and are also important for mitotic progression as they recruit the mitotic kinases Plk¹ and Aurora A². The minus ends of the microtubules are nucleated from the spindle poles and the plus ends of the microtubules grow towards the chromosomes, which progress to the equator of the cell. The kinetochores at the centromere of each chromosome function as the attachment site for microtubules from each spindle pole, to form bipolar attachments (Figure 1-2). Kinetochores are conserved multiprotein complexes and they support the spindle microtubule anchoring by nucleating short microtubule stubs themselves ^{3,4}. Only end-on, balanced microtubule attachments stabilise each sister kinetochore to its respective pole. Incorrect attachments are labile and become disattached through the activity of Aurora B⁵⁻⁹. At metaphase, all chromosomes align at an equatorial plan and in some species oscillate due to fluctuations in the balance of microtubule tension (Figure 1-2). During anaphase, the sister chromatids are separated by separase protease that cleaves cohesin at the kinetochores (Figure 1-2)¹⁰, and the separated sister chromatids segregate to opposite cell poles as a result of depolymerisation of the plus-ends of microtubules and the acting of minus-end directed motors. A surveillance mechanism, the 'Spindle Assembly Checkpoint' (SAC), functions at kinetochores to prevent the separation of any sister chromatids until all kinetochores are attached to microtubules and the chromosomes are perfectly aligned at the metaphase plate ¹¹. The cell poles move further apart in anaphase B as a result of the sliding of overlapping spindle pole microtubules of opposite polarity. The spindle reorganises in late anaphase and the resulting 'central spindle' participates in organising the cleavage furrow that enables cell membranes to form between the telophase nuclei. Cytokinesis divides the cell into two identical daughters.

The interphase that follows mitosis is separated into three events, G_1 -phase, S-phase and G_2 -phase. Cells can enter an additional state in G_1 -phase, the dormancy or G_0 -phase, when they do not progress to S-phase due to unfavourable conditions such as limiting growth factors or lack of nutrients. Otherwise, G_1 -phase is the main phase of cell growth and the

time at which centrosome duplication begins. Chromosomal DNA is regulated during Sphase, and the subsequent G_2 -phase is characterised by final cell growth and the completion of centrosome duplication.

The centrosome comprises of a pair of centrioles (mother and daughter) surrounded by PCM (pericentriolar material). In addition to their mitotic function as MTOCs to organise the formation of the bipolar spindle, the mother centriole at their core can template formation of cilia and flagella.



Figure 1-2 Attachment of microtubules to the kinetochores and subsequent sister chromatid separation. In prometaphase the spindle microtubules attach to the kinetochores of the centromeres, leading to bipolar attachment. The chromosomes oscillate, align at the central metaphase plate and the attached spindle microtubules cause tension at the centromere. Activated separase then cleaves the sister chromatids at anaphase and they are pulled to opposite poles. Figure reproduced with modifications and permission from ¹¹.

1.2 The Centrosome and cell cycle

In the late 19th century, Van Beneden and Theodor Boveri described two dots within the spindle poles that Boveri named the centrosome. But only in the mid 20th century did electron microscopy reveal the organisation of centrioles at their core ^{12,13}. In a little more than a decade, we have begun to understand the assembly and function of centrioles and centrosomes at the molecular level.

Centrioles are present in eukaryotic species which form cilia and flagella but not in higher plants and higher fungi, which do not form these structures. Centrosomes participate in many cellular and developmental processes, including cell polarity, cell motility and cell division. To form a cilium or flagellum, the mother centriole of a centriole pair converts into the basal body at the cell membrane in the G₀ phase of the cell cycle. The basal body then assembles cilia and flagella which function in signal transduction and cell motility. Many diseases are linked to structural, functional and numerical abnormal centrioles, including ciliopathies and cancer.

The duplication cycle of centrioles is generalised in Figure 1-3. This process begins at the G_1 - to S-phase transition when one new daughter centriole (procentriole) begins to form orthogonally at the proximal end of each of the two linked mother centrioles; progresses through S-phase and into G_2 -phase where the daughter centrioles elongate to their full size. At this point the only physical difference between mother and daughter centrioles are distal and subdistal appendages at the mother centrioles. At entry into mitosis, the linker between the two mother centrioles dissociates, the mother centrioles recruit PCM, and the two centrosomes separate and migrate to opposite sides of the nucleus where they will function as MTOCs. Each centrosome consists of a mother-daughter pair of centrioles with PCM recruited to surround the mother and each centrosome forms one spindle pole of the mitotic spindle. As mitosis progresses, the daughter centriole becomes licensed to recruit PCM in the next cycle. After mitosis, each of the two resulting daughter cells receives one centriole

pair that consist of a mother and daughter centriole that separate but remain connected by a protein linker.

The coupling of centrosome duplication and the cell cycle is a major regulating mechanism. But each can occur independently, for example Aphidicolin blocks α -DNA polymerase and therefore DNA replication but centrosome duplication remains unperturbed in many cell types.



Figure 1-3 Centriole duplication. After mitotic exit two centrioles are loosely linked by a protein linker. At the G_1 /S-phase transition, each of the centrioles functions as a mother centriole and procentriole formation is initiated at their proximal ends. The daughter centriole assembly continues throughout S-phase until it reaches its full length in G_2 -phase. The mother centriole then recruits pericentriolar material and the two centrosomes separate by the removal of the protein linker. Each of the centrosomes then migrates to opposite sites of the nucleus where they function as MTOCs and generate the mitotic spindle. Figure reproduced with modifications and permission from ¹⁴.

1.3 Centriole structure and cartwheel

The process of centriole duplication is tightly regulated and linked to cell cycle progression to guarantee correct centriole numbers. The initial step in centriole duplication is the formation of the procentriole at one single site on the proximal end of the mother centriole. The hierarchy of protein recruitment to form the daughter centriole was first described in *C. elegans* and extensive RNA interference (RNAi) and genetic screens identified five proteins

as essential for centriole duplication; Spd2 (spindle defective 2), the Serine/Threonine kinase Zyg-1 (zygotic defective: embryonic lethal 1), Sas6 (spindle assembly abnormal 6), Sas5 and Sas4 (spindle assembly abnormal 5 and 4 respectively) $^{15-23}$. Table 1-1 shows the homologues of *C. elegans* in *Drosophila* and *Homo sapiens*. Their sequential recruitment was analysed by electron tomography of staged *C. elegans* one-cell embryos. This revealed firstly, the formation and elongation of a central tube and secondly, the assembly of nine singlet microtubules during daughter centriole formation. The pathway of centriole formation is believed to be conserved between species and in *C. elegans* it requires the coiled-coil protein Spd2 to recruit the protein kinase Zyg-1, followed by recruitment of the Sas6-Sas5-protein-complex as prerequisite for procentriole assembly, and Sas4 recruitment for microtubules assemble onto the central tube.

In this section I will discuss what we know of the structure of these proteins or their orthologues in *C. elegans* and other organisms. I will return to what we know of their role in centriole duplication in section 1.4.

Table 1-1 Homologues of centriole duplication proteins of *C. elegans*, *Drosophila* and *Homo sapiens*.

Homologues				
C. elegans	Drosophila	Homo sapiens		
Spd2	-	Cep192		
Zyg-1	Plk4	Plk4		
-	Asterless	Cep152		
Sas6	Sas6	Sas6		
Sas5	Ana2	STIL		
Sas4	Sas4	CPAP		
-	Bld10	Cep135		

The microscopy techniques, especially in the area of super-resolution, have advanced in the recent years, and in *Drosophila*, it is now possible to view the centriole as a cylinder which

can be differentiated into five different regions and into which different centriole duplication proteins have been localised (Figure 1-4) ^{24–30}.



Figure 1-4 The division of *Drosophila* **centrosome into five zones.** (A) The schemata shows the mother and daughter centriole and PCM. Zones I-II represent the core centriole; zone III-IV represent the PCM and zone V represents the distal end. Figure reproduced with modifications and permission from ²⁴. (B) Schematic proximal view of a centriole; indicating the localisation of the named proteins at each zone during interphase and mitosis.

Centrioles are characterised by a precise 9-fold symmetry evident in the central cartwheel and in the organisation of its microtubules ^{31–33}. The cartwheel is believed to represent a conserved building mechanism. The cartwheel appears first during procentriole formation at the proximal end of the centriole. It consists of an inner hub from which nine spokes radiate

outwards, which then each connect to an A-microtubule (Figure 1-5). These microtubules are stable due to tubulin modifications (e.g. tubulin glutamylation)³⁴ and comprise of triplets in most species but in Drosophila and C. elegans, duplets or singlets respectively predominate. Each A-microtubule is comprised of 13 α - and β -tubulin-containing protofilaments, followed by anti-clockwise assembly of the B- and C-microtubules of which each comprises 10 a- and β -tubulin-containing protofilaments ^{35–37}. Each of the partial microtubules forms a complete tubule by sharing 3 protofilaments with the preceding microtubule and each A-microtubule links with the neighbouring spoke's microtubule, to form the outer cylindrical ring of the centriole. The centriole microtubules show polarity, with the minus ends located at the proximal end of the centriole, which coincides with the site of cartwheel assembly. Sas4 protein is necessary for polymerisation of centriolar microtubules and it localises to the microtubules wall ²⁴. Overexpression of the human homologue of Sas4, CPAP, causes centriole elongation ³⁸⁻⁴⁰; Sas4/CPAP also interacts with STIL and Cep135 ⁴¹⁻⁴⁴ but the function of these interactions are still unknown. Additionally, y-tubulin is necessary for the assembly of microtubules. It is part of the y-tubulin ring complex and localises to the minus end microtubules of the A-microtubules ⁴⁵⁻⁴⁹.

Mother centrioles carry appendages at their distal end (Figure 1-5 B and C). The subdistal appendages function in anchoring of the minus ends of the cytoplasmic microtubules to organise radial arrays of microtubules. And the distal appendages function in anchoring the basal body to the cell membrane during ciliogenesis. Once the daughter centriole has passed through mitosis it will mature into a mother centriole and also carry these appendages ⁵⁰.



Figure 1-5 Centriole and cartwheel structure. (A) Ultrastructure of a cross-section of the proximal end of a *Trichonympha* reveals the cartwheel. At the central hub there are nine radiating spokes, which join the microtubules triplets. (B) Ultrastructure of a human centriole and procentriole; arrow indicates the distal and subdistal appendages next to the mother centriole. (C) Schemata of A and B. Additionally indicating the pinhead structures connecting the cartwheel spokes with the A-microtubules, which are in turn connected to the B-microtubules, and to the C-microtubules (left); the A-C-microtubules-linker (left); and the stack of cartwheels (right). Figures reproduced with modifications and permission; (A) from ⁵¹; (B) and (C) from ⁵².

During procentriole formation, stacks of cartwheel form in the proximal part of the centriole, which vary in size between species, e.g. in *Drosophila* sperm, basal bodies are 2.5µm long whereas *C. elegans* centrioles are 150nm ⁵³. Mammalian centrioles lose their cartwheels during mitosis ^{37,54,55}. The *Trichonympha* centriole on the other hand is formed of many hundred cartwheels in approximately 90% of its centriole length ⁵⁶. This proves ideal for structural studies by cryo-electron tomography ^{36,51}. These reveal that neighbouring spokes of the cartwheel layers merge 20nm from the hub and end in a pinhead structure, which consist of the pinbody and two pinfeet that connect it to the A-microtubules (Figure 1-6) ³⁶.

The vertical distance between the merged spokes is 17nm, that correlates with the size of two tubulin dimers.



Figure 1-6 Characteristics of the proximal centriole region and cartwheel stack. (A) 3D representation of *Trichonympha* cartwheel stack showing the individual layers which show the central hub and nine radiating spokes each, which end in the pinhead structure. (B) 3D representation of the *Chlamydomonas* cartwheel-pinhead-microtubules triplet. (C) Longitudinal section of the cartwheel spokes (C-SP), which comprise of the spoke arm (SP-A), the spoke junction (SP-J), and the spoke tip (SP-T); connecting to the pinhead (partially indicated). Figure reproduced with modifications and permission from ³⁶.

Despite the structural knowledge of the cartwheel and the microtubules the basis for the 9fold symmetry is still unknown. In most organisms, the cartwheel appears before microtubule assembly ^{57–60} but *C. elegans* centrioles adopt 9-fold symmetry in the absence of any cartwheel structure ⁵³. Moreover, in *Paramecium*, the circular microtubules become arranged before cartwheel formation in basal bodies ⁶¹. That the cartwheel contributes to the 9-fold structure has been demonstrated by multiple mutants that show structural defects. Also a *Chlamydomonas* null-mutant in Bld10p, which encodes a Sas6-interacting protein, lacks centriolar microtubules ⁶² and a truncated Bld10p mutant leads to cartwheels with nine shorter spokes that recruit only eight microtubules due to reduced circumference based on shorter cartwheel spokes ^{62,63}. On the other hand, depletion of its respective homologue in *Drosophila* and human, Bld10 and Cep135 respectively, still permits centriole formation but they appear unstable ^{32,64–66}. This suggests that Bld10p/Bld10/Cep135 localis to the distal part of the cartwheel spokes and might function in extending the cartwheel to its full length and/or in stabilising the connection between cartwheel and microtubules ^{65,67}. This is supported by the observations that Bld10p/Cep135's N-terminus interacts with microtubules in human cells ^{43,68}; and that Bld10p/Cep135 C-terminus interacts with the cartwheel protein Sas6 ^{43,63}.

Additionally the cartwheel protein Sas6 is required for the 9-fold symmetry of centrioles in zebrafish, human cells, *Drosophila*, *C. elegans* and *C. reinhardtii*^{63,69–71}. A null-mutant of the homologue bld12 in *Chlamydomonas* causes loss of the central hub and cartwheel spokes ⁷⁰; and a mutant leads to 20% of cells with circular centrioles of which 30% have abnormal numbers of microtubules ranging between seven to 11 triplets ⁷¹. Similar findings were made in *Drosophila*. Thus, bld10p/Bld10/Cep135 and bld12/Sas6 all contribute to the 9-fold symmetry of the centriole ^{54,72,73}.

Structurally, Sas6 is characterised by a N-terminal head domain with a PISA motif (present in Sas6; region of homology), a coiled-coil domain and a small, poorly conserved and unstructured C-terminal domain ⁷². The protein forms parallel homodimers via its coiled-coil domains, which exhibit a coiled-coil rod with two N-terminal globular domains, with the latter being positioned next to each other but in mirror image position (Figure 1-8). Each Nterminal head of the dimer weakly interacts via hydrophobic bonds with an N-terminal head of another Sas6 dimer, leading to the assembly of nine Sas6 dimers to the inner hub/ring like structure with the nine homodimerised coiled-coil domains of the protein radiating out (Figure 1-8). Its structure has been elucidated for *C. elegans, C. reinhardtii, Chlamydomonas* and zebrafish using X-ray crystallography, analytical gel-filtration, and *in silico* structural modelling ^{63,69,74,75}. In solution, Sas6 molecules are able to oligomerise and form ring like structures similar to the cartwheel hub ^{63,69}. This gives important insight into the nature of the 9-fold symmetry of centrioles. It predicts a 42° angle between the homodimers and a ring of 23nm diameter, which is close to the expected 40° angle from a 9-fold radially symmetry cartwheel and the observed 20-25nm diameter observed for the central hub by electron microscopy ^{60,69,76}, with the model for Sas6 *C. reinhardtii* in Figure 1-7. On the other hand, *C. elegans* exhibits a tube like structure rather than a cartwheel ⁵³ and X-ray crystallography shows that its Sas6 dimerise to a right-handed helical filament with 9-fold radial symmetry, leading to the tube rather than cartwheel formation (Figure 1-9) ^{77,78}. Just like the cartwheel, the tube can function as a scaffold for microtubule assembly. It was also suggested that two Sas6-spirals might be intertwined to form the central tube in *C. elegans* (Figure 1-9 C and D) ⁷⁸. The ability of Sas6 to self-assemble might explain why some centrioles can form *de novo*. But it also suggests there must be a tightly regulated process for Sas6 oligomerisation to prevent spontaneous cartwheel assembly. Therefore, Sas6 is the likely candidate to establish the universal 9-fold symmetry of centrioles.



Figure 1-7 Bld12p (Sas6 homologue) oligomer model of *C. reinhardtii.* Organisation of nine coiled-coil homodimers according to their interacting N-terminal domains leads to a 9-fold symmetric cartwheel ring, exhibiting a diameter of 23nm, with nine radiating spokes. Figure reproduced with modifications from ⁶⁹.



Figure 1-8 3D model of a Sas6 ring assembly. Sas6 dimers form by homodimerisation of their coiled-coil domains. Nine homodimers interact weakly via their N-terminal head domains and form the 9-fold symmetry of the centriolar cartwheel. Figure reproduced with modifications and permission from ⁶³.



Figure 1-9 Sas6 forms a spiral in *C. elegans* which provides the basis for the 9-fold symmetry of the centriole. (A and B) Model of a single Sas6 spiral with nine homodimers (numbered, orthogonally viewed). (C) Model of two Sas6 spirals intertwined. (D) Centrosomal model of *C. elegans* containing the Sas6 double spiral, of which four turns account for the central tube. Original figure reproduced from ⁷⁸.
Zone 5 of the centriole was described as a distal 'cap' to which the centriolar proteins CP110 and Cep97 localise and function in the regulation of centriole length ^{39,79,80}. The two proteins are co-ordinately recruited with Cep97 being required to stabilise CP110 at the centriole ⁸¹. The loss or depletion of CP110 from human cell culture leads to elongated centriole microtubules ³⁹. In contrast, the depletion of CP110 in *Drosophila* cells leads to shortened centriolar microtubule apparently as a result of the 'exposure' of the centriole to Klp10A, a depolymerizing kinesin-like protein ⁸².

1.4 Centriole duplication and its proteins Plk4, Sas6 and Ana2

1.4.1 Plk4

Plk4 is the conserved master kinase of centriole duplication ^{73,83–85}. Its counterpart in *C. elegans* is Zyg-1 which, although more divergent, has the distinct domains of all other Plk4 kinases ⁸⁶. *Drosophila* Plk4 is structurally similar to other members of the polo-like kinase family but there are some significant differences; all Plks carry an N-terminal catalytic domain but Plk4's C-terminal part contains three Polo box (PB) motifs compared to the two PBs in other family members (Figure 1-10) ⁸⁷. The polo-box motifs function to direct protein interactions, intracellular targeting, substrate binding, dimerization and auto-inhibition of kinase activity ^{1,86,88–90}.



Figure 1-10 Polo-like kinase family and their domains of *Homo sapiens* and *Drosophila.* All kinases contain an N-terminal kinase domain. Plk1-3 contain two Polo box domains. But Plk4 is characterised by three polo boxes (PB) of which PB1 and PB2 function as a cryptic polo box. After homodimer-dependent autophosphorylation of Plk4, SCF^{Slimb/βTrCP} ubiquitin ligase recognises the phosphodegron 'downstream regulatory element' (DRE), leading to degradation (see Figure 1-11). Figure reproduced with modifications and permission from ⁸⁷.

The localisation of Zyg-1/Plk4 to the site of centriole duplication requires Spd2 in *C. elegans* ^{53,91}, Asterless in *Drosophila* ⁹² and the homologues of both proteins, Cep192 and Cep152 respectively, in mammalian cells ^{93,94}. Plk4 localises around the whole circumference of zone 3 of the centriole in G1 but becomes focused at a single site at the initiation of duplication ⁹⁵. This cannot be explained by its interaction with Cep192/Spd2 and Cep152/Asterless, as both localise around the entire centriole following the completion of centriole to centrosome conversion. How Plk4 becomes localised at a single site is not clear. The important role of Plk4 in centriole duplication is reflected by loss of centrioles after depletion of Plk4, and by the over-amplification of centrioles in many cell types and species when Plk4 is overexpressed ^{73,83–85,96,97}. Overexpression can also lead to *de novo* centriole formation in *Drosophila* eggs which lose their centrioles during oogenesis ²⁰. When Plk4 is overexpressed, multiple sites of centriole duplication are observed on the mother centriole to form a 'centriole rosette' ^{73,84}. Both, upregulation and downregulation of Plk4 have been associated with tumorigenesis ^{99–101}.

The regulation of Plk4's activity for centriole duplication requires transcriptional control, localisation, regulated degradation and auto-inhibition of the kinase activity (Figure 1-11) ^{1,90,102–106}. A major mode of regulation of Plk4 appears to be through autoinhibition, achieved through homodimerisation of polo-box 1 and polo-box 2 (cryptic polo box; Figure 1-11 A and B) ⁸⁷. Homodimerisation itself or the recruitment of an unknown binding partner of PB3 to move the linker 1 (L1) away from the kinase's activation loop allows for auto-phosphorylation of a phosphodegron ^{104,107–109} (Figure 1-11C). This permitts for binding of the ubiquitin ligase complex SCF^{Slimb/βTrCP 103–105,107,110,111} (Figure 1-11D) and initiates Plk4 self-destruction by targeting it to the proteasome (Figure 1-11E) ^{103,105,108,109,112}. Although we have this outline of this aspect of Plk4 regulation, we still have much more to learn to fully understand how it controls centriole duplication.



Figure 1-11 Speculative model for activation and regulation of Plk4. (A) Plk4 is autoinhibited by a link of Linker 1 (L1) and Activation loop (AL), which allows for homodimerisation by Polo Box 1 and 2 (PB1, PB2). (B) In the homodimerised stage, a binding partner of PB3 moves L1 away from AL which leads to autoinhibition relief. (C) This allows for autophosphorylation of Plk4. (D) Followed by SCF^{Slimb/βTrCP} recruitment and ubiquitination of PB1. (E) And separation of the dimers. Original figure reproduced from ¹⁰⁶.

The recruitment of Sas6 to the procentriole in human cells is independent of Plk4. However its maintenance at the procentriole depends upon Plk4. This is similar to the relationship between Sas6 and Zyg-1 in C. elegans, where recruitment of Sas6 is directly regulated by Zyg-1 but is independent of Zyg-1 kinase activity ^{15,91}, whereas the Zyg-1-phosphorylation of Sas6 at Ser123 is suggested for Sas6 maintenance ^{54,113}. However, this residue is not conserved in other species. Also, the recruitment hierarchy of human Sas6 and CPAP corresponds to that of Sas6 and Sas4 in C. elegans; HsSas6 depletion prevents the recruitment of CPAP whereas HsSas6 is still recruited after CPAP depletion, suggesting Sas6 is recruited upstream of CPAP/Sas4. Some species-specific differences are also seen from overexpression experiments. Overexpression of non-degradable HsSas6 causes amplification of centrioles whereas overexpression of DmSas6 in syncytial embryos leads to de novo formation of MTOCs that lack centrioles at their core 7^{1} . However, when Drosophila Sas6 and Ana2 are co-expressed, they assemble into extended tubes that interact with proximal ends of centrioles and bear structural resemblance to the inner cartwheel of centrioles, when also co-overexpressed with Plk4¹¹⁴. This suggests, that Drosophila Sas6 and Ana2 together drive cartwheel formation of centrioles, in a Plk4 dependent manner.

It is of great interest to know how the basic ring of Sas6 homodimers is stabilized to promote formation of a mature centriole. Two mechanisms have been proposed for regulating HsSas6 protein levels. First, that Sas6 is targeted for degradation by APC/C^{Cdh1} through its C-terminal KEN-box ^{54,115}. This keeps Sas6 levels low and could limit the number of procentrioles per mother centriole to one. Second, that SCF targets Sas6 for degradation by ubiquitination via Fbxw5 (Fbox protein) ¹¹⁵. Fbxw5 on the other hand is regulated by degradation by the APC/C in mitosis before it accumulates at G₁/S-phase. Plk4 phosphorylates Fbxw5 which then suppresses the ubiquitination and consequently full degradation of Sas6 in S-phase ¹¹⁵. This linkage would guarantee a timely increase and decrease of Sas6 protein levels to control centriole assembly. But there is still little structural information on how the mother centriole recruits Sas6 to a single site of procentriole formation and how the nascent cartwheel and centriole are linked to the mother centriole.

1.4.3 Ana2

It has been suggested that Drosophila Ana2 and human STIL are homologues of C. elegans Sas5, despite their limited sequence homology. Significantly, there is an approximately 20aa coiled-coil domain in the central part of each protein together with a conserved STAN motif in the C-terminus. The STAN motif is a region off approximately 90aa that exhibits 31% sequence identity between Ana2 and STIL and is even more distantly related to Sas5¹¹⁶. Finally there is a conserved TIM (truncated in microcephaly) motif at the very C-termial end of Ana2, STIL and Sas5 that has been identified ¹¹⁷. In human cells, STIL exhibits an asymmetric localisation to the daughter centriole and is essential for procentriole formation. In cultured human cells Sas6 is thought essential for STIL recruitment ^{41,117}. However there it is uncertain whether reciprocally STIL supports the recruitment of HsSas6 to centrioles ^{41,117,118}. This is in contrast to *C. elegans*, where Sas5 and Sas6 protein localisation is codependent ⁷². Additionally, when Sas6 and/or Sas5/Ana2/STIL are overexpressed, it leads to over-amplification of centrioles, which is similar to Plk4 overexpression, which causes overamplification and *de novo* formation (in unfertilized eggs) of centrioles ^{41,54,72,117–119}. In Drosophila spermatocytes, co-overexpression of Sas6 and Ana2 leads to the assembly of cartwheel-like structures ¹¹⁴. Recently, it was suggested that the Ana2-Sas6 complex could function as the so far poorly understood linker between the procentriole and mother centriole, which retains the linkage between the two centrioles until their disengagement late in cell division ¹¹⁴. STIL is recruited to the proximal end of the mother centriole after the G₁-S phase transition, where its signal increases gradually and reaches its maximum at the poles of pro- and prometaphase cells. This is followed by degrease in intensity from the metaphase-to-anaphase transition onwards until it appears absent in late anaphase and telophase cells ¹¹⁷. A similar path of regulation to the one described above for Sas6 is claimed for STIL. The APC/C^{Cdc20-Cdh1} brings about dependent proteasomal degradation of STIL after the metaphase-anaphase transition, with Cdc20 being the major APC/C adaptor and the C-terminal Ana2 KEN box being recognised by APC/C at the end of mitosis ¹¹⁷. Interestingly, the KEN box was observed to be lost in MCPH mutants of STIL, leading to accumulation of STIL protein in the cytoplasm and resulting in centriole amplification rather than interference with STIL function ¹²⁰. The degradation of STIL is initiated by its relocalisation from the centriole to the cytoplasm at nuclear envelope breakdown, dependent on Cdk1 (cyclin-dependent kinase 1) ^{117,120}. The mother and daughter centriole linkage also provides a physical input for regulating STIL levels, whereas their disengagement at the end of mitosis licenses them for reduplication in the next cell cycle ^{121,122}. It was shown that overexpressed STIL localises as a ring around the proximal end of the mother centriole and causes the near-simultaneous formation of multiple daughter centrioles, which co-localise with Sas6¹¹⁷. This observation supports the theory that STIL and Sas6 function together in centriole duplication in human cells, just as do Sas5 and Sas6 in C. elegans. Therefore, it was the more surprising that it has not been possible to detect stable STIL-Sas6-complexes. On the other hand, depletion of STIL by siRNA has a negative effect and suppresses centriole duplication ^{41,117} but it did not affect the localisation of Plk4 nor Cep152 to the centrioles. By contrast, Plk4 depletion disrupts STIL localisation to the centriole ⁴¹. This suggests that STIL is recruited to the daughter centriole downstream of Cep152 and Plk4. Indeed, STIL recruitment to the centriole was shown to depend on the interaction of its central coiled-coil domain with Plk4 ^{95,123}. Structurally, it has been shown that Ana2 and Sas6 both form homo-oligomers, and that the central coiled-coil domain of Ana2 is necessary to form a tetramer with an unusual parallel-coil topology, which occurs also but more weakly with STIL ¹²⁴. An Ana2 mutant that cannot tetramerise in vitro lacks ability for efficient centriole duplication in vivo but still allows for the formation of some centrosome like structures which can concentrate at spindle poles ¹²⁴. Controversially, an Ana2 tetramer was also observed but requiring dynein light chain (LC8) ¹²⁵. This led to the suggestion that the previously mentioned central coiled-coil domain of Ana2 might lead to the Ana2 tetramer formation and that the Ana2-LC8 interaction might rather be important for spindle orientation. Our knowledge of Ana2, its precise role in centriole duplication, and its interaction with other centriole duplication proteins is still very limited and requires further study.

1.5 Centriole maturation and PCM recruitment

The process of daughter centriole assembly to the mother centriole is followed by maturation of the centriole to centrosome conversion for which the mother centriole recruits PCM material. The PCM serves multiple functions: it is the site of microtubule nucleation from tubulin subunits ¹²⁶, it organises the formation and anchors the mitotic spindle, and it is important for the accumulation of cell cycle regulators ¹⁴. In the past it was believed that the PCM is an amorphous unstructured cloud of proteins surrounding the centriole but more advanced microscopy techniques in recent years, especially super-resolution microscopy, has started to elucidate that the PCM is a highly ordered layer system with hierarchical protein recruitment ^{24,26,28,127,128}. Many proteins of the PCM have been identified from purified centrosomes and RNAi and localisation screens in *C. elegans* ¹²⁹, *Drosophila* ^{130,131} and human cells ^{132,133}. The molecular interactions of PCM components with each other begin to be uncovered but further study is necessary to understand their complex interacting network at the centriole, how the PCM is regulated and how it functions.

Asterless, which localises to zone III of the centriole, was suggested as a PCM recruiting protein¹³⁴, as it links the centriole with the PCM by direct interaction with Sas4 (zone II)⁹² and as it is necessary for Cnn recruitment (zone IV)^{135,136}. Sas4 also has PCM functions, as Sas4 null-mutant flies show reduced levels of PCM in testes ^{137,138}. But how the PCM expands to zone IV of the centrosome is still unknown. A possible regulator is Polo kinase whose inhibition prevents γ-tubulin assembly, phosphorylation of Cnn and Pericentrin (zone IV) and PCM expansion ^{131,139–141}. Additionally, Plk1 maintains the PCM at the centrosome throughout mitosis ¹⁴². Aurora A, which assembles microtubule-nucleating complexes and proteins such as γ-tubulin ^{143,144}, activates Plk1 in conjunction with Bora ^{145,146}.

How the PCM and its proteins are dissociated from the centrosome after mitosis is not fully known. It is suggested that dephosphorylation plays an important part. Inhibition of Polo kinase activity leads to the removal of Pericentrin and γ -tubulin in human centrosomes ¹⁴². Candidate phosphatases that might mediate this are protein phosphatase 4 (PPH4)¹⁴⁷⁻¹⁴⁹

1.6 Centriole disengagement

Once the cell has gone through mitosis and the mitotic spindle and the centrosomal PCM are disassembled, the two centrioles disengage by loosening their orthogonal connection but they remain connected by a linker. How this process is regulated still remains unknown but it licences the daughter centriole for duplication in the next cell cycle ^{122,155}. It is suggested that Plk1 and separase regulate the disengagement ¹⁵⁶. Plk1 is suggested to activate separase which in turn loosens cohesion at the centrioles and leads to disengagement ^{122,156–160}. Supporting this suggestion is the finding that overexpression of Plk1 leads to centriole disengagement in G₂-phase. Cohesion cleavage by Plk1 dependent separase activity also occurs earlier during the metaphase to anaphase transition at the sister chromatids. However a mechanism that would regulate dissociation of two different targets at two different time points has not been found ^{157,161–164}. Pericentrin has been suggested to be the separase substrate permitting disengagement as it gets cleaved at the meta-/anaphase transition but remains at the centrosome until anaphase ¹⁶⁵.

After disengagement, the two centrioles remain linked and both function as mothers in the following cell cycle when new daughter centrioles are assembled. The details about the linker are still emerging but dependency studies suggest that C-Nap1 (Nucleosome assembly protein 1) localises and functions as a docking site for rootletin connecting the two centrioles at their proximal ends ^{166–169}. Bld10 is a candidate for the connection between the linker and the centriole ¹⁷⁰. The eventual separation of the two centrioles at the G₂/M-phase transition is proposed to be triggered by Nek2 phosphorylation of C-Nap1 and rootletin because overexpression of Nek2 leads spontaneous separation of the centrioles and decreased Nek2 levels inhibit separation ^{167,168,171–174}. Additionally, the motor protein Eg5

might support the linker separation by forcefully pulling the centrosomes apart before it separates them spatially ¹⁷⁵.

1.7 The Golgi, GoRab and cilia signalling pathways

Both the centrosome and the Golgi apparatus have microtubule nucleation abilities ^{176,177}. At the centrosome, microtubule nucleation and anchoring occurs in the PCM and relies on ytubulin complexes ¹⁷⁸. Similar multiprotein complexes are also necessary for microtubule nucleation at the cis-Golgi. A well organised microtubule cytoskeleton is important for the organisation of the cell and the regulation of cellular processes. In general, the Golgi apparatus of the cell functions in organising secretory pathways, but interestingly, its structure varies depending on the organism (Figure 1-12). In yeast, the Golgi apparatus consists of dispersed cisterns ¹⁷⁹; in green algae, it consists of parallel aligned stacks of cisterns ¹⁸⁰; in fungi, plants and *Drosophila* multiple Golgi stacks are individually scattered in the cytoplasm but always linked to an individual ER exit site ^{181–183}; and in mammalian cells multiple Golgi stacks are laterally connected to form a ribbon-like structure ^{184,185}, that localises near the centrosome and the nucleus in a manner dependent on centrosomal microtubules ^{186,187} and dynein ¹⁸⁸. In mammalian cells, the Golgi apparatus undergoes fragmentation in late G₂-phase, and this appears to be necessary for Golgi inheritance and mitotic entry^{189,190}. The protein GMAP210 (Golgi microtubules associated protein of 210kDa) has been suggested to anchor the Golgi to the centrosome ^{191,192}. In *C. elegans*, GMAP210 functions in Golgi organisation and regulation of cilium length ¹⁹³, reflecting its role as a receptor of the intraflagellar transport protein IFT20 (see also below). It is suggested that GMAP210 and IFT20 function together in the sorting or transport of cargo destined for cilia in mammalian cells ¹⁹⁴. Microtubules originate directly from the Golgi membrane ¹⁹⁵ and their nucleation is dependent on PCM and the cis-Golgi protein AKAP450 (A-kinase anchor proteins, Drosophila homologue Plp), that in turn is recruited by the cis-Golgi protein GM130 ¹⁹⁶, the *trans*-Golgi CLASPs (cytoplasmic linker-associated proteins) ¹⁷⁷, and additional proteins in a multiprotein complex ^{197,198}. Whereas the precise role of AKAP450 in nucleating microtubules at the Golgi is not understood yet, such microtubules formation is independent of the centrosome ¹⁷⁷ and might serve to link and fuse Golgi stacks ^{199,200}. Coordinated function of the centrosome, Golgi and Golgi microtubules are required in cell polarity and migration ^{186,196,201}.



Figure 1-12 Golgi apparatus forms Golgi stacks in *Drosophila* S2 cells and Golgi ribbon in mammalian HeLa cells. The function of the Golgi apparatus for secretory pathways is conserved but it exhibits structural differences. In fungi, plant and *Drosophila*, Golgi stacks are dispersed in the cell but always linked to an ER exit site (example: *Drosophila* S2 cells). The mammalian Golgi apparatus consists of Golgi stacks that are laterally connected and form the Golgi ribbon. At late G₂-phase, the Golgi ribbon gets fractioned into Golgi stacks, which then disassemble for mitosis. Figure reproduced with modifications and permission from ¹⁸³.

In this study I will focus on the uncharacterised Golgi protein CG33052, which is named Dragon from here onwards. GoRab, also known as SCYL1BP1 (Scyl1 binding partner), is the human counterpart of Dragon and it is highly expressed in skin and osteoblasts. The protein GoRab localises to the Golgi and appears to be an effector of the GTPase Rab6 since it binds the active GTP-bound form of Rab6²⁰². The Golgi apparatus consists of stacked cisternae, through which biosynthetic cargo proteins pass and are modified (Figure 1-13)²⁰³. It is also the site of synthesis of complex polysaccharides^{204–206}. The function of

GoRab at the Golgi is unknown. However, a null mutant of GoRab has been identified in patients exhibiting gerodermia osteodysplastica ²⁰². A missense mutation resulting in similar phenotypes as the null mutant has also been described ²⁰⁷. The phenotypes of this autosomal recessive disorder include osteoporosis, spontaneous bone fractures, above average joint dislocations, anomalies in the white matter of the brain but normal mental development. Patients have characteristic facial features with jaw hypoplasia, variable levels of growth retardation and wrinkly skin with severe elastin abnormalities ²⁰⁸⁻²¹³. GoRab was previously identified as an interactor with the pseudo protein kinase Scyl1, that is found in association with COPI vesicles and appears to be required for retrograde flow from the Golgi to the ER^{214,215}. But the function of their interaction is unknown, particularly as Scyl1 localises to the *cis*-Golgi and GoRab polarises to the *trans*-Golgi-network (TGN) ^{202,216}. However, depletion of Scyl1 affects Golgi homeostasis which leads to an increased Golgi volume and surface area, decreased order in Golgi structure, and decrease in trafficking of the KDEL (Lysine/ Aspartic acid/ Glutamic acid/ Leucine) receptor by COPI ²¹⁵. But the Golgi polarity remains undisturbed. Similarly, the closely related Scyl3 associates with clathrincoated vesicles ²¹⁷, which are derivatives of Golgi transport vesicles. However, fibroblasts of patients carrying the GoRab null-mutant do not show any defects in Golgi or changes in the distribution of the Golgi proteins yadaption (a TGN marker), Rab6 (a trans Golgi marker) or GM130 (a cis Golgi marker) 202. It is debatable whether GoRab should be classed as a Golgin since although it interacts with Rab6 and Golgi it has a single characteristic Cterminal coiled-coil domain, whereas Golgin proteins typically exhibit poorly structured coiled-coil domains throughout the whole protein. An understanding of the disease resulting from GoRab mutations is desirable, to understand how it leads to the typically ageing-related features on skin and bone, potentially by interfering with functional or secretory pathways²¹⁸. A function of GoRab as a regulator of the MDM2-p53 feedback loop has also been suggested in which case it would function indirectly as a tumour suppressor ²¹⁹. GoRab triggers the self-ubiquitination and degradation of MDM2 (mouse double minute gene number 2) and thereby stabilising p53 levels ²²⁰⁻²²². This results in apoptosis, cell growth inhibition and tumour prevention ²¹⁹.



Figure 1-13 The currently proposed model of Golgi compartments and maturation. Structurally, COPI vesicles functions in the carbohydrate synthesis stage by transferring proteins between medial and *trans*-Golgi, as well as protein recycling from the *cis*-Golgi to the ER. COPII vesicles export proteins from the ER and bud into new *cis* Golgi cisterna, during the cisternal assembly stage. And carrier formation occurs at the TGN where cisterna disintegration leads to secretory and clathrin-coated vesicles. Figure reproduced with modifications and permission from ²²³.

Centrioles function not only at the core of centrosomal MTOCs but also as basal bodies to template cilia. There are two types of cilia, mobile and primary or non-mobile cilia. One obvious difference between the two forms is the composition of their axonemes. These originate from the basal body that is derived from the mother centriole of the cell's centrosome. Motile cilia have 9 peripherally arranged microtubule doublets plus one microtubule pair in their centre, which together with radial spokes and dynein arms enable its motility (9+2) ²²⁴. Primary cilia assemble in G_0 -phase and disassemble prior to mitotic entry. They consist only of 9 peripheral microtubule pairs and are missing the central microtubule pair (9+0) ^{224,225}. Primary cilia play an important part in cell signalling/signalling pathways ^{226,227} and regulate key processes during embryo development and tissue homeostasis, such

as differentiation, re-entry into the cell cycle, cell division and apoptosis. Therefore, defects in the cilia structure or function lead to developmental abnormalities and diseases affecting many organs, known as ciliopathies. These include skeletal defects, blindness, obesity, polycystic kidney disease, retinal degeneration, infertility, Bardet-Biedl syndrome and many more ²²⁸⁻²³⁴. To assemble the primary cilium, the centriole pair migrates to the plasma membrane, allowing the mother centriole to function as the basal body by anchoring itself to the plasma membrane by its distal appendages (Figure 1-14A). This is followed by elongation of the axoneme from the mother centriole on the surface of the plasma membrane. It is also proposed that the mother centriole may also attach with its distal appendages to a nearby Golgi vesicle (Figure 1-14A). The axoneme of the primary cilium grows from the mother centriole then indents the vesicle, which in turn extends with the growing axoneme by budding and fusion with other secondary vesicles, while remaining connected to the appendages/transition fibres. The structure then migrates to the cell surface where the Golgi vesicle fuses to the plasma membrane; and the primary cilium emerges on the cell surface, where it matures to its full length ^{235,236}. In this second intracellular path of cilia assembly, the primary cilia is partially intracellular and protrudes from the ciliary pocket, that is a membrane invagination. This ciliary pocket is important in membrane trafficking and signalling pathways, and consists of the ciliary membrane, transition fibres (the transformed distal appendages of the mother centriole) and the ciliary necklace (proposed to be the original site of docking to the Golgi vesicle) ²³⁷. Despite being continuous, the ciliary membrane has a denser and distinct composition compared to the plasma membrane ²³⁸⁻²⁴¹. It is a complex barrier that restricts the diffusion of proteins between the plasma and the ciliary membrane, and functions in the selection of proteins that can transit into the ciliary membrane and intra-ciliary space from vesicle trafficking ²⁴²⁻²⁴⁴. The primary cilia does not synthesise proteins itself. Instead, proteins are supplied by vesicles that travel to, dock and fuse with the ciliary membrane ²⁴⁵. These vesicles are derived from the Golgi ^{246,247} and carry ciliary specific cargo that is pre-sorted mainly in the trans-Golgi network ²⁴⁸. Their delivery requires specific ciliary targeting signals needed for the sorting and fusion into the primary cilia. The movement of selected cargo in the mammalian primary cilia is organised by intraflagellar transport complexes (IFT) (Figure 1-14B), which are essential for the growth and maintenance of the primary cilia ²⁴². Proteins are transported by the anterograde path from the primary cilia base, along the microtubules of the axoneme and to the primary cilia tip, and by the retrograde path from the primary cilia tip to the base ^{249–254}. Transport is mediated by IFT-particles/IFT-trains together with ciliary building complexes, as well as kinesin 2 motor proteins for the anterograde path and cytoplasmic dynein 2 for the retrograde path ^{255–258}. The primary cilia has highly significant but highly diverse functions in signalling pathways, with one primary cilia being able to have different receptors and channels at the same or at different times. Signalling via primary cilia is used in sensory (Rhodopsin) and in a variety of developmental pathways in vertebrates (Hedgehog and Wingless) in response to, for example, mechanical force, hormones and growth factors ^{233,259–268}. The abnormal activation or lack of cilia and therefore disrupted cilia signalling is linked to abnormal cell division and cancer ^{269–281}. In summary, vesicle trafficking and protein sorting dictate the assembly of the primary cilia and participate in their function in development and cell-cycle regulation. This accounts for the pleiotropic phenotypes associated with ciliopathies.



Figure 1-14 Cilia assembly and intraflagellar transport (IFT). (A) The mother centriole of a centriole pair functions as basal body in cilia assembly. Two different pathways are suggested. Firstly, the mother centriole anchors at the plasma membrane and the cilia is assembled from there on the cell surface. Alternatively, a Golgi vesicle is anchored by the distal appendages of the mother centriole in the cytoplasm, followed by the growth of the axoneme and the according growth of the vesicle by vesicle fusion. The growing cilia then migrates to the plasma membrane, where it is exposed to the cell surface by fusion of vesicle and plasma membrane. This creates the ciliary pocket at the cilia base. (B) Golgi vesicles are transported to the cilia, where they fuse with the ciliary membrane and release their cargo for anterograde and retrograde intraflagellar transport (IFT) by IFT particles and ciliary complexes, with the aid of Kinesin II and Dynein 2 respectively. The transition zone contains transition fibres and the ciliary necklace. It restricts protein diffusion from the cytoplasm, and functions as a protein selection barrier to the ciliary membrane and intraciliary space. Figure reproduced with modifications and permission from ²⁴⁵.

1.8 Aims of this thesis

The tight regulation of centriole duplication is important for the maintenance of genomic stability, but only little is known about the molecular regulation of centriole duplication. Therefore the overall goal of this thesis is to further elucidate the protein interactions at the centriole and the mechanisms that govern centriole duplication.

My aim was to identify the physical and functional interactions of the centriole duplication proteins. I approached this by re-analysing and performing *in vivo* protein purifications from cultured *Drosophila* cells and syncytial *Drosophila* embryos; performing a direct *in vitro* protein-protein interaction assay screen; and performing yeast-2-hybrid protein interaction assays to design a centriole protein network of protein-protein interactions in relation to their localisation at the centriole (Chapter 3).

I further aimed to specifically elucidate the interaction of Ana2 and Sas6, as it is known from *C. elegans* that their homologues Sas5 and Sas6 interact with each other and that a Sas5-Sas6-complex is recruited to the procentriole. My objective was to perform *in vitro* interaction studies of Ana2, Sas6 and Plk4, with the latter being the master kinase of centriole duplication. In collaboration with Dr. Dzhindzhev, I showed that Plk4 phosphorylates Ana2 at its STAN motif. Thus, I aimed to study non-phosphorylatable Ana2 versus phosphomimicking Ana2 and to identify their effect on centriole duplication in *Drosophila* cell culture in collaboration with Dr. Dzhindzhev (Chapter 4). My next objective was to study the effect of Plk4-mediated Ana2-STAN phosphorylation on Ana2's ability to interact with other centriole duplication proteins and specifically Sas6 by combined phosphorylation and direct binding assays *in vitro* (Chapter 4). This identified an interaction between Ana2 and Sas6 that is dependent on Plk4-phosphorylation of the Ana2-STAN motif. This led me to determine the minimal structural domains within Ana2 and Sas6 that are necessary for protein-protein interaction. To this end, I generated truncated protein constructs of both proteins and tested their direct binding abilities *in vitro* (Chapter 4).

The studies of *in vivo* Sas6 purifications from *Drosophila* cell culture repeatedly identified the uncharacterised protein CG33052, which we named Dragon. Its human homologue GoRab localises to the Golgi. My aim was to confirm or deny Dragon localisation at the Golgi and the centrosome. Additionally, I aimed to identify if Dragon is essential for centriole duplication by studying its effect on centrosome numbers after Dragon depletion; and to determine if Dragon interacts directly with the centriolar cartwheel protein Sas6 (Chapter 5). Centriolar localisation of Dragon by structured illumination microscopy was shown in collaboration with Dr. Tzolovsky. After showing that Dragon localises to the centriole and directly interacts with the centriolar cartwheel protein Sas6, I aimed to identify the smallest protein domains of Sas6 and Dragon necessary for their interaction (Chapter 5). My next objective was to generate a Dragon mutant that abolishes interaction with Sas6 and study its effect on centriole duplication by performing rescue experiments in *Drosophila* cell culture (Chapter 5). For my final objective I asked whether there is a similar requirement for the human homologue GoRab for centriole duplication (Chapter 5).

Chapter 2

Materials and Methods

2 Materials and Methods

2.1 Cloning

2.1.1 Gateway cloning to generate tagged protein constructs

Gateway[®] cloning is an Invitrogen[™] cloning system, applying recombination att sequence sites and BP and LR Clonase[®] enzyme mixes to transfer DNA fragments between plasmids and generate tagged proteins.

Full-length cDNAs (BDGP Gold Collection, Drosophila Genomics Resource Center) were amplified by PCR, using Pfu Ultra™ DNA Polymerase AD (Agilent, 600389-51), followed by agarose gel electrophoresis analysis and gel extraction (QIAquick® Gel Extraction Kit, QIAGEN, 28706). Utilised were the following cDNAs from the Drosophila Genomics Resource Centre (DGRC): Ana1 (LD07765 and IP16240 to generate a full-length Ana1 cDNA), Ana2 (LD22033), Asterless (GH02902), Bld10 (LD35990), Cep97 (RE26466), Rcd4 (SD16838), Sas6 (AT29216), Plk4 (RE70136), Dragon (RE68977). To generate the pENTR clones, the cDNA products were recombined with pDONR221 (Invitrogen[™], Thermo Fisher Scientific, 12536-017) using BP Clonase® II Enzyme Mix (InvitrogenTM, Thermo Fisher Scientific, 11789-020). The fusion vectors were transformed into Library Efficiency® DH5α™ Competent Cells (InvitrogenTM, Thermo Fisher Scientific, 18263-012), amplified, purified (QIAprep® Spin Miniprep Kit, QIAGEN, 27106) and sequenced (Source BioScience LifeScience or GATC Biotech). To generate the pDEST clones, the pENTR clones were recombined with the Gateway® destination vectors, using LR Clonase® II Enzyme Mix (InvitrogenTM, Thermo Fisher Scientific, 11791-100). The Drosophila Gateway Vectors were used to generate expression vectors that drive expression of proteins with the N- or Cterminal tag eGFP (pAGW, pAWG, Thermo Fisher Scientific), 3xFLAG (pAFW, pAWF, Thermo Fisher Scientific), 6xmyc (pAWM, Thermo Fisher Scientific), 6xHis (pDEST42, Thermo Fisher Scientific), GST (pDEST24, Thermo Fisher Scientific) or MBP (pKM596,

Addgene plasmid 8837). Additionally, pAct5c-PrA and pMT-cPrA (with the copper-inducible *Metallothionein* A (CG9470) promotor) were used, that were originally generated in the lab ²⁸². To generate plasmids that express untagged proteins, the pENTRs with the protein sequence and a C-terminal STOP codon were recombined into destination vectors for C-terminal tagging. The STOP-codon between the coding sequence and the tag leads to protein translation without the tag.

2.1.2 Regular cloning to generate constructs for Yeast-2-Hybrid method

PCR products that carry specific restriction enzyme sequences upstream and downstream of the protein sequences were amplified and cloned into the yeast-2-hybrid vectors pGBT9 and pGAD424. Pfu Ultra[™] DNA Polymerase AD (Agilent, 600389-51) was utilised for the PCRs. Digests were performed consecutively or simultaneously, depending on the buffer conditions of the restriction enzymes used. The digested vectors were additionally treated with CIP (Alkaline Phosphatase, Calf Intestinal; New England BioLabs, M0290S) for 1 hour at 37°C, which catalyses the dephosphorylation of the 5' and 3' endings of the linearised vectors to prevent religation, followed by 15 minutes at 75°C to inactivate the CIP enzyme. The linearised vectors and digested PCR products were subjected to ligation at 16°C over night, using T4 ligase and reaction buffer (10x reaction buffer is 300mM Tris-HCI (pH 7.8 at 25°C), 100mM MgCl₂, 100mM DTT and 10mM ATP) (Promega, M1801). The ligation reaction was transformed into XL10-Gold ultracompetent cells (Stratagene, Agilent Technologies, 200314) according to the manufacturer protocol.

2.2 Site-directed mutagenesis

Table 2-1 Primers used for site-directed mutagenesis reactions. Listed are the forward (FW) and reverse (RV) primers applied in site-directed mutagenesis reactions of protein vectors to create the listed mutated protein (name). Blue represents final mutated sequence; red represents deletion between the two highlighted nucleotides.

Name	Primer	Primer sequence 5' to 3'
Dragon sequence correction	FW	CCAGAAGACGGCGGCGGAGTCGCGAA <u>A</u> GATCGAGGAGATCCGCCACGAGCTGT
	RV	ACAGCTCGTGGCGGATCTCCTCGATCTTCGCGACTCCGCCGCCGTCTTCTGG
Dragon∆aa197-259	FW	CATCTCGCTGAAGGACTTCGAACAGTGCATACATTTTGCCAATGTAGAAA
	RV	TTTCTACATTGGCAAAATGTATGC <mark>AC</mark> TGTTCGAAGTCCTTCAGCGAGATG
Dragon 1 00210 244	FW	AATGCTGTACCAGGCCATCGAGCA <mark>GC</mark> TGGCCGTGGACGTAGCTCTGCTGA
Dragon∆aaz 19-244	RV	TCAGCAGAGCTACGTCCACGGCCAGCTGCTCGATGGCCTGGTACAGCATT
Dragon A 22/14/250	FW	CGAGCTGTCCAAGCTGGAAAGTGATTGCATACATTTTGCCAATGTAGAAA
Diagonizaaz44-259	RV	TTTCTACATTGGCAAAATGTATGCAATCACTTTCCAGCTTGGACAGCTCG
Dragon 4 00 286 220	FW	GCGGGCCAAGATAGAGCTGCACAATGGTCTGTCGCCAACCGATGATTGCC
Diagonizaaz80-320	RV	GGCAATCATCGGTTGGCGACAGACCATTGTGCAGCTCTATCTTGGCCCGC
Dragon 4 00 202 220	FW	AGAGCATCTATGCACAGTAATTGCCGGTCTGTCGCCAACCGATGATTGCC
Diagonizaa505-520	RV	GGCAATCATCGGTTGGCGACAGACCGGCAATTACTGTGCATAGATGCTCT
Dragon 4 ap 220, 219	FW	AATGCTGTACCAGGCCATCGAGCAGAAAGTGGGTCTGTCGCCAACCGATG
Diagonizaazzo-318	RV	CATCGGTTGGCGACAGACCCACTTTCTGCTCGATGGCCTGGTACAGCATT
Dragon (00220, 286	FW	AATGCTGTACCAGGCCATCGAGCAGCATCCGAAAAGAAGGAGCTGCTCA
Dragon∆aa220-266	RV	TGAGCAGCTCCTTCTTTTCGGATG <mark>CC</mark> TGCTCGATGGCCTGGTACAGCATT
Dragon (00260, 286	FW	GCTGAGGAAGCAGATCGACAATGCCCGCATCCGAAAAGAAGGAGCTGCTCA
Diagoniaa200-280	RV	TGAGCAGCTCCTTCTTTTCGGATGCGGCATTGTCGATCTGCTTCCTCAGC
Dragon 4 22260, 266	FW	GCTGAGGAAGCAGATCGACAATGCCCGAAAAACAATACGTCAAAATCGAGG
Diagonizaazoo-zoo	RV	CCTCGATTTTGACGTATTGTTTTTCGGCATTGTCGATCTGCTTCCTCAGC
Dragon 4 22/267 281	FW	CTGCATACATTTTGCCAATGTAGAAATAGAGCTGCACAATGCATCCGAAA
Diagonizaazor-zon	RV	TTTCGGATGCATTGTGCAGCTCTATTTCTACATTGGCAAAATGTATGCAG
Dragon 4 22 282 286	FW	CGAGGCTCAGTTCTTGCGGGCCAA <mark>GG</mark> CATCCGAAAAGAAGGAGCTGCTCA
Diagonizaazoz-zoo	RV	TGAGCAGCTCCTTCTTTTCGGATG <mark>CC</mark> TTGGCCCGCAAGAACTGAGCCTCG
	FW	AGCGACCTGATGAGCGCCATATGGAGATGTGTGGAACTCCGAACTATAT
PIK4-1172E	RV	ATATAGTTCGGAGTTCCACACAT <u>CTC</u> CATATGGCGCTCATCAGGTCGCT
DILA KA2M	FW	ACACTCACCAGGATGTGGCCATAATGATGATCGATAAAAAACTAATCCA
FIK4-K43W	RV	TGGATTAGTTTTTATCGATCATCATTATGGCCACATCCTGGTGAGTGT
A==0 0040A	FW	ACTGGCCAAGCCCAACACCGAGAAGGCAATGGTGATGAACGAGCTGGCGCTGA
Anaz-5318A	RV	TCAGCGCCAGCTCGTTCATCACCATIGCCTTCTCGGTGTTGGGCCTGGCCAGT
A	FW	GATCGACAACATAGGCCACGCGCAGGCACCAAACGACATATCCAATGCTTCGT
Ana2-5365A	RV	ACGAAGCATTGGATATGTCGTTTGGTGCCTGCGCGTGGCCTATGTTGTCGATC
4	FW	CCACGCGCAGAGTCCAAACGACATAGCAAATGCTTCGTACAAGTATCTCAAAA
Anaz-5370A	RV	TTTTGAGATACTTGTACGAAGCATT <u>TGC</u> TATGTCGTTTGGACTCTGCGCGTGG
Arr = 0 0070A	FW	GAGTCCAAACGACATATCCAATGCTGCATACAAGTATCTCAAAAAAATACCGTC
Anaz-5373A	RV	GACGGTATTTTTTGAGATACTTGTATGCAGCATTGGATATGTCGTTTGGACTC
4702.24	FW	CCACGCGCAG <u>GCA</u> CCAAACGACATA <u>GCA</u> AATGCT <u>GCA</u> TACAAGTATCTCAAAAAATACCGTC
Anaz-3A	RV	GACGGTATTTTTTGAGATACTTGTATGCAGCATTTGCTATGTCGTTTGGTGCCTGCGCGTGG

To introduce point mutations or deletions within Dragon, the QuikChange II XL Site-Directed Mutagenesis Kit (Agilent Technologies, 200521) was used with Dragon cDNA or Dragon+STOP in pDEST42 (invitrogen[™], Thermo Fisher Scientific, 12276010). The mutagenesis reaction mixes of 25µl final volume contained: 50ng DNA, 1x buffer, 600µM NTPs, 240nM forward primer, 240nM reverse primer, 1.5µl Quik Solution, 0.5µl *Pfu* Ultra high-fidelity DNA Polymerase; and the following temperature cycling program was used: 1. 95°C for 1 minute, 2. 18x cycles of 95°C for 50 seconds, 60°C for 50 seconds and 68°C for 3 minutes, 3. 68°C for 10 minutes, 4. Final storage at 4°C. The method uses the supercoiled

double-stranded DNA vector and two primers that are complementary to opposite strands of the vector and contain the desired mutation. The primers are extended during the temperature cycles and contain staggered nicks. After the cycling program, the template DNA was digested by DpnI enzyme for 1 hour at 37°C, which targets for methylated and hemimethylated DNA (target sequence: 5'-Gm6ATC-3'). The remaining generated nicked vector products were transformed into DH5α cells.

2.3 Immuno-Histo-Staining and Microscopy

2.3.1 Immuno-Histo Stainings

For immune-staining of Drosophila cell culture 22 x 22 mm cover slides (VWR, 48376-049) were used. Therefore, the cell culture concentration was counted with a Hemocytometer and diluted to 500,000 to 800,000 cells per ml culture. Cover slides were pre-treated with concanavalinA (ConA, Sigma), which stretches the cells horizontally and allows an easier observation of the centrioles. The cells were incubated on the cover slide for 3 hours at 25°C before fixation with ice cold methanol. To fix the cells, the medium was taken off, 3ml ice cold methanol (left on dry-ice for 30 minutes beforehand) was flushed quickly onto the cover slides and remained on dry ice for 5 minutes. The methanol was taken off quickly and the cover slides were washed twice with 1x PBS. For long term storage, PBS-0.1%NaN₃ was added to prevent bacteria growth. To prepare the cells for staining, the cover slides were washed with PBS-0.1%TritonX-100 and transferred onto parafilm. The cells were blocked with PBS-10%FBS-0.1%TritonX-100 for 1 hour at room temperature, followed by incubation with primary antibodies (in PBS-10%FBS-0.1%TritonX-100) over night at 4°C, 3 washes with PBS-0.1%TritonX-100, and incubation with secondary antibodies (in PBS-10%FBS-0.1%TritonX-100) for 1 to 3 hours at room temperature (commonly Alexa Fluor® antibodies from Novex[™] (Thermo Fisher Scientific) were used). After incubation, the cover slides were washed 3 times with PBS-0.1%TritonX-100 and stored in 1x PBS until mounting the same day. The cover slides were briefly rinsed in ddH₂O before mounting to microscope slides with VECTORSHIELD mounting medium for fluorescence with DAPI (for DNA staining) (Vector Laboratories, H-1200) and nail varnish was used to seal off the edges.

Antibody	Dilution	Raised in	Location
Anti-Ana2	1:1000	Rabbit	Glover lab
Anti-Asterless	1:2000	Sheep	Glover lab
Anti-Dragon	1:1000	Guinea-pig	Glover lab
Anti-FLAG M2	1:1000	Mouse	Sigma, F3165
Anti-GM130	1:1000	Rabbit	Abcam, ab52649
Anti-Golgin245 G-7	1:1000	Mouse	Santa Cruz Biotechnology, sc-514775
Anti-D-Plp	1:1000	Chicken	Glover lab
Anti-Sas6	1:1000	Rat	Glover lab
Anti-GFP	1:600	Mouse	Thermo Fisher Scientific, A6455
Anti-myc 9E10	1:1000	Mouse	Thermo Fisher Scientific, 13-2500
Anti-α-tubulin DM1A	1:1000	Mouse	Sigma, T6199
Anti-γ-tubulin	1:250	Mouse	Sigma, T6557

Table 2-2 Summary of primary antibodies that were used in IF analyses.

Antibody	Dilution	Species	Location
AlexaFluor® 488	1:333	Goat anti-chicken	Thermo Fisher Scientific, A11039
AlexaFluor® 568	1:333	Goat anti-chicken	Thermo Fisher Scientific, A11041
AlexaFluor® 594	1:333	Goat anti-chicken	Thermo Fisher Scientific, A11042
AlexaFluor® 647	1:333	Goat anti-chicken	Thermo Fisher Scientific, A21449
AlexaFluor® 488	1:333	Goat anti-guinea-pig	Thermo Fisher Scientific, A11073
AlexaFluor® 568	1:333	Goat anti-guinea-pig	Thermo Fisher Scientific, A11075
AlexaFluor® 594	1:333	Donkey anti-guinea-pig	Jackson ImmunoResearch, 70-586-148
AlexaFluor® 488	1:333	Donkey anti-mouse	Thermo Fisher Scientific, A21202
AlexaFluor® 594	1:333	Donkey anti-mouse	Thermo Fisher Scientific, A21203
AlexaFluor® 488	1:333	Donkey anti-rabbit Thermo Fisher Scientific, A21206	
AlexaFluor® 594	1:333	Goat anti-rabbit	Thermo Fisher Scientific, A11012
AlexaFluor® 405	1:333	Goat anti-rabbit	Thermo Fisher Scientific, A-31556
AlexaFluor® 488	1:333	Goat anti-rat	Thermo Fisher Scientific, A11006
AlexaFluor® 594	1:333	Goat anti-rat	Thermo Fisher Scientific, A21213
AlexaFluor® 488	aFluor® 488 1:333 Donkey anti-sheep Jackson ImmunoResearch, 713-546-1		Jackson ImmunoResearch, 713-546-147

2.3.2 Microscopy

2.3.2.1 Structured illumination microscopy

The method was applied in collaboration with Dr. Tzolovsky and as describes in ²⁴. In short, the OMX-V3 system was used with a 63x/1.4NA oil Olympus lens to acquire super-resolution images (512x512ppi), followed by images being reconstructed and registered using the package SoftWorx Linux and processing of the images to obtain the maximum intensity projections. Final figures were cropped and assembled in Photoshop v6.

2.3.2.2 Fluorescent microscopy

Microscopic analyses of *Drosophila* cells and U2OS cells after histo-immuno-staining were performed on a Carl Zeiss Axiovert 200M microscope with 40x/1; 63x/1.25 and 100x/1.4 Plan Apochromat objectives. Acquiring of images was performed with a Photometrics Cool SNAP HQ2 camera, analyses of images were performed with the Metamorph software (v7.7).

2.4 Western Blot

For Western Blotting, proteins were run on a SDS-PAGE gel and transferred onto Hybond-ECL membran (GE Healthcare, RPN3032). Membranes were stained with Amido Black to visualise total protein. The membranes were then blocked for 1 hour in PBS-0.1%Tween-4% milk solution, followed by incubation over night with the primary antibody in PBS-0.1%Tween-4% milk solution at 4°C. The membranes were washed 3 times for 5 minutes in PBS-0.1%Tween and incubated for one hour with the secondary peroxidase conjugated antibody in PBS-0.1%Tween-4% milk solution at 4°C. After 3 washes in PBS-0.1%Tween for 5 minutes at room temperature the proteins were detected using Immobilon Western Chemiluminescent HRP Substrate reagent (WBKLS0500, Millipore). For this membrane was incubated with the mixed solutions (5ml ddH₂O, 2.5ml substrate solution, 2.5ml luminol solution) for 5 minutes, the majority of the solution was aspirated off and the membrane developed in the dark room.

Antibody	Dilution used	Raised in	Location
Anti-DragonN (aa1-171)	1:1500	guinea-pig	Glover lab
Anti-FLAG M2	1:20,000	mouse	Sigma, F3165
Anti-GFP	1:2000 or 1:10,000	rabbit	Thermo Fisher Scientific, A6455
Anti-myc	1:5000	mouse	Abcam, ab18185
Anti-myc 9E10	1:6000	mouse	Thermo Fisher Scientific, 13-2500
Anti-Plk4	1:2000	sheep	Glover lab
Anti-α-tubulin DM1A	1:1000	mouse	Sigma, T6199

Table 2-4 Summary of primary antibodies that were used in Western Blot analyses.

Table 2-5 Summary of secondary antibodies that were used in Western Blot analyses.

Antibody	Dilution	Location
Peroxidase AffiniPure Goat Anti-Guinea Pig IgG (H+L)	1:333	Jackson ImmunoResearch, 106-035-003
Peroxidase AffiniPure Goat Anti-mouse IgG (H+L)	1:333	Jackson ImmunoResearch, 115-035-003
Peroxidase AffiniPure Goat Anti-rabbit IgG (H+L)	1:333	Jackson ImmunoResearch, 111-035-144
Peroxidase AffiniPure Rabbit Anti-sheep IgG (H+L)	1:333	Jackson ImmunoResearch, 313-035-045

2.5 Expression and purification of tagged proteins from *E. coli* for *in vitro* assays and antibody generation

2.5.1 Expression and purification of tagged proteins from E. coli

Proteins were tagged with GST (Glutatione S-Transferase) or MBP (Maltose Binding Protein) using gateway cloning technology and transformed into Chemically Competent *E. coli* cells One Shot® BL21 Star[™] (DE3) or BL21 Star (DE3) pLysS (Thermo Fisher Scientific). Colonies were tested for protein expression by inoculation of an overnight culture at 37°C,

220 rpm, followed by dilution to 1:50 and growth of the culture until it reached an OD of 0.4 to 0.6. At this time point a 1 ml sample of bacteria culture was taken for further analysis on SDS-PAGE and 1mM IPTG was added to the main culture to induce protein expression. The culture was left at 37°C and 1 ml culture samples were taken at different time points, up to 6 hours after induction, to analyse the level of protein expression on SDS-PAGE. After the timed protein expression, the cell cultures were centrifuged at 8600 rpm for 12 minutes, resuspended in 1x PBS and instantly stored at -20°C or -80°C. The samples for SDS-PAGE analysis were centrifuged at 13.000 rpm for 1 minute, the pellets were resuspended in PBS/1%Benzonase, left for 1 minute at RT, followed by adding 3x sample buffer containing 15% β -Mercaptoethanol to the sample and boiled at 96°C for 5 minutes.

Alterations of the expression conditions were undertaken where the above described protocol did not result in efficient protein expression. Expression levels were tested at 25°C or 16°C with increased expression times of up to 20 hours. The construct containing the HsSas6 protein sequence was kindly provided by Dr. Tzolovsky, followed by PCR to attach att overhangs for Gateway® cloning into pDONR221 and the expression construct pDEST15 (N-terminal GST tag).

For the protein purification, the bacteria suspension was defrosted and 1x Protease Inhibitor mix (cocktail tablets, complete EDTA-free, Roche, 11873580001), 10% PMSF (Sigma, 93482), 4% TritonX-100 (Sigma, T8787) and 10% Glycerol (Sigma, G5516) were added. In the case of Sas6 purification, PMSF was not added. Additionally, for the proteins stored on resin described in chapter 3, Sodium lauroyl sarcosinate (Sarkosyl, Sigma, 61747) was used instead of Glycerol, to increase solubility of GST fusion proteins ²⁸³. The bacteria mix was then sonicated at 4°C until it was not viscous but of a fluid character, followed by a centrifugation step at 18,000 rpm for 30 minutes, 4°C. To purify the fusion protein, and rotated at 4°C for 2 to 3 hours. For GST fusions, Glutathione Sepharose 4B (GE Healthcare, 17-075601) and for MBP fusions, Amylose resin (BioLabs E8021L) were used. Each of the resin solutions were washed in PBS-2%TritonX-100 (T-PBS). For storage of the proteins on

beads, 250µl beads baid volume were used (proteins bound to resin was stored at -20°C in 1x PBS with 50% glycerol); and for final protein elutions, 500µl beads baid volume were used for binding. After the binding, the beads were washed once with 0.5% T-PBS, once with 0.1% T-PBS and twice with Wash Buffer (50mM TrisHCI, 150mM NaCI, 0.1% TritonX-100). For further experiments with tagged protein bound to beads, they were stored at -20°C in 1x PBS with 50% glycerol. For elution of the proteins off the beads, Elution Buffer (10mM TrisHCI, 30mM NaCI, 0.02% TritonX-100, plus 15mM L-Glutathione for GST tagged proteins or 15mM Maltose for MBP tagged proteins) was added as twice the volume of the resin bait volume. Each protein was eluted 3 times at 4°C on a rotating wheel, for 2 hours or overnight for the first and second elution and for 2 hours for the third elution, and stored at -20°C. For use of the protein as an antigen in the generation of antibody, the protein was dialysed against 1x PBS overnight and again for 10 hours in fresh 1x PBS. In the case of MBP-Plk4-T172E and MBP-Plk4-T172E-K43M; the proteins were eluted in kinase buffer (20mM Na-HEPES pH7.5, 100mM NaCl, 10mM MgCl₂, 10mM MnCl₂, 1mM DTT), supplemented with 15mM D-Maltose, and stored at -80°C in Plk4-Kinase Buffer supplemented with 50% glycerol. Concentrations were measured by spectrophotometry and quality was analysed by SDS-PAGE.

	Chapter 3	Chapter 4	Chapter 5
GST		MBP-PIk4-T172E	GST-Sas6
	MBP	MBP-PIk4-T172E-K43M	GST-HsSas6
	GST-Ana2	MBP-Sas6	GST-Dragon
	AsI-GST	MBP-Ana2	
	GST- Cep97	GST-Ana2-N (aa1-280)	
	GST-CP110 (aa1-400)	GST-Ana2-C (aa281-420)	
	GST-CP110 (aa360-570)	GST-Ana2-4D	
	MBP-Plk4	GST-Ana2-4A	
	GST-Rcd4	GST-Ana2-C-4A	
	GST-Sas4	GST-Ana2-S318A	
		GST-Ana2-S365A	
		GST-Ana2-S370A	
		GST-Ana2-S373A	
		GST-Ana2-C-S318A	
		GST-Ana2-C-S365A	
		GST-Ana2-C-S370A	
		GST-Ana2-C-S373A	
		GST-Ana2-aa315-384 (STAN only)	
		GST-Ana2-aa305-394	
		GST-Ana2-aa295-404	
		GST-Ana2-aa315-420	

Table 2-6 Summary of expressed and purified proteins as of their first appearance in the chapters of this thesis.

2.5.2 Lambda-phosphatase bandshift assay

The λ -phosphatase bandshift assay was used to analyse the kinase activity of purified MBP-Plk4-T172E by its migration on SDS-PAGE. MBP-Plk4-T173E was resuspended in λ phosphatase buffer (1x NEBuffer, 1x MnCl₂ Buffer, up to with ddH₂O, all NEB, P0753) and half the sample was treated with exogenous λ -phosphatase (NEB, P0753) for 1 hour at 30°C, followed by adding 3x sample buffer containing 15%β-Mercaptoethanol and boiling of the sample at 96°C for 5 minutes. Samples were subjected to SDS-PAGE and compared to the migration of kinase dead MBP-Plk4-T172E-K43M.

2.5.3 Antibodies generation and purification

Protein expression, purification and elution for the production of antibodies was performed as previously described (section 2.5.1). Antibodies applied in this study: MBP-Ana2 (full length) and GST-Sas6-C (aa236-472). The concentrated protein (150µg for 4 to 6 injections) was send to IMBC - instituto de biologia molecular e cellular, Porto, Portugal; to be used as antigen to generate IgG immunoglobulins specific for the antigen in rat. The received rat serum was stored in 50% glycerol at -80°C and used for antibody purification. The purification of the antibodies was performed as an IgG purification on rProteinA : ProteinG Sepharose (GE Healthcare, 17-1279-01, 17-0618-01 respectively) and were done small scale with 200µl resin suspension and 1000µl serum. This method allowed purification of all the IgGs present in the serum. The principle for the purification of IgG, IgG fragments and subclasses, is the high affinity of proteinA and proteinG for the Fc region of polyclonal IgGtype antibodies. ProteinA and ProteinG are bacterial proteins from Staphylococcus aureus and Streptococcus respectively, which were coupled to sepharose and can be used to isolate IgGs from serum. ProteinA has five regions for the Fc region of IgG to bind. Additionally, the used rProteinA (recombinant protein A) has been engineered to include a Cterminal cysteine which enables a single-point coupling to sepharose, allowing an increased binding capacity. ProteinG is a cell surface protein from Group G streptococci and a type III Fc-receptor, which binds through a non-immune mechanism. Compared to ProteinA, it binds more strongly to several polyclonal IgGs. Therefore a mixture of 50% rProteinA : ProteinG was used for serum from rat (anti-Ana2 and anti-Sas6). For the purification of sheep serum (anti-Plk4) only ProteinG and for the purification of rabbit serum (anti-Asterless and anti-Ana2-N) only rProteinA was used.

For the purification, the serum was diluted 10 times with PBS and centrifuges for 10 minutes at 14.000 rpm, 4°C to remove aggregates. Then it was mixed with the resin for binding on a rotating wheel for 60 minutes at 4°C, followed by two wash steps with PBS-0.1%TritonX-100 and two rinses with 1x PBS. The elutant was 0.1M Glycine-HCL pH3, which was added to the resin, mixed for 10 to 20 seconds and then removed and neutralised with 1M Tris-HCl

pH8. Each antibody was eluted up to 4 times to win the highest protein concentration. For long term storage, the antibodies were concentrated by dialysing against a 50% Glycerol-PBS solution at 4°C overnight.

2.6 *In vivo* assays and Mass spectrometry

2.6.1 *In vivo* ProteinA and GFP-trap purification from *Drosophila* cell culture

For the identification of protein complexes *in vivo*, a combination of the methods of cell culture, single step ProteinA affinity or GFP trap purification and Mass Spectrometry has proven to be successful in mitotic and cytokinetic complexes. The method is based on the tagging of a bait protein with two IgG binding domains of Protein A or GFP, followed by stable expression in *Drosophila* cell culture, and isolation of the tagged bait protein together with its interacting partners by a single affinity purification step. The isolated protein complexes were then analysed Mass Spectrometry.

The cells for Mass Spectrometry analysis were expanded to 6 or 8 cell culture flasks of 175cm^2 , using Express Five® SFM (1x) cell culture medium (GibcoTM, Thermo Fisher Scientific, 10486-025) supplemented with 2mM L-glutamine (GibcoTM, Thermo Fisher Scientific, 25030), and 100 U/ml penicillin and 100μ g/ml streptomycin (GibcoTM, Thermo Fisher Scientific, 15140). The cells were grown at 25°C until confluent, followed by passage. Cells were treated with 25µM MG132 for up to 5 hours to inhibit proteasomal degradation. For proteins which express from a pMT promoter, 1mM CuSO₄ was added to the medium for 22 hours to induce expression of the protein. 50% of each cell line was additionally treated with 50nM okadaic acid for 9 to 16 hours to inhibit the protein phosphatase PP2A and keep proteins in their phosphorylated state.

2.6.1.1 ProteinA purifications

For ProteinA purifications, the cells were harvested in PBS, resuspended in cold extraction buffer (75mM Na-HEPES pH7.5, 150mM NaCl, 2mM MgCl₂, 0.1%NP-40, 5mM DTT, 2mM EGTA, 5% glycerol, 1 tablet complete protease inhibitor per 50 ml), homogenised on ice and centrifuged at 4°C to pre-clear the soluble material. The supernatant was transferred to new tubes and magnetic rlgG-Dynabeads M-270 Epoxy (InvitrogenTM, Thermo Fisher Scientific, 143.02D) were added. The mixture was incubated on a slowly spinning wheel at 4°C for 2 hours, to allow the rabbit IgG to bind to the complexes associated with the ProteinA tagged bait. After incubation, the beads were washed 5 times with extraction buffer, followed by elution using an elutant (0.5M NH₄OH, 0.5mM EDTA). For the analysis of the proteins, the eluted protein samples were desiccated to a volume of 100µl and an aliquot was taken for analysis using the SilverQuestTM Silver Staining Kit (NovexTM, Thermo Fisher Scientific, LC6070). The proteins were then precipitated in small volumes with Acetone, dried in a speedvac centrifuge (Eppendorf, Concentrator 5301) and send for gel-free mass spectrometry analysis (Mass Spectrometry Laboratory, Institute of Biochemistry and Biophysisc, Warsaw, Poland).

The following purifications by Cunha-Ferreira, Dzhindzhev, Psternak, Schneider* and Weiskopf were reanalysed in chapter 3 and 5: pMT-Ana2-PrA*, pAct5-PrA-Ana2+pMT-Plk4*, Act5-PrA-Asl, Act5-Asl-PrA, Act5-Asl(aa531-994)-PrA, pMT-PrA-Cep97, pMT-Cep97-PrA, pMT-PrA-CP110, pMT-CP110-PrA, Act5-PrA-Plk4, pMT-PrA-Plk4, pMT-Rcd4-PrA, pMT-Sas4-PrA, pMT-PrA-Sas6. Additional purifications were performed but did not yield centrosomal duplication proteins in complex with the bait*: pAct5-PrA-Ana1, pAct5-Ana1-PrA, pAct5-PrA-Ana2, Act5-Ana2-PrA+pMT-Plk4, pAct5-PrA-Bld10, pAct5-PrA-Sas6. The constructs and cell lines were kindly provided by Dr. Dzhindzhev.

2.6.1.2 GFP-trap purifications

The GFP-trap purifications were performed in the cold room at 4°C and all reagents were kept at 4°C if not otherwise stated. The confluently grown Drosophila cells in 6x175cm² flasks (Corning®, 431079) were harvested with a cell scraper and centrifuged at room temperature and 900g for 5 minutes, followed by a 1x PBS wash and combining of all the cells into one 50ml falkon tube (Greiner Bio-One, 227261). The cells were then resuspended in 8ml Lysis Buffer 1 (20mM Tris pH7.5, 150mM NaCl, 2mM MgCl₂, 1mM DTT, 0.1% NP-40, 5% glycerol, 1x EDTA-free complete protease inhibitor cocktail (PIC, Roche) and 1mM PMSF (for samples other than tagged Sas6 purifications)) and homogenized at power 6 for 5-6 times for 30 seconds with breaks of 15 seconds (Fisherbrand PowerGen 125, FB70300). The lysate was clarified at 10,000 rpm for 15 minutes at 4°C. In the meantime the GFP-trap agarose bead suspension (ChromoTek, gta) was pre-equilibrated: 120µl of beads were added to 10ml LB1 and gently mixed 4-6 times, followed by centrifugation at a maximum of 2400g for 3 minutes at 4°C with a low deceleration speed and removal of the final supernatant. The supernatant of the cell lysate was then mixed with the GFP-trap beads and incubated on a rotating wheel (15-20 rpm) for 2-3 hours at 4°C. Thereafter, the beads were centrifuged at a maximum of 2400g for 3 minutes at 4°C with a low deceleration speed and the supernatant was removed. The beads were then washed twice in 10ml cold LB1 at 20rpm for 10 minutes, at 4°C; followed by transfer of the beads to a new pre-chilled Falcon tube and two wash steps in 10ml LB2 (same as LB1 but without PMSF and PIC). Beads were then transferred to a 1.5ml Eppendorf tube, adjusted to 1ml with LB2 and send for mass spectrometry. The protein complexes were mixed with 1x Laemmli sample buffer and analysed by Western Blotting.

The GFP-trap purifications from *Drosophila* cell culture stably expressing pMT-Dragon-GFP or pUb-GFP-Dragon (kindly provided by Miss Chu) were performed and analysed. Additionally, the purifications of pMT-PrA-Sas6 by Dr. Dzhindzhev was reanalysed.

2.6.2 Large scale collection and *in vivo* GFP-trap purification from *Drosophila* syncytial embryos

2.6.2.1 Large scale Drosophila embryo collection

For the large scale collection of 0-4 hours old syncytial Drosophila embryos that express poly-Ubiquitin-GFP-Dragon (flies kindly provided by Miss Chu), the flies were expanded to 9 large maintenance bottles and transferred into 2 large population cages (Genesee Scientific, FS59-104) for the collection of 1g of fresh embryos for GFP-trap purification. The population cages were kept at a 12/12 hours reversed light/dark cycles, with a room temperature of 25°C and a room humidity of 70%. On day 1 (morning), 2 chippy trays with grape juice agar and yeast paste were added to each cage, and replaced every 12 hours for a period of 48 hours. This stimulates the flies to the food-rich environment, which avoids eggs retainment and hence, synchronised egg laying. On day 3 (morning), a final change of chippy trays with yeast paste was added to the population cages for one hour to finalise full synchronisation. Thereafter new chippy trays with small amounts of yeast paste were added and replaced every 4 hours. The embryos were collected from the chippy trays with fine brushes and washed in mesh sieves with dH₂O, followed by a quick drying step with a paper towel pressed against the underneath of the sieve. For dechorionation, the embryos were transferred into a small beaker with 60ml 50% bleach (Kemtec) for 3-5 minutes, which was gently swirled manually. The dechorionated embryos were transferred into a small mesh sieve, washed with water, then wash buffer (0.7%NaCl+0.01% TritonX-100), to remove the vitelline membrane, and transferred into 2ml tubes and briefly centrifuged for collection. For long term storage, the decorionated embryos were frozen in liquid nitrogen.

2.6.2.2 In vivo GFP-trap purification from Drosophila syncytial embryos

1g of fresh Drosophila syncytial embryos (0-4 hours) expressing poly-Ubq-GFP-CG33052 were homogenised with a Dounce tissue grinder (Wheaton) in 10ml Extraction Buffer (EB: 20mM Tris-HCl pH7.5, 150mM NaCl, 2mM MgCl₂, 0.5mM Na-EGTA pH8, 1mM DTT (dithiothreitol), 0.1%NP-40, 5% glycerol, 1mM PMSF (phenylmethanesulfonyl fluoride), EDTA-free complete protease inhibitor cocktail (Roche)) at 4°C. 10ml of EB were then added to the sample, which was then vortexed for 10 seconds and passed through a needle and pre-chilled syringe three times, followed by a centrifugation step at 5000g for 20 minutes at 4°C. The supernatant was carefully transferred to a new tube, avoiding to remove any white fatty matter with it, and mixed with pre-equilibrated GFP-trap agarose beads (50-100µl per sample, gently mix in 5ml EB in 15ml conical tubes, sediment beads at 500g for 3 minutes at 4°C) for 30-150 minutes, at 18 rpm on a spinning wheel at 4°C. Thereafter, the beads were washed four times in 10ml Wash Buffer (same as EB) for 5 minutes each, at 4°C; sedimented and transferred to a new 15ml conical tube, washed two times in 10ml Final Wash Buffer (FWB: 20mM Tris-HCl pH7.5, 150mM NaCl, 2mM MgCl₂, 0.5mM Na-EGTA pH8, 1mM DTT) by gently rotating for 10 minutes at 4°C; again sedimented, transferred and twice washed with FWB; and finally all buffer was removed, and beads were stored at 4°C until on-beads tryptic digestion and mass spectrometry analysis.

The purifications of pUb-Sas6-GFP from *Drosophila* syncytial embryos by Dr. Dzhindzhev were reanalysed; these purifications were performed with normal NaCl concentration or with a high 440mM NaCl concentration and plus/minus okadaic acid.

2.6.3 Mass spectrometry and Phospho-peptide/residue mapping

The Mass Spectrometry data was generated by Dr. Dubski at the Mass Spectrometry Laboratory, Institute of Biochemistry and Biophysics, Pawinskiego 5a, 02-106, Warszawa, Poland. GST-Ana2 protein was phosphorylated by active Plk4 *in vitro* and ProteinA-Ana2

was phosphorylated by co-expressed non-degradable Plk4ND in *Drosophila* cell culture (*in vivo*). The protein samples were digested with trypsin (Promega V5111) and the peptide mixtures were analysed by LC–MS/MS (high-performance liquid chromatography tandem mass spectrometry) using Nano-Acquity (Waters) LC system and Orbitrap Velos mass spectrometer (Thermo Electron Corp.). The raw data was then analysed by Mascot Distiller followed by Mascot Search (Matrix Science) against the FlyBase database. The values of Mascot scores for individual proteins ('Protein score') and 'number of identified peptides' were analysed as a measure of ability for certain baits to co-purify with the prey protein. The Mascot score is a statistical score that represents how well the experimental data matches the database sequence (FlyBase). A 95% confidence level is required to identify a positive protein. The final Mascot score is generated from the summed scores of peptide masses and peptide fragment ion masses for the individual peptides that match a given protein.

2.7 Yeast-2-Hybrid – testing for direct interactions in an *in vivo* system

For the Yeast-2-Hybrid assay, each protein sequence was cloned into the vector pGBT9 and pGAD424 and then co-transfected into the yeast strain AH109. The method is based on the activation of the GAL promotor by its transcription factor, which is split into Binding Domain (BD) and Activation Domain (AD). The bait plasmid (pGBT9) contains the GAL4 DNA-Binding Domain (BD) and the prey plasmid (pGAD424) contains the GAL4-Activation Domain (AD). When proteins cloned into these plasmids interact directly with each other, they bring the BD and AD together, allowing for GAL promotor transcription and translation, which leads to colonies that grow on X- α -GAL to turn blue (colonies turn blue after up to 6 days at 30°C when a protein interaction occurs). If the co-transformation has been successful but the proteins do not interact with each other, the yeast can grow on the selection plates, which select for -Leu (pGD424) and –Trp (pGBT9), but they stay white and do not turn blue. If a transformation has not been successful with neither or only one of the plasmids, then the yeast strain cannot grow on the selection media.
For the co-transformation, the overnight culture of AH109 is diluted in 330ml YPD medium with OD600 = 0.3, then grown until OD600 = 0.6. The cells are centrifuged at RT, 1000g, 5 minutes, resuspended in 1x TE, centrifuged and resuspended in 1.5ml 1x TE/ 1x LiAc. 100µl of competent cells are added to 0.1µg plasmid DNA 1 + 0.1µg plasmid DNA 2 + 0.1mg carrier DNA and mixed by vortexing. 600µl of PEG/LiAc solution are added and the tube is vortexed for 10 seconds. The cells then incubate at 30°C, 220 rpm for 30 minutes. 70µl of DMSO is added to the cells and gently inverted, followed by a heat shock for 15 minutes at 42°C and 2 minutes on ice. Then the cells are resuspended in 1x TE, 100µl are plated on dropout media containing X-α-GAL and the plates are incubated at 30°C for up to 6 days.

Table 2-7 List of proteins that were cloned into pGAD424 or pBGT9 vectors. The vectors carry a GAL4-AD (activation domain) or GAL4-BD (binding domain) respectively; including plasmids used as positive and negative controls. The plasmids were used in yeast-2-hybrid interaction studies.

Vector	Domain	Proteins	Control
pGAD424	GAL4-AD	Asl, Ana2, Bld10, Cep97, CP110, Plk4, Rcd4, Sas4, Sas6, Polo and Spd2	-
pBGT9	GAL4-BD	Ana2, Bld10, CP110, Sas4 and Sas6	-
pGAD424	GAL4-AD		negative
pBGT9	GAL4-BD		negative
pGAD424	GAL4-AD	Mis12	positive
pBGT9	GAL4-BD	Nnf1a	positive
pGAD424	GAL4-AD	Nnf1a	positive
pBGT9	GAL4-BD	Mis12	positive



Figure 2-1 Schematic diagram of the GAL promotor activation in the yeast-2-hybrid system. Binding of bait and prey protein bring together the GAL4-AD and GAL4-BD which forms the transcription factor for the GAL promotor.

2.8 In vitro binding assays

2.8.1 In vitro binding assay

For the analysis of *in vitro* protein-protein-interactions, the methods of *in vitro* transcription – translation (IVTT), followed by binding assays and pull-downs were performed.

The method is divided into the production of two different sets of reagents, ³⁵S-Methioninelabelled proteins and tagged protein immobilised on resin (section 2.5.1). Every protein to analyse was amplified from cDNA in T7 containing promotors or from PCR products that carry the T7 promoter sequence 5'-GAATTAATACGACTCACTATAGGG-3', the Kozak sequence 5'- AGAGCCGCCACC-3', the start codon for protein transcription and the protein coding sequence. Alternatively, proteins were amplified from the pHY22 vector which contains a T7 promotor followed by the start codon and protein sequence. For the transcription-translation reaction, the TnT® T7 Quick Coupled Transcription/Translation System kit (Promega, L1170) was used. It contains a TnT® T7 Quick Master Mix, to which radioactively labelled ³⁵S-Methionine (Perkin Elmer, NEG709A001MC), RNasin Plus RNase Inhibitor (Promega, N2611), T7 TNT PCR Enhancer, protease inhibitor cocktail and the cDNA, PCR product or pHY22 vector with the protein sequence were added. The reaction of in vitro transcription/translation reaction was performed in a volume of 50µl, at 30°C for 30 to 120 minutes. The synthesised and radioactively labelled proteins were then used for binding assays. The cDNAs of Drosophila centriole duplication proteins were sourced from the BDGP Gold Collection, Drosophila Genomics Resource Center. The human GoRab variant 3 was sourced from Source Bioscience, followed by PCR to amplify att sequence overhangs and include a STOP codon after the protein sequence for Gateway® cloning into pDEST42 (C-terminal His tag). The human GoRab variant 1 was generated by PCR from a U2OS cDNA cell library, which was kindly provided by Dr. Lipinszki.

For the binding assay, each tagged protein on beads (bait) was mixed with each radioactively labelled protein (prey) in individual reactions in 800µl Binding Buffer (50mM

Hepes pH7.5, 1mM EGTA, 1mM MgCl₂, 1mM DTT, 100mM NaCl, 0.1%Triton X-100, 1x Protease Inhibitor, 0.5mg/ml BSA). The mixture rotated on a spinning wheel for 30-60 minutes at RT, followed by 3x5 minutes washes in Wash Buffer (50mM Hepes pH7.5, 1mM EGTA, 1mM MgCl₂, 1mM DTT, 100mM NaCl, 0.1%Triton X-100), to remove the radioactively labelled proteins that were not directly bound to the protein on beads. The resins were transferred into new tubes and 3xsample buffer containing 15%β-Mercaptoethanol was added. To analyse if interaction occurred between 2 proteins, the resin samples were subjected to SDS-PAGE followed by Western Blot or the drying of the SDS-PAGE, exposure to hypersensitive film (Kodak BioMax MS film, 8222648) at -80°C and autoradiography. The resulting exposure signals were categorised into: no interaction (-), weak interaction (+), interaction (++) and strong interaction (+++). Visually compared were the 'input versus negative control' signal, which in turn support the comparison of the 'interaction versus input' and 'interaction versus negative control' signal, to categorise the analysed interaction.





Chapter 3	Chapter 4	Chapter 5
Ana1	Sas6 (pHY22)	Dragon
Ana2	Sas6-aa1-180	Sas6-aa1-402
Ana3 Exon 1 (aa1-1146)	Sas6-aa181-408	Sas6-aa1-392
Ana3 Exon 2 (aa1146-1978)	Sas6-aa1-408	Dragon-aa1-171
Asterless	Sas6-aa181-472	Dragonaa172-339
Bld10	Sas6-aa221-472	Dragon-aa1-113
Cep97	Sas6-aa261-472	Dragon-aa114-243
CP110	Sas6-aa266-472	Dragon-aa244-339
Plk4	Sas6-aa271-472	Dragon-aa191-318
Rcd4	Sas6-aa276-472	Dragon∆aa219-244
Sas4	Sas6-aa291-472	Dragon∆aa244-259
Sas6	Sas6-aa295-472	Dragon∆aa286-320
Cnn	Sas6-aa341-472	Dragon∆aa303-320
D-Plp-N (aa1-1603)	Sas6-aa351-472	Dragon∆aa220-318
D-Plp-C (aa1604-2727)	Sas6-aa361-472	Dragon∆aa220-286
Polo	Sas6-aa371-472	Dragon∆aa260-286
Spd2	Sas6-aa381-472	Dragon∆aa260-266
	Sas6-aa1-462	Dragon∆aa267-281
	Sas6-aa1-452	Dragon∆aa282-286
	Sas6-aa1-442	GoRab variant 1
	Sas6-aa1-437	GoRab variant 3
	Sas6-aa1-432	
	Sas6-aa1-427	
	Sas6-aa1-422	
	Sas6-aa1-414	
	Sas6-aa1-412	

Table 2-8 Summary of proteins that were generated by IVTT reaction. ³⁵S-Methionine</sup> labelled proteins used in this study (arranged as of their first appearance by chapter).

2.8.2 *In vitro* PIk4 kinase assay (MBP-PIk4-T172E phosphorylation assay using ³²P-γ-ATP)

To analyse if a protein is phosphorylated by active MBP-Plk4-T173E kinase a phosphorylation reactions was performed. The protein kinase or kinase dead (typically 4-10 μ g) was added to a reaction mix of 20-50 μ l, which contained Kinase Buffer (20mM Hepes, 100mM NaCl, 10mM MgCl2, 10mM MnCl2, 1mM DTT), 2.5mM ³²P- γ -ATP, 5-10 μ M cold ATP, tagged proteins bound to resin, ddH₂O. For non-radioactive kinase assays, 250 μ M cold ATP was used instead. The mix was incubated at 30°C for 45 minutes, followed by removal of the supernatant, adding 3x sample buffer containing 15% β -Mercaptoethanol and boiling of

the sample at 96°C for 5 minutes. Samples were subjected to SDS-PAGE for protein separation, followed by drying of the SDS-PAGE, direct exposure to hypersensitive film (Kodak BioMax MS film, 8222648) at -80°C and autoradiography.

2.8.3 In vitro binding assay of Sas6 with pre-treated Ana2

To study the in vitro interaction of Ana2 and Sas6 in chapter 4, it is necessary to prephosphorylate Ana2 with active Plk4 kinase; including the necessary controls. For this, 4-5µg of GST-Ana2/GST on resin were gently mixed in Kinase Buffer (20mM Na-HEPES pH 7.5, 100mM NaCl, 10mM MgCl₂, 10mM MnCl₂, 1mM DTT) with 250µM ATP; and ~4.5µg of active or kinase dead MBP-Plk4, and incubated at 30°C for 60 minutes, with a gentle mix every 3 to 5 minutes. After the incubation time, 400µl ice-cold Binding Buffer (50mM Na-HEPES pH 7.5, 100mM NaCl, 2mM MgCl₂, 1mM EGTA, 1mM DTT, 0.1%Triton-X100, 1.1 tablets of PhosStop/10ml BB, 1 tablet of PIC/35 ml BB, 100nM okadaic acid, 0.5mg/ml BSA) and ³⁵S-Methionine-labelled Sas6 were added to the reaction, and the samples were incubated for 2 hours at 15 rpm on a rotating wheel at 4°C. Adding PhosStop (Roche, 04906837001) gives a complete protection of proteins against a broad range of phosphatases according to manufacturer. The samples were then centrifuged at 1200 rpm for 3 minutes at 4°C, the supernatant was removed and the beads washed three times with 800µl Wash Buffer 1 (as Binding Buffer but without BSA) for 5 minutes at 4°C. The beads were then transferred into new chilled tubes and washed with 1ml Wash Buffer 1, followed by two washes with Wash Buffer 2 (same as WB1 but contains 10mM NaCl and 0.2%Triton-X100). Finally, 3x sample buffer containing $15\%\beta$ -Mercaptoethanol were added and the samples boiled at 96°C for 5 minutes, followed by analysis on SDS-PAGE, drying of the gels and direct exposure to hypersensitive film (Kodak BioMax MS film, 8222648) at -80°C and autoradiography.

2.9 Drosophila cell culture and Human U2OS cell culture experiments

2.9.1 Cell cultures

Drosophila cell cultures were grown in Express Five SFM medium (Gibco[™], Thermo Fisher Scientific, 10486-025) supplemented with 2mM L-glutamine (Gibco[™], Thermo Fisher Scientific, 25030-024) and Pen Strep (Gibco[™], Thermo Fisher Scientific, 15140-122). To generate stable cell lines, FuGENE HD Transfection Reagent (Promega, E2311) was used and procedures were performed as for transient transfection described in section 2.9.2, with the addition that 0.5µg of 'helper' plasmid carrying a Blasticidin resistance (pCoBlast) were added. The antibiotic selection started 48hours post-transfection with 20µg/ml Blasticidin. After 1 to 2 days the cells with antibiotic resistance start dividing, and once they are confluent, they were split and kept under 20µg/ml Blasticidin treatment for 6 to 8 passages until stably expression was reached. For localisation studies, *Drosophila* cell lines stably expressing Act5-myc-Dragon, poly-Ubiquitin-Dragon-GFP and poly-Ubiquitin-GFP-DragonΔ[™] were generated.

2.9.2 Co-IP experiment

Drosophila cells were transiently co-transfected with poly-Ubiquitin-GFP, poly-Ubiquitin-GFP-Dragon or poly-Ubiquitin-GFP-Dragon^{ΔIM} and Act5-6xmyc-Sas6, followed by GFP immunoprecipitated after 24-36 hours with 50nM okadaic acid (Calbiochem, 459620) in the lysis buffer, and subsequent Western Blot analysis. For the transient transfection 4.5x10⁶ cells were seeded in each well of a 6 well plate (Corning, 3516) and topped to 2ml with Express Five® SFM medium (Gibco[™], Thermo Fisher Scientific, 10486-025), after 2 hours a mix of 3µg of vectors DNA in 100µl nuclease-free water and 15µl FuGENE® HD Transfection Reagent (Promega, E2311) was incubated for 15 minutes and then added dropwise to the cells. The input samples of all three transient transfection confirmed the presence of Sas6 by anti-myc antibody staining (anti-myc 9E10, 1:6000, mouse), GFP/GFP-Dragon/GFP-Dragon^{Δ IM} by anti-GFP antibody staining (anti-GFP, 1:2000, rabbit) and as a control anti- α -tubulin (anti- α -tubulin DM1A, 1:2000, mouse). Secondary antibodies from Jackson ImmunoResearch were used at a 1:333 dilution (Table 2-5).

In collaboration with Dr. Lipinszki, *Drosophila* cells were transiently co-transfected with Actin5C-promoter-driven constructs encoding 3xFLAG-Ana2 (WT or 4A), Sas6-6xMyc or Plk4 (ND or NDKD) for 22 hours. Cells were treated with 25 μ M MG132 (Sigma-Aldrich, 133407-82-6) for 2.5hours before harvest. For the immunoprecipitation, the supernatants were mixed with anti-FLAGM2 magnetic beads (Sigma) for 3 hours at 4°C. After several washes proteins were eluted with 150 μ g/ml 3xFLAG peptide, mixed with 3x sample buffer and subjected to SDS-PAGE followed by Western Blotting. Proteins were detected using the antibodies anti-Plk4 (1:2000, sheep), anti-FLAG (clone M2, 1:20,000, mouse), anti-myc (clone 9E10, 1:6000, mouse) and anti- α -tubulin (clone DM1A, 1:2000, mouse). Secondary antibodies from Jackson ImmunoResearch were used at a 1:333 dilution (Table 2-5).

2.9.3 RNAi – RNA interference

RNAi was performed using TransFast[™] transfection reagent (Promega, E2431). In the morning 1.5x10⁶ cells were transferred into wells of 6 well plates (Corning, 3516) with 2 to 4ml Express Five SFM medium (Gibco[™], Thermo Fisher Scientific, 10486025) and transfection was performed 4 hours after. To prepare the transfection mix, 25µg of dsRNA were diluted in 1ml Express Five SFM medium, 20µl TransFast[™] transfection reagent was added and the whole mix was briefly vortexed, followed by 15 minutes incubation in which the complexes form. The medium was removed from the cells, which had attached to the bottom of the well, and the transfection mix was gently aspired in drops over the cells. The cells were incubated with the transfection mix for exactly 60 minutes at 25°C, after which 3ml

of Express Five SFM medium was added. The cells remained in the transfection-mediummix for 2 or 4 days, after which 500,000 to 800,000 cells per ml culture were transferred onto ConA coated cover slides for methanol fixation and Histo-Immuno-Staining. Additionally, 1.5x10⁶ cells were transferred for a second round of knock down by RNAi and the above protocol was followed repeatedly for further rounds of knock down. In collaboration with Dr. Dzhindzhev, the *Drosophila* cell lines stably expressing pAct5-Ana2-WT, pAct5-Ana2-4A and pAct5-Ana2-4D were used in RNAi experiments. Additionally, RNAi experiments were performed on wild-type *Drosophila* cells and cells expressing poly-Ubiquitin-GFP-Dragon or poly-Ubiquitin-GFP-Dragon^{ΔIM}.

Table 2-9 Summary of oligonucleotide primers used to generate dsRNA. Listed are the name of the primer, FW primer (FW), reverse primer (RV) and the primer sequence 5' to 3'. Red: T7 promoter sequence; CDS (coding sequence); UTR (untranslated region). For efficient dsRNA-based silencing of endogenous Ana2, a 225 bp-long hybrid DNA template containing a combination of T7 promoter sequence (red), Ana2's 5'UTR (black directly downstream of red T7 promoter sequence), 15 first nucleotides of the Ana2 CDS (green) and Ana2's 3'UTR (black downstream of green), was generated by Overlap Extension PCR.

Name FW or RV Primer sequence 5' to 3'				
Pod4	FW	GAATTAATACGACTCACTATAGGGAGAATGCCTCACAAACGTAGGAACCGAGTAC		
RC04	RV	GAATTAATACGACTCACTATAGGGAGACTAGTTGTATGTTCTCCTATATGCGCCG		
Dragon CDS	FW	GAATTAATACGACTCACTATAGGGAGAATGACTGAGAAATTCAATGGTTTTA		
Diagon CDS	RV	GAATTAATACGACTCACTATAGGGAGAGCGGCGATGCTGTTCGAAGTCCTTC		
Drogon 2" ITD	FW	GAATTAATACGACTCACTATAGGGAGAACACGTAACACGTGTAAATTCAACTTC		
Diagon SUTK	RV	GAATTAATACGACTCACTATAGGGAGACACATAACATATACATATTTATT		
	FW	GAATTAATACGACTCACTATAGGGAGAACTCCACTCGTTCTGTTTGCATTTG		
Diagon SUTK	RV	GAATTAATACGACTCACTATAGGGAGATGGTGTTTAACTTAGGGATAATTAGC		
COT	FW	TAA TACGACTCACTA TAGGGAGAAAGGTGA TAAA TGGCGAAACAAAA		
631	RV	TAATACGACTCACTATAGGGAGACAACATCAAGAGCGTCATACAACA		
Actoricos	FW	TAATACGACTCACTATAGGGAGAATGAACACGCCAGGTATAAG		
Asteriess	RV	TAA TACGACTCACTATAGGGAGA TATTGGAGCACGTCTCTTT		
DIk4	FW	TAATACGACTCACTATAGGGAGAATACGGGAGGAATTTAAGCAAGTC		
FIK4	RV	TAA TACGACTCACTA TAGGGAGA TTA TAACGCG TCGGAAGCAGTCT		
Ano2 CDS	FW	GAATTAATACGACTCACTATAGGGAGAATGTTTGTTCCCGAAACGGAGG		
Ana2 CDS	RV	GAATTAATACGACTCACTATAGGGAGACAGAGCCGCCAGATCACTCTTA		
Ana2 UTR		GAATTAATACGACTCACTATAGGGAGACAGATTCTCCCCGCTCGAATTTAATTCATCGGCAAATATAAACAAAT ACGCTCCAAATGTTTGTTCCCGAACCGAA		

2.9.4 siRNA in U2OS cells

U2OS cells were maintained in growth medium DMEM (1X) + GlutaMAX[™]-I (Gibco® Thermo Fisher Scientific, 31966-021) with antibiotics and FBS (Gibco® Thermo Fisher Scientific, 10500) at 37°C, 5% CO₂, in a humidified incubator; and were passaged after trypsination from the flask with 0.05% Trypsin-EDTA (1X) (Gibco® Thermo Fisher Scientific, 25300-054). For the siRNA experiment (Figure 2-3), 1x10⁵ cells were plated in 2ml of growth medium without antibiotics per well of a 6-well plate (Corning, 3516) on day 1, to reach 30-50% confluence before starting the siRNA experiment. On day 2, firstly, 125µl Opti-MEM® Medium I (Gibco® Thermo Fisher Scientific, 31985-047) and 7.5µl Lipofectamine RNAiMAX reagent (invitrogen[™] Thermo Fisher Scientific, 13778-030), and secondly, 125µl Opti-MEM® Medium I (Gibco® Thermo Fisher Scientific, 31985-047) and 25pmol siRNA were each mixed and incubated for 3 minutes at RT. The diluted siRNA was then added to the diluted Lipofectamine RNAiMAX reagent, mixed by pipetting, and incubated for 10 minutes at RT. In the meantime, the medium of the U2OS cells was replaced with medium without antibiotics for 10 minutes, followed by adding the siRNA-lipid complex mix to the cells. On day 3 (24 hours after transfection), the media was replaced with fresh complete media and 4µM Aphidicolin and 1.5mM Hydroxyurea were added to induce S-phase arrest of the cells. The cells were then fixed to sterile and 1x PBS-washed cover slides 72 hours after siRNA transfection by cold methanol. GoRab was depleted via three target siRNAs (Silencer® Select siRNAs, 4392420, IDs: s40927, s40928, s40929), and GFP siRNA (Silencer® Select siRNA, Ambion[™], Thermo Fisher scientific, AM4626) was used as a negative control. The cells were stained with anti-γ-tubulin (1:250, mouse, Sigma, T6557) and secondary antibody AlexaFluor® 594 donkey anti-mouse (1:333, Thermo Fisher Scientific, A21203) for centrosomes. When U2OS cells are blocked in S-phase by Aphidicolin and Hydroxyurea, DNA duplication and therefore cell division was prohibited, but centriole duplication still occurred as normal. This leads to an increase in the number of centrosomes within each cell under control conditions.

 Table 2-10 Summary of the three GoRab Silencer® Select siRNAs. Listed are the sense and antisense strand siRNAs of the GoRab Silencer® used.

GoRab siRNA	sense	antisense
ID s40927	CAGAGACCAUGAAACUAAATT	UUUAGUUUCAUGGUCUCUGCC
ID s40928	CCAUGAUGGUCACAACAAUTT	AUUGUUGUGACCAUCAUGGGA
ID s40929	CAGCAAAGCUAGAUAUACATT	UGUAUAUCUAGCUUUGCUGCA



Figure 2-3 Time line of treatment of U2Os cells to study centrosome numbers after GFP and GoRab siRNA. U2Os cells were seeded at time point zero; siRNA transfection was performed 24 hours after; followed by arrest of cells in S-phase from 24 hours later by adding 4µM Aphidicolin and 1.5mM HydroxyUrea to the cell culture; and final fixation of cells 48 hours later.

2.9.5 Standard error and t-test

2.9.5.1 Standard error

The standard error was calculated for experiments were centrosomes were counted. Normally, three data points were generated; for all *Drosophila* cells 3 times 200 different cells were counted and for U2OS cells 3 times 100 different cells were counted. Initially, the Sample Standard Deviation was calculated by the square root of the Variance, which is the squared differences from the Mean divided by the 'number of data points minus 1', with the Mean being the average of the data points. From there the Standard Error was calculated by dividing the Standard Deviation by the square root of the 'number of data points'. Data set: a, b, c

Mean: M = (a+b+c) / n (n=population)

Sample Standard Deviation: $\sigma = \sqrt{\left[\left((a-M)^2 + (b-M)^2 + (c-M)^2\right)/(n-1)\right]}$

Standard Error: SE = σ / \sqrt{n}

2.9.5.2 t-test

For statistical analysis the paired t-test was used. It compares the population means of two correlated samples. Samples are classes as significant if p<0.05; and are categorised into statistically significant with p<0.05 (*) or p<0.01 (**) and statistically highly significant with p<0.001 (***).

2.10 Alignments and predictions

2.10.1 Protein sequence alignments

For the alignment of protein sequences to study their homology/orthology, protein sequences were acquired from http://www.flybase.org and alignments were performed with Clustal Omega ²⁸⁴ on http://www.ebi.ac.uk/Tools/msa/clustalo/.

2.10.2 Predicted secondary structure

For proteins of unknown secondary structure prediction softwares were used to indicate for potential secondary structure characteristics from protein sequences. Used were 'psipred' ²⁸⁵

and 'coils server' ²⁸⁶ on http://bioinf.cs.ucl.ac.uk/psipred/ and http://www.ch.embnet.org/software/COILS_form.html respectively. The resulting 'windows number' in the latter were described in ²⁸⁶; in short the higher the window number, the better the distinction between coiled-coil and other regions.

2.10.3 Phosphorylation sites prediction

Generic phosphorylation site predictions were generated with the NetPhos 2.0 server on http://www.cbs.dtu.dk/services/NetPhos/. It generates neural network predictions for serine, threonine and tyrosine phosphorylation sites as was published in ²⁸⁷. Blotted are 'Phosphorylation potential' against the sequence position. A residue is predicted not to be phosphorylated if its 'phosphorylation potential' lies below the threshold.

Chapter 3

Physical interaction screen to elucidate protein interactions governing centriole duplication

3 Physical interaction screen to elucidate protein interactions governing centriole duplication

3.1 Introduction

Two genome wide dsRNAi screens in *Drosophila melanogaster* cell culture identified a total of eighteen proteins required for centriole duplication. Out of these, eleven, Asterless (AsI), Ana1, Ana2, Ana3, Bld10, Cep97, CP110, Plk4, Rcd4, Sas4 and Sas6 showed specific centriole localisation and are therefore likely to be directly involved in the process ^{131,288}. Many of these individual proteins are currently investigated and their role in centriole biogenesis is becoming clearer. However, still very little is known about the precise molecular mechanisms and the physical and functional interplay of these proteins in the pathway as a whole. It has been shown that the core proteins identified in *C. elegans* show similarities in their assembly and function in other systems, suggesting that the relationship between the centriole duplication proteins is conserved ^{90,289–292}. It is believed that Polo like kinase 4 (Plk4) is the functional homologue of Zyg-1 in insects and vertebrates, and that it is the key regulator of centriole duplication ^{83–85}.

In this chapter I wished to study and identify the physical interactions between the proteins AsI, Ana1, Ana2, Ana3, Bld10, Cep97, CP110, Plk4, Rcd4, Sas4 and Sas6 and how they act together to control centriole duplication. For this purpose, I have generated antibodies against most of these proteins and I have performed *in vivo* and *in vitro* assays to test for direct and indirect interactions between these proteins. It is my aim to analyse the relationship of the proteins involved in the complex centriole duplication network. For this purpose, I firstly analysed mass spectrometry data of the ProteinA purifications generated in our group by Cunha-Ferreira, Dr. Dzhindzhev, Psternak, Schneider and Weiskopf and generated further purifications from *Drosophila* cells expressing proteins of the centriole duplication process (section 3.2.1), followed by an *in vitro* interaction screen to supplement

the *in vivo* findings by identifying direct protein-protein interactions (section 3.2.2) and applying the additional method of yeast-2-hybrid interaction (section 3.2.3).

3.2 Results

3.2.1 An *in vivo* protein interaction network of centriole duplication proteins designed from studies by ProteinA affinity purification

The tight regulation of centriole duplication is important for the maintenance of genomic stability, but only little is known about its molecular regulation. Therefore, my aim is to determine and map the physical interactions within the centriole duplication protein network using both *in vivo* and *in vitro* approaches. In this chapter I revisit ProteinA affinity purifications undertaken in our group; carry out and analyse additional ProteinA purifications of centriole duplication proteins; and create an interaction network considering the localisation of these proteins at the centrosome (Figure 3-1). To achieve single step affinity purifications, I expanded cell lines each expressing a centrosomal protein fused to ProteinA. I used IgG-coated resin to purify the expressed tagged protein and other endogenous proteins bound to it.

3.2.1.1 Plk4 – a master regulator forms complexes with the majority of proteins involved in centriolar duplication *in vivo*

Plk4 is described as the master kinase in centriole duplication and so it was of interest to identify its partners and substrates. Therefore, I focused on re-analysing previous ProteinA affinity purifications of ProteinA-tagged Plk4 purified from cultured cells and analysed by mass spectrometry, performed by K. Weiskopf and Dr. Dzhindzhev (complete lists in Appendix A). Of the possible Plk4 interactors, Asterless was the most striking showing a high Mascot score when co-purified with Plk4, indicating that peptides derived from Asterless were abundant in the purification (Table 3-1A). This is significant because genetic analysis shows that overexpression or depletion of Asterless results in similar phenotypes to

overexpression and depletion of Plk4 92. In reciprocal purifications of Asterless tagged with ProteinA, Plk4 was also found as an interacting partner (Table 3-1B). Asterless was shown to recruit Plk4 to the centriole ⁹². In addition to Plk4, Sas4 was also identified as a binding partner of Asterless. This suggests that Asterless is required for centriole duplication to form a scaffold that binds Plk4 and Sas4 92,293,294. Such a scaffold would bring Plk4 close to Sas4 or other centriolar proteins, to allow for their phosphorylation by Plk4. The purifications of Plk4 tagged to ProteinA also identified centriolar proteins (Table 3-1 A). Components of zone 1: Bld10 and Ana2; components of zone 2: Ana1, Sas4 and Spd2; components of zone 3: Asterless and D-Plp; components of zone 4: Cnn and Spd2, and in zone 5: CP110. The localisation of Ana3, also found in the purification, remains unknown in the centrosome (Figure 3-1, locations according to ^{24,30}). The localisation of these proteins might be important for the characterisation of the precise role of Plk4 at the centrosome and in identifying its substrates. As Asterless is known to recruit Plk4 directly, I also re-analysed affinity purifications of Asterless from cultured Drosophila cells, to identify potential additional interactors of the Asterless scaffold ⁹². This identified Ana1, Bld10, D-Plp, Sas4, Spd2 and Plk4 (Table 3-1B). In summary, these purifications identify the proteins Ana1, Bld10, D-Plp, Sas4 and Spd2 in complex with Plk4 and Asterless. On the other hand, only Ana2, Ana3, Cnn and CP110 are specific in complex with Plk4 but not with Asterless.

Table 3-1 Mass spectrometry data from purifications of Plk4 (A) and Asterless (B) confirms centriole duplication proteins. ProteinA tagged Plk4 and Asterless were expressed and purified from *Drosophila* cell culture, followed by gel-free mass spectrometry analysis. The tables show the Mascot 'score' and 'number of peptides' of each according centriolar duplication and maturation protein identified in the purification data. OA, okadaic acid. MG132 treatment to inhibit proteasomal degradation. Complete lists in Appendix A.

A) Plk4 purifications

CG #	Score	# of peptides	Full name					
Act5-PrA-Plk4								
CG7186	3411	118	Plk4					
CG2919	636	25	Asterless					
CG33957	460	19	D-Plp					
CG4832	257	9	Cnn					
CG17081	147	5	Bld10					
CG10061	126	2	Sas4					
CG6631	95	2	Ana1					
CG14617	69	2	CP110					
CG17286	53	1	Spd2					
	рМТ	-PrA-Plk4 (MG132	:)					
CG7186	8544	205	Plk4					
CG2919	3542	148	Asterless					
CG33957	468	13	D-Plp					
CG4832	176	4	Cnn					
CG6631	160	4	Ana1					
CG17081	143	3	Bld10					
CG10061	53	2	Sas4					
	pMT-P	r A-Plk4+OA (MG1	32)					
CG33957	4029	116	D-Plp					
CG7186	3011	111	Plk4					
CG2919	1778	53	Asterless					
CG6631	1776	55	Ana1					
CG17081	1107	33	Bld10					
CG4832	927	22	Cnn					
CG10061	409	19	Sas4					
CG13162	175	3	Ana3					
CG8262	134	2	Ana2					

B) Asterless purifications

CG # Score		# of peptides	Full name				
Act5-PrA-Asl							
CG2919	2736	138	Asterless				
CG33957	772	29	D-Plp				
CG6631	229	11	Ana1				
CG17081	123	5	Bld10				
CG17286	97	3	Spd2				
CG7186	49	2	Plk4				
CG10061	52	1	Sas4				
		Act5-Asl-PrA					
CG2919	10717	465	Asterless				
CG33957	798	24	D-Plp				
CG6631	628	26	Ana1				
CG7186	224	9	Plk4				
CG17081	174	6	Bld10				
CG17286	87	4	Spd2				
CG10061	71	1	Sas4				
	Act	5-Asl (531-994)-PrA	١				
CG33957	542	13	D-Plp				
CG7186	512	20	Plk4				
CG2919	432	41	Asterless				
CG17081	188	4	Bld10				
CG6631	69	3	Ana1				
CG10061	38	1	Sas4				

3.2.1.2 *In vivo* studies of the centriole duplication proteins Ana2, Asterless, Cep97, CP110, Plk4, Rcd4 and Sas4 suggests a protein network

Additional ProteinA affinity purifications and mass spectrometry studies were then performed with Ana1, Ana2, Bld10, Cep97, CP110, Rcd4, Sas4 and Sas6, to search for candidates for their interacting proteins. The affinity purified complexes were analysed via gel free mass spectrometry. In the majority of cases, proteins were tagged with ProteinA on both their N-and C-terminus, to exclude possible interference of the affinity tag with binding. The affinity purifications of Ana1, Bld10 and Sas6 tagged to ProteinA did not identify any candidates involved in centriole duplication. However, the following proteins were found complexed to other centriole proteins: 1.) Ana2 purification identified Ana1, Plk4, Polo and Sas4; 2.) Sas4 purification identified Ana2, D-Plp and Polo; 3.) Rcd4 purification identified Ana2 and Ana3; 4.) Cep97 purification identified Ana2, CP110, D-Plp and Polo; and 5.) CP110 purification identified Cep97, Cnn, D-Plp and Polo (Table 3-2).

Interestingly, Ana2 was identified in complex with Sas4 and Plk4, and in the reciprocal ProteinA purifications the proteins Sas4 and Plk4 were identified in complex with Ana2, which strengthens the confidence of a potential interaction of Ana2 with Sas4 and Plk4 (Table 3-1, Table 3-2).

It is also noticeable that treatment of the *Drosophila* cells expressing Sas4 with okadaic acid seems to stabilise Polo in complex, as it was not identified when the cells were untreated. Thus Polo's association with Sas4 might be phospho-dependent.

Similarly, only when cultured *Drosophila* cells expressing Cep97 were treated with okadaic acid, was CP110 found in the complex. This suggests that CP110 complexes with Cep97 in a phosphorylation-dependent manner.

Based upon these interactions I have constructed an interaction network between these proteins positioned at their known sites within the 3D structure of the centrioles as described by 3D-SIM (Figure 3-1) ^{24,30}.

Table 3-2 Mass spectrometry data of centriole duplication proteins purified from *Drosophila* cell culture expressing ProteinA tagged Ana2, Sas4, Rcd4, Cep97 and CP110. Shown are the Mascot 'score' and 'number of peptides' identified of centriolar duplication and maturation proteins that were analysed in the purifications by mass spectrometry. OA, okadaic acid. MG132 treatment to inhibit proteasomal degradation. Complete lists in Appendix A.

CG #	Score	# of peptides	Full name				
pMT-Ana2-PrA (MG132)							
CG8262	4562	80	Ana2				
CG10061	24	1	Sas4				
	pMT-Ana2-PrA+OA (MG132)						
CG8262	11127	177	Ana2				
CG6631	24	1	Ana1				
	oAct5-PrA	A-Ana2 + pMT-Plk	4 +OA				
CG8262	7098	138	Ana2				
CG12306	41	1	Polo				
CG7186	32	1	Plk4				

CG #	Score	# of peptides	Full name					
pMT-Sas4-PrA (MG132)								
CG10061	Sas4							
	pMT-Sas4-PrA+OA							
CG10061	24851	848	Sas4					
CG12306	281	9	Polo					
CG33957 132 2 D-Plp								
CG8262	123	2	Ana2					

CG #	Score	# of peptides	Full name					
pMT-Rcd4-PrA (MG132)								
CG17295	698	32	Rcd4					
CG13162	199	8	Ana3					
CG8262 70		1 Ana2						
	pMT-Rcd4-PrA+OA (MG132)							
CG17295	438	17	Rcd4					
CG13162	207	8	Ana3					

CG #	Score	# of peptides	Full name				
pMT-PrA-Cep97+OA (MG132)							
CG3980	1465	Cep97					
CG14617	7 178 5 CP110						
CG33957	44	1	D-Plp				
	pMT-Cep97-PrA (MG132)						
CG3980	7109	208	Cep97				
CG8262	235	3	Ana2				
CG12306	41	1	Polo				
	pMT-Ce	p97-PrA+OA (MG	132)				
CG3980	16796	437	Cep97				
CG14617	330	11	CP110				
CG12306	31	1	Polo				

CG #	Score	# of peptides	Full name				
pMT-PrA-CP110 (MG132)							
CG14617	2046	46	CP110				
CG33957	148	5	D-Plp				
CG12306	56	1	Polo				
	pMT-PrA-CP110+OA (MG132)						
CG14617	1506	33	CP110				
CG4832	19	1	Cnn				
	pMT-CF	110-PrA+OA (MG	132)				
CG14617	2607	72	CP110				
CG12306	104	5	Polo				
CG3980	84	3	Cep97				



Figure 3-1 *In vivo* connections of centriolar duplication and maturation proteins and their localisation within the centrosome. (mass spectrometry data from Cunha-Ferreira, Dzhindzhev, Psternak, Schneider and Weiskopf; localisation studies from Fu^{24,30}). Localisation of Ana3 and Rcd4 is unknown. Polo and Spd2 are localised in zone 2 and 4. Black lines connect proteins involved in centriole duplication. Blue lines connect to proteins involved in centriole maturation. Asl interaction with Plk4 and Sas4 was shown in ⁹².

As the localisation of Rcd4 within the centrosome had not been described, I depleted the protein by RNAi in cultured *Drosophila* cells. Cells were fixed and stained to reveal the centrosome marker D-Plp. This clearly showed that the knock down of Rcd4 over a 16 day interval resulted in a reduction of the number of centrosomes (Figure 3-2; 52.5% +/-2.5% of cells lost their centrosomes). The effect of Rcd4 depletion was less efficient than the positive control, depletion of Asterless, which causes loss of almost all centrosomes after 16 days of RNAi (90.8% +/-0.3%) but significantly greater than control GST RNAi (9.6% +/-1.8%). This confirms the findings of Dobbelaere *et al.* ¹³¹ that Rcd4 is required for centrole duplication.



Figure 3-2 Effect of Rcd4 depletion on centrosome numbers in *Drosophila* **cell culture.** Rcd4 RNAi, Asterless RNAi (positive control) and GST RNAi (negative control) for 16 days with knock down every 4 days. High loss of centrosomes after Rcd4 and Asterless depletion. 3x200 cells; error bars represent standard error.

3.2.2 *In vitro* protein interaction assays confirm and expand interactions between centriole duplication proteins identified *in vivo*

To attempt to determine which of the above interactions might be direct I chose to carry out *in vitro* interaction assays. To this end, I asked whether the eleven centriolar duplication proteins (Ana1, Ana2, Ana3, AsI, Bld10, Cep97, CP110, Rcd4, Sas4, Sas6 and Plk4) and the pericentriolar proteins Cnn, D-Plp, Polo and Spd2, involved in the centrosome maturation process, would interact. For this study, I generated one putative partner that was ³⁵S-Methionine-labelled by coupled transcription-translation reactions and the other partner expressed as a fusion in *E. coli* (section 2.8.1, section 2.5.1). The binding complex was subjected to SDS-PAGE, followed by autoradiography. I simultaneously analysed a negative control (the tag alone bound to resin) and 1% input of the total radioactively labelled protein. I successfully expressed and purified eight tagged full length proteins (Ana2, Asl, Bld10,

Cep97, Rcd4, Sas4, Sas6 and Plk4), and two fragments of CP110 (aa1-400 and aa360-570) for which the pENTR clones were kindly shared with me by Dr. Fu. I was not successful in my cloning strategy for Ana3. Moreover Ana1 and CP110 (aa571-666) could not be expressed successfully. I compared the autoradiographic signals for the protein interactions with the input and the corresponding negative control, and categorised the strength of the signal as: no interaction (-), weak interaction (+), interaction (++) and strong interaction (+++), with "d" indicating, that the strongest signal was observed as degraded protein (individual autoradiographic signals in Appendix B). I excluded tagged Sas6 and tagged Bld10 from the analyses, as these proteins exhibited strong non-specific binding to other proteins, most likely due to aberrant folding of Sas6 and Bld10. I was still able to analyse the reciprocal experiment following the binding properties of ³⁵S-Methionine labelled Sas6 and Bld10. All interactions are summarised in Table 3-3^{24,30}. The strongest direct protein interactions observed in vitro (+++) are highlighted in blue in Table 3-3. These are also indicated in relation to the localisation of the potential partner proteins within the centrosome in Figure 3-3; where black connecting lines highlight protein interactions that were also found in vivo (section 3.2.1); red connecting lines highlight strong protein interactions identified only in vitro. Good in vitro protein interactions (++) that verify in vivo protein interactions are highlighted in green in Figure 3-3.

In summary, the *in vitro* analyses of direct protein interactions suggest that some proteins found in complex *in vivo* correspond to direct interactions, namely Ana2 with Sas4, Ana2 with Plk4, CP110 with Polo, Asl with Plk4, Asl with Spd2 as well as Asl with Sas4 ⁹². Additional interactions were only identified *in vitro*. These include CP110, which localises in the cap of the centriole (zone 5) that interacts strongly with Sas4 (zone 2) and vice versa *in vitro*. Additionally, CP110 is also linked to Ana3 (zone 1), Sas6 (zone 1) and Ana1 (mainly zone 2) by an *in vitro* interaction; and Sas4 (zone 2) is linked to Ana1 (mainly zone 2) and Rcd4 by direct *in vitro* interaction. Figure 3-3 also highlights potential protein interactions in green that were identified as a good interaction *in vitro* (++) and were also found associated in complex *in vivo*. These include interactions of Plk4 with Ana3, Bld10, CP110, D-Plp and Sas4; Ana2 with Cep97, Polo and Rcd4; Sas4 with D-Plp, Plk4 and Polo; CP110 with Cep97

and Cnn; Rcd4 with Ana3; and Cep97 with Ana2, Polo and CP110 (Table 3-1, Table 3-2, Figure 3-3). The assays also revealed strong interactions of Ana2, Rcd4 and CP110 with themselves but should be studied more carefully in future.

Table 3-3 Direct interaction levels of centriolar proteins using *in vitro* binding assays. Binding assays of radioactively labelled protein and tagged full length protein. Signals were categorised into no interaction (-), weak interaction (+), good interaction (++) and strong interaction (+++, blue background), with "d" indicating degraded protein size. The zones relate to the different layers of centrioles as described in ^{24,30}; ? indicates unknown protein localisation in the centrosome. GST-CP110 1/3 (aa1-400), GST-CP110 2/3 (aa360-570), D-Plp-N (aa1-1603), D-Plp-C (aa1604-2727). Individual autoradiographic signals in Appendix B.

			tagged protein							
		Zone	GST- Ana2	Asl- GST	GST- Cep97	GST- CP110 1/3	GST- CP110 2/3	MBP- Pik4	GST- Rcd4	GST- Sas4
	Ana1	2	-	+	+	(+)	+++	(+)	+d	+++
	Ana2	1	+++	-	++	+	++	++	+	++
	Ana3 Exon1	?	(+)	(+)	+	(+)	++	++	+	(+)
	Ana3 Exon2	?	++	++	++	+++	+++	++	++	++
ein	Asl	3	+	++	++	++	++	+++	++	++
ī	Bld10	1	+	+	+	(+)	++	++	-	++
d p	Cep97	5	++	++	+	-	++	+	(+)	++
elle	CP110	5	++	++	++	+	+++	++	++	+++
lab	Plk4	3	+++	+++	(+)d	(+)d	(+)d	++	- d	++d
ne	Rcd4	?	++	++	++	++	++	++	+++	+++
oni	Sas4	2	+++	+++	++	+++	++	++	++	++
ethi	Sas6	1	(+)	(+)	+	+	+++	(+)	+	++
ž										
35 S	Cnn	3, 4	(+)	-	+	-	++	-	(+)	+
	D-Plp-N	3	-	+	+	(+)	(+)	++	-	++
	D-Plp-C	3	-	-	+	-	-	-	-	-
	Polo	2, 4	++	++	++	++	+++	-	++	++
	Spd2	2, 4	++	+++	++	-	++	-	(+)	-



Figure 3-3 The protein network of centriole duplication after *in vivo* and *in vitro* interaction studies. Black connections stand for protein complexes analysed *in vivo* and confirmed as strong interactions *in vitro* (+++). Green lines stand for *in vivo* complexes confirmed as a good interaction *in vitro* (++). Red lines represent interactions only detected *in vitro* but with a strong autographic signal (+++).

3.2.3 Confirmatory studies using the Yeast-2-Hybrid Assay

The *in vivo* and *in vitro* analyses of complexes that I have described each have their advantages and disadvantages. The advantages of the *in vitro* method are its high sensitivity and its detection of direct interactions. On the other hand, the *in vivo* method detects proteins which form complexes between proteins that are correctly folded due to post-translational modifications. The *in vitro* method has the drawback that some protein interactions could only be observed in one direction but not reciprocally; for example: bacterially expressed Plk4 interacted well with ³⁵S-Methionine-labelled Rcd4 whereas bacterially expressed Rcd4 did not interact with ³⁵S-Methionine-labelled Plk4. The *in vivo*

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method is much less sensitive than in the in vitro approach. Thus certain interactions could only be detected in vitro but were not represented in complexes present in vivo. This could represent inaccessibility of a complex or formation of a complex at a specific time during the centriole duplication cycle. The yeast-2-hybrid system combines elements of the in vitro and in vivo methods, as it tests for direct protein-protein interactions but is performed within a eukaryotic cell and allows for post-translational protein modifications. I therefore applied the yeast-2-hybrid system in an attempt to confirm or deny protein interactions that were detected in only one of the previously applied methods. Methodically, the yeast-2-hybrid system is based on the activation of the GAL promotor by its transcription factor, which is split into a Binding Domain (BD) and an Activation Domain (AD). Each protein is tagged with these domains individually. Hence, when two proteins interact directly, they bring the AD and BD together, forming the functional transcription factor and activating the GAL4 transcription (section 2.7). The use of X- α -GAL gives a visual indication (colonies turn blue after up to 6 days at 30°C when a protein interaction occurs), if the two proteins interact directly and activate the GAL promotor. For the yeast-2-hybrid analysis, I generated 11 proteins in pGAD424 tagged with the GAL4 AD (Ana2, Asl, Bld10, Cep97, CP110, Plk4, Rcd4, Sas4, Sas6, Polo and Spd2), five proteins in pBGT9 tagged with the GAL4 BD (Ana2, Bld10, CP110, Sas4 and Sas6), two negative controls (AD-only, BD-only), and as positive controls I used BD-tagged Nnf1a and AD-tagged Mis12, and vice versa. Mis12 and Nnf1a are two interacting proteins in the Mis12 complex of the kinetochore ²⁹⁵. All constructs were tested for autoactivation of the GAL promotor, of which only BD-Asl tested positive for autoactivation. Hence, only AD-Asl was used for interaction studies of Asterless.

My hybrid screen focused on centriolar proteins that localise to zone 1 and zone 2 of the centrosome and identified protein-protein interactions (highlighted in blue in Table 3-4). These confirm protein interactions found *in vitro* and in *in vivo* complexes (***), confirm protein interactions only found *in vitro* (a equals strong interaction (+++); b equals good interaction (++)), and suggest additional protein interactions (blue filled cells only). These interactions are summarised in relation to their localisation within the centrosome in Figure 3-4. Interestingly, the yeast-2-hybrid method confirms the interactions of Ana2 with Plk4,

Sas4 and Polo, as previously described by the *in vitro* and *in vivo* tests (section 3.2.1, section 3.2.2). These are highlighted by black connection lines in Figure 3-4. The yeast-2-hybrid also confirms strong protein interactions (+++) observed *in vitro* of CP110 and Sas6, and the strong interaction of CP110 and Ana2 with themselves (marked 'a' in Table 3-4), and additionally confirming some good protein interactions observed *in vitro* (++) of Sas4 with itself, Sas6 with Sas4, and Spd2 with Ana2, Cep97 and CP110 (marked 'b' in Figure 3-4). The yeast-2-hybrid method also identified additional protein interactions which were not described in section 3.2.1 and 3.2.2. These include Sas6 with Ana2, Ana2 with Bld10, Sas6 with itself, Sas6 with Polo and Spd2, and Bld10 with Spd2 which are highlighted in orange in Figure 3-4.

Table 3-4 Confirmation of protein interactions found *in vivo* and/or *in vitro* applying the yeast-2-hybrid system. pGBT9 containing the GAL4-BD. pGAD424 containing the GAL4-AD. Blue highlighted boxes: observed protein interactions applying the yeast-2-hybrid method. White boxes: no protein interactions observed by yeast-2-hybrid. Additional symbols *** for interactions previously detected *in vivo* and *in vitro* (as good (++) or strong (+++) interactions); 'a' for interactions previously detected as strong interactions *in vitro* only (+++); 'b' for interactions previously detected as good interactions *in vitro* only (++).

		pGBT9					
		Ana2	Bld10	CP110	Sas4	Sas6	Spd2
pGAD424	Ana2	а			***		b
	Asl						
	Bld10						
	Cep97						b
	CP110			а		а	b
	Plk4	***					
	Rcd4						
	Sas4	***			b		
	Sas6				b		
	Polo	***					
	Spd2			b			



Figure 3-4 Diagram summarising the protein interactions detected by yeast-2-hybrid and confirming protein interactions identified by *in vivo* and *in vitro* methods. Black lines confirm proteins found in complex *in vivo* and as direct protein interactions *in vitro* (strong and good protein interactions). Red lines confirm interactions previously detected by strong or good *in vitro* interaction only. Orange lines indicate protein interactions newly detected by yeast-2-hybrid or previously identified as a (very) weak *in vitro* interaction.

3.3 Discussion

The studies I report in this chapter suggest that Plk4, master regulator of centriole duplication, directly or indirectly interacts with and regulates proteins localised in complex present in vivo within every zone of the centrosome. Additional ProteinA affinity purifications indicate a complex network of interacting proteins that participate in centriole duplication and centrosome maturation proteins (Figure 3-1). The in vitro interaction studies I carried out to identify direct protein-protein interactions gave some suggestions on functionally important interactions. It was previously shown that Asterless functions as a scaffold to recruit Plk4 and Sas4 to the daughter centriole, with the Asterless/Plk4 interaction being necessary for centriole duplication ⁹². Significantly, Plk4 localises in the outer layer of the centrosome (zone 3) and Sas4 localises in the inner layer (zone 2), which goes in line with the recent discovery that their interacting protein partner Asterless localises mainly to zone 3 but also partially to zone 2 30. I was able to demonstrate these interactions as direct protein interactions in vitro. Plk4 interacts strongly with Asterless and vice versa; additionally, Asterless interacts with Sas4 and vice versa in the performed binding assays (Table 3-3). Hence, the in vitro method appears reproducible and reliable, and sheds further light on the finding of interactions in vivo. As seen in Figure 3-1, Plk4's partners are present in every zone of the centrosome, implying potentially diverse regulatory roles. Alternatively the large number of centriole duplication proteins purifying with Plk4 could indicate direct or indirect interactions occurring in the cytoplasm prior to incorporation into the centriole; for example Bld10 localises to zone 1 in the centriole but its interaction with Plk4 has not previously been described. At the time these in vivo analyses were carried out, neither direct substrates of Plk4 nor the timing of their interactions were known. Recently, it was discovered that Ana2 is a substrate of Plk4 and must be phosphorylated by Plk4 to allow for interaction and recruitment of Sas6 to the site of procentriole formation (Chapter 4)²⁹⁶. Significantly, Ana2 and Plk4 were detected in the reciprocal in vivo purifications (Table 3-1, Table 3-2) but with a low Mascot score and a low 'number of peptides'. The reason for this is not clear but could be explained if the interactions of the kinase with its substrates are only transitory. The interaction of Plk4 and Ana2 was confirmed as a direct interaction *in vitro* and additionally confirmed by the yeast-2-hybrid method.

Plk4 localises in zone 3 of the centrosome together with D-Plp and Asterless. The high Mascot scores of D-Plp in the Plk4 and Asterless purifications suggest a robust complex of these proteins. D-Plp is found predominantly on the mother centriole for most of the duplication cycle. D-Plp's C-terminus is localised at the centriole wall, from where it radiates outwards into the matrix, D-Plp could be a possible candidate for the recruitment of Asterless to the centriole ^{24,27}. Although recently it was shown that Bld10, Ana1 and Asterless are recruited sequentially in the centriole-to-centrosome conversion, that Asterless and Ana1 interact with each other, and that depletion of Ana1 leads to failure of Asterless and D-Plp localisation to the metaphase daughter centriole ³⁰. This suggests that D-Plp might be recruited to the centriole upstream of Asterless. Additionally, D-Plp has been shown to interact with Sas4 during PCM recruitment but its role in centriole duplication still needs to be investigated further ^{137,297}.

On the other hand, in *C. elegans*, it was shown that Sas4 is recruited to the centriole by Sas5 (the Ana2 homologue) ^{53,91}. In accord with this I observed an interaction of Sas4 and Ana2 *in vivo*, *in vitro* and by yeast-2-hybrid, suggesting the possibility of a similar role of the Sas4/Ana2 interaction in *Drosophila*.

Of additional interest is the observation that Sas4 interacts directly with Cep97, CP110 and D-Plp *in vitro* but I identified only Cep97 and CP110 in complex with D-Plp *in vivo*. Sas4 has been associated with the process of PCM recruitment ^{11,20,25}. And a link to the cartwheel is supported by Sas4's interaction with proteins in zone 1 (Ana2) and zone 3 (Asterless, D-Plp) of the centrosome. In human cell culture, overexpression of CPAP (Sas4 homologue) leads to increased centriole length by enhanced accumulation of centriolar tubulin ^{38–40}. Elongated centrioles have also been observed after depletion of CP110, suggesting that CPAP and CP110 have antagonistic functions during centriole elongation and control centriole length ³⁹, and Cep97 and CP110 function in cilia formation and length regulation ^{79,81}. On the other hand, in *Drosophila*, CP110 seems to restrict centriole length in a microtubule-depolymerising kinesin-like protein 10A (KLP10A) dependent manner ^{80,82}.

Spd2 was also found in complex with Plk4 and Asterless, a finding of interest, as Spd2 exhibits a dual-localisation in zone 2 of the centrosome during interphase and mitosis, but additionally localises in zone 4 (PCM) after the onset of mitosis. This is also the case for Polo, which localises in zone 2 of the centrosome during interphase but also largely localises to zone 4 from metaphase onwards, where it is required for PCM recruitment ²⁴. In contrast to Spd2, Polo was also identified in complex with centriole duplication proteins that are in the core of the centrosome in zone 1, 2 and 5 (Ana2; Sas4; and Cep97 and CP110 respectively). This was confirmed by *in vitro* interaction studies, and the yeast-2-hybrid method confirmed the Polo and Ana2 interaction. Polo was only identified in the Sas4 purification when the cells were treated with okadaic acid, suggesting a potential phosphorylation-dependency of the Sas4/Polo interaction.

The connection between Ana3 and Rcd4 is of interest, as pilot experiments have linked Rcd4 to zone 1 or zone 5 by structured illumination microscopy on cultured cells expressing GFP-tagged Rcd4 (data not shown; cell lines by Mr Meghini; microscopy by Dr. Tzolovsky). The initial data suggests that Rcd4 recruitment to the centriole starts in interphase and reaches similar protein levels as Sas6 in metaphase (data not shown). Further studies will conclude the localisation of Rcd4 and give suggestions for Ana3 localisation.

The yeast-2-hybrid method confirms *in vitro* findings of potential self-interactions of Ana2, CP110 and Sas4. This accounts with the homodimerisation potential of Sas6 with itself, which has since been described in structural studies but was not detected in previous *in vivo* nor *in vitro* analyses ^{63,69}. Most interestingly, the interaction of Ana2/Sas6 was found using yeast-2-hybrid but not by *in vivo* and *in vitro* approaches. Significantly, at the time of the experiments, it was known that the interaction of *C. elegans* Sas5 and Sas6 is necessary in centriole duplication ⁵³ but we showed only later that they also interact in *Drosophila* but in a manner dependent on Plk4 phosphorylation of Ana2 (Chapter 4) ²⁹⁶. This was also confirmed in human cell culture for STIL and Sas6 ^{95,299,300}. The interaction of Ana2 and Bld10 was only detected by yeast-2-hybrid but not by *in vivo* or *in vitro* binding tests. Both proteins localise to zone 1 of the centriole and could possibly contribute to the formation or stability of the 9-fold

symmetry of the cartwheel/centriole. Further studies need to confirm or dismiss the interaction of Bld10 and Ana2.

In conclusion, the studies I describe in this chapter have analysed proteins of centriole duplication and maturation that form complexes *in vivo* and were shown to interact directly by *in vitro* binding assays. Proteins that were found in complexes *in vivo* but did not interact *in vitro* might be connected indirectly. On the other hand, strong interactions found *in vitro* but that were not reflected in *in vivo* complexes could represent transient interactions in the centriole duplication cycle. The additional application of the yeast-2-hybrid method combines the advantages of testing for direct protein interactions in a system that allows for post-translational modifications. It confirmed protein interactions that were identified both *in vivo* and *in vitro*, and also protein interactions that were identified by the more sensitive *in vitro* approach only.

In summary, the application of *in vivo*, *in vitro* and yeast-2-hybrid methods in a screen to identify interactions of centriole duplication proteins has proven to be a guide to further studies rather than providing totally reliable conclusions. Each method in itself can be a strong and reliable method but needs to be accompanied by additional and more specific evidence of functional interaction to be conclusive.

Chapter 4

Interaction of Ana2 and Sas6 – Mediated by Plk4 phosphorylation of Ana2 and enabling procentriole formation
4 Interaction of Ana2 and Sas6 – Mediated by Plk4 phosphorylation of Ana2 and enabling procentriole formation

4.1 Introduction

Five proteins have been described to be essential in the centriole duplication pathway in *C. elegans*; Spd2, Zyg-1, Sas6, Sas5 and Sas4 ^{16–20,22,23,72,301}. My attempt to define the direct protein interactions of the *Drosophila* homologues and further centriole duplication proteins (Chapter 3) did not give the expected understanding how these *Drosophila* centriole duplication proteins interact with each other. Thus they gave little insight into molecular mechanisms underlying centriole duplication. The similarities of the core proteins identified in *C. elegans* in their assembly and function in other systems indicates that interactions between centriole duplication proteins are conserved ^{90,289–292}. The *Drosophila* proteins Ana2 and Sas6 were of particular interest and here I focus on their interactions. Their *C. elegans* homologues, Sas5 and Sas6, are recruited together to the procentriole, after Spd2 mediates recruitment of Zyg-1 ^{114,302}. However, how *Drosophila* Ana2 and Sas6 might interact was not clear. The substrates of the master kinase of centriole duplication Plk4 were also unknown. As in *C. elegans*, Zyg-1 is recruited upstream of the Sas5-Sas6 complex, I asked whether Ana2 and Sas6 interact, if they are substrates of the Plk4 kinase and function together in the centriole duplication process.

4.2 Results

4.2.1 Plk4 directly interacts with and phosphorylates Ana2 but not the centriole cartwheel protein Sas6

The recruitment of centriole duplication proteins is well described in *C. elegans* with Spd2 recruiting Zyg-1, the Plk4 homologue, followed by recruitment of Sas5 and Sas6 to the nascent procentriole, and recruitment of Sas4 for microtubules assembly ^{53,91}. In *Drosophila melanogaster*, the protein recruitment hierarchy of centriole biogenesis is similar to *C. elegans* but with some differences. Rather than Spd2, Asterless (Asl), a protein not present in *C. elegans*, recruits Plk4, the Zyg-1 homologue to the procentriole ⁹². In human cells, both Cep152 and Cep192, the homologues of Asterless and Spd2 respectively cooperate in Plk4-recruitment in centriole biogenesis ⁹³. One question still remaining is what ensures the timely and functional recruitment of the *Drosophila* homologues of Sas5 (Ana2), Sas6 and Sas4 to the pro-centriole, especially in the light of Plk4s' characterisation as the master kinase for centriole duplication. We know that Plk4 is recruited to the centriole by Asterless and that Asterless interacts with Sas4 ⁹². But despite this knowledge, we do not know the critical substrates that are phosphorylated by Plk4 during centriole duplication.

4.2.1.1 Ana2 and Plk4 interact *in vitro* but neither shows binding with Sas6

To address the above questions, I first attempted to determine which centriole proteins interact with each other during centriole duplication in *Drosophila*. Therefore, I performed an *in vitro* interaction screen in which I expressed tagged centriole duplication proteins (with MBP or GST) in *E. coli* and purified them on resins to determine whether they would interact with individual ³⁵S-Methionine-labelled centriole duplication proteins produced in an *in vitro*

transcription-translation system. This allowed me to directly test whether two proteins bind each other by combining a) protein bound to resin with b) ³⁵S-Methionine-labelled protein in an *in vitro* interaction assay (section 2.8.1). The resin was then washed and subjected to SDS-PAGE, directly followed by protein transfer onto nitrocellulose membrane and autoradiography at -80°C. Such experiments revealed that Plk4 and Ana2 interact directly with each other *in vitro* (Figure 4-1). The autoradiogram in Figure 4-1A shows 1% input of ³⁵S-Methionine labelled Ana2 (lane 1) and the analysed interaction complexes of MBP and MBP-Plk4 with ³⁵S-Methionine-labelled Ana2 (lane 2 and 3 respectively). ³⁵S-Methioninelabelled Ana2 does not interact with MBP alone. Therefore, the observed signal with MBP-Plk4 is due to direct interaction of Ana2 with Plk4. The reciprocal assay is shown in Figure 4-1B and confirms the observations from Figure 4-1A. The autoradiogram in Figure 4-1B shows 1% input of ³⁵S-Methionine-labelled Plk4 (lane 1) and the interaction complexes of GST and GST-Ana2 with ³⁵S-Methionine-labelled Plk4 (lane 2 and 3 respectively). Plk4 does not interact with GST but the detected signal of ³⁵S-Methionine-labelled Plk4 with GST-Ana2 confirms that Plk4 directly interacts with Ana2 *in vitro*.



Figure 4-1 Ana2 and Plk4 protein interact directly *in vitro*. (A) MBP and MBP-Plk4 immobilised on resin were incubated with ³⁵S-Methionine-labelled Ana2 in an *in vitro* binding assay, subjected to SDS-PAGE and autoradiography. (B) GST and GST-Ana2 immobilised on resin were incubated with ³⁵S-Methionine-labelled Plk4 *in vitro*, subjected to SDS-PAGE and autoradiography. Autoradiograms show that Ana2 is found in complex with Plk4 (A) and Plk4 is found in complex with Ana2 (B).

The *in vitro* interaction assays shown in Figure 4-1 show that Plk4 and Ana2 interact directly with each other. It is known from *C. elegans*, that Sas5 and Sas6 are recruited to the

centriole after Zyg-1 recruitment ^{53,91}, with Ana2 and Sas6 being the respective homologues in *Drosophila*. This raises the question of whether *Drosophila* Sas6 can interact with Plk4 or Ana2. To address this, I applied the direct binding assay as described above using ³⁵S-Methionine-labelled Sas6 and MBP or MBP-Plk4 (Figure 4-2 A) and with GST or GST-Ana2 (Figure 4-2 B). I found no direct interaction of Sas6 with either of the two proteins, either with Plk4 or the negative control MBP (Figure 4-2A) or Ana2 or the negative control GST (Figure 4-2B).



Figure 4-2 Plk4 and Ana2 proteins do not bind Sas6 directly *in vitro.* ³⁵S-Methioninelabelled Sas6 was incubated with MBP and MBP-Plk4 bound to resin (A) and GST and GST-Ana2 bound to resin (B). 2% ³⁵S-Methionine-labelled Sas6, as input, and the resin complexes were subjected to SDS-PAGE and autoradiography. The autoradiograms show that Sas6 was not associated with Plk4 (A) nor with Ana2 (B).

4.2.1.2 Plk4 phosphorylates itself and Ana2 in vitro but not Sas6

Initially, I expressed and purified MBP-Plk4-T172E-K43M and MBP-Plk4-T172E, the Nterminal MBP-tagged kinase dead and active form of Plk4 respectively. The expression constructs for MBP-Plk4-T172E-K43M and MBP-Plk4-T172E were generated by Dr. Dzhindzhev. MBP-Plk4-T172E carries a mutation at aa172 from T (Threonine) to E (Gutamic acid), located in the T-loop within the cryptic polo box of Plk4. MBP-Plk4-T172E-K43M carries an additional mutation at aa43 from K (Lysine) to M (Methionine), which is located in the kinase domain of Plk4 and corresponds to the kinase dead Plk4 version. Plk4 is known to auto-phosphorylate in a self-regulatory fashion ^{107,109}. This autophosphorylation is also observed with MBP-Plk4, as a bandshift of the MBP-Plk4 protein can be observed when the protein is analysed on SDS-PAGE. To test if the purified batch of MBP-Plk4-T172E protein is an active Plk4 form and has phosphorylation ability, I incubated MBP-Plk4-T172E with lambda-phosphatase buffer and analysed its mobility on a SDS-PAGE in comparison to a) the active version treated with lambda phosphatase and b) the kinase dead version MBP-Plk4-T172E-K43M (Figure 4-3). A protein shift can be observed with MBP-Plk4-T172E treated with lambda phosphatase (lane 4) and MBP-Plk4-T172E-K43M (lane 1), confirming that MBP-Plk4-T172E is active and auto-phosphorylates. MBP-Plk4-T172E treated with lambda phosphatase (lane 4) has a similar mobility to kinase dead MBP-Plk4-T172E-K43M (lane 1). Thus the mobility shift between MBP-Plk4-T172E-K43M and MBP-Plk4-T172E results from auto-phosphorylation of the latter; and MBP-Plk4-T172E is an active form of Plk4 which was used in subsequent experiments.



Figure 4-3 MBP-PIk4-T172E auto-phosphorylates but kinase dead MBP-PIk4-T172E-K43M does not. SDS-PAGE showing bandshift due to auto-phosphorylation of MBP-PIk4-T172E compared to the kinase dead MBP-PIk4-T172E-K43M. Bandshift and phosphorylation of MBP-PIk4-T172E is reverted to the level of kinase dead MBP-PIk4-T172E-K43M after treatment with lambda-phosphatase.

Experiments in *C. elegans* have shown that Sas5 (Ana2 homologue) and Sas6 are recruited to the procentriole after Zyg-1 (Plk4 homologue) ^{53,91}; that the recruitment of Sas6 to the

procentriole is independent of Zyg-1 (Plk4 homologue); and that the kinase is necessary for the maintenance of Sas6 at the centriole which is achieved by Zyg-1 mediated phosphorylation of Sas6 at Ser123¹¹³. To study whether Ana2 or Sas6 are substrates of Plk4 phosphorylation in centriole duplication, I applied a similar binding assay as above. I incubated active MBP-Plk4 kinase with several centriolar proteins, which were expressed in *E. coli* and purified onto resin before addition of ³²P-γ-ATP in kinase buffer. The proteins tested as potential substrates were MBP-Ana2 and MBP-Sas6; MBP was used as a negative control. After incubation, the resins were washed and subjected to SDS-PAGE; the gel was dried and exposed at -80°C. The autoradiograms showed that MBP-Ana2 but neither MBP nor MBP-Sas6 are Plk4 substrates.



Figure 4-4 Active Plk4 phosphorylates Ana2 but not Sas6. Coomassie stained SDS-PAGE gel and correlating autoradiogram. SDS-PAGE shows MBP, MBP-Ana2 and MBP-Sas6, following incubation with active MBP-Plk4 and ³²P-γ-ATP. Autoradiogram shows radioactive signal only for MBP-Ana2, that was phosphorylated directly by active MBP-Plk4. MBP and MBP-Sas6 were not phosphorylated by active Plk4.

After showing that N-terminally MBP-tagged Ana2 is a substrate of Plk4 (Figure 4-4), I tested N-terminally GST-tagged Ana2 protein by *in vitro* phosphorylation assay (Figure 4-5), to confirm that GST-Ana2 can be phosphorylated by active Plk4. For this, I treated GST alone (negative control) or GST-Ana2 on resin, with either MBP-Plk4^{KD} (kinase dead Plk4) or active

MBP-Plk4, under addition of ³²P-γ-ATP. This revealed that only GST-Ana2 but not GSTalone was phosphorylated by the active form of Plk4 (Figure 4-5).



Figure 4-5 Ana2 is phosphorylated by Plk4. GST and GST-Ana2 bound to resin were treated with active MBP-Plk4 or kinase dead MBP-Plk4^{KD} in the presence of ³²P-ATP and then subjected to SDS-PAGE and autoradiography. Coomassie stained gel shows protein inputs and bandshift of GST-Ana2, treated with active MBP-Plk4. Bandshift of MBP-Plk4 due to phosphorylation state, as confirmed by ³²P signal in the autoradiogram.

4.2.2 Plk4 phosphorylates Ana2 at four main phosphorylation sites which are localised in the conserved Ana2-STAN motif

As shown in section 4.2.1.2, Ana2 is phosphorylated by active Plk4. To identify the Plk4phosphorylation sites within Ana2, I generated Plk4 phosphorylated Ana2 *in vitro* (GST-Ana2 protein was phosphorylated by active Plk4) and Dr. Dzhindzhev generated Plk4 phosphorylated Ana2 *in vivo* (ProteinA-Ana2 was affinity purified from *Drosophila* cell culture expressing non-degradable Plk4ND), and both samples were analysed by phospho-peptide mapping by mass spectrometry by Dr. Dubski. Table 4-1 summarises the frequency of particular phospho-peptides detected *in vivo* or *in vitro*. This identified two tryptic peptides which are highly present in the *in vitro* and *in vivo* samples; namely S318, and the grouped S365, S370 and S373. Significantly, the identified phosphorylated peptides are within the conserved STAN motif of Ana2 (Figure 4-6, Figure 4-7). Other tryptic peptides, which were phosphorylated by Plk4, were also identified by phospho-peptide mapping by mass spectrometry of Ana2 phosphorylated *in vitro* and/or *in vivo* but at a lesser spectral count (Table 4-1). Several of these were previously reported as phosphorylated in *Drosophila* Kc 167 cells in a phospho-proteome analysis ³⁰³.

Figure 4-6 shows the schematic localisation of the identified Plk4 phosphorylation sites within Ana2 in red, the predicted coiled-coil region in green and the conserved STAN motif in blue. The four main Serine residues that are phosphorylated by Plk4 (S318, S365, S370, S373) lie within the conserved Ana2-STAN motif. And all four Serine residues are conserved as Serine/Threonine sites in the STAN motif throughout the analysed species *Homo sapiens*, *Gallus gallus, Xenopus laevis, Danio rerio,* and *Drosophila melanogaster* (Figure 4-7).

Having determined that full length Ana2 is phosphorylated by Plk4 throughout its sequence, with the C-terminal residues S318, S365, S370 and S373 in the conserved STAN motif being particularly prominent sites, I wished to test the separated N- and C-terminal parts as substrates. I generated two constructs splitting Ana2 to cover aa1-280 and aa281-420. In collaboration with Dr. Dzhindzhev, we then performed an *in vitro* kinase assay using the generated GST-tagged Ana2 fragments bound to resin (GST-Ana2-N, residues 1-280aa and GST-Ana2-C, residues 281-420aa) and treated them with active MBP-Plk4 kinase and ³²P-γ-ATP. This indicated that active MBP-Plk4 is able to phosphorylate both GST-Ana2 fragments, GST-Ana2-N and GST-Ana2-C (Figure 4-8). Significantly, the phosphorylation efficiency of GST-Ana2-C is ~2.5 times higher than the GST-Ana2-N fragment.



Figure 4-6 Localisation of the Plk4 phosphorylation sites within Ana2 identified by phospho-peptide mapping by mass spectrometry and listed in Table 4-1. Schematic of Ana2 showing the Plk4 phosphorylation sites (red), predicted coiled-coil domain (green) and the conserved STAN motif (blue). The four main Serines phosphorylated by Plk4 *in vitro* and *in vivo* are S318, S365, S370 and S373, which localise within the conserved STAN motif of Ana2.

Table 4-1 Plk4 phosphorylates Ana2 predominantly at residues S318, S365, S370 and S373 within the STAN motif *in vitro* and *in vivo* as identified by phospho-peptide mapping by mass spectrometry. GST-Ana2 was phosphorylated by MBP-Plk4 *in vitro* and *in vivo* ProteinA-Ana2 was affinity purified from *Drosophila* cell culture co-expressing PrA-Ana2 and non-degradable Plk4ND. Each sample was subjected to phospho-peptide mapping by mass spectrometry. The table summarises the number of times a particular phospho-peptide was detected from the *in vitro* and *in vivo* samples. Two tryptic peptides were preferentially phosphorylated, S318 and S365-373 (consisting of S365, S370 and S373).

	Total number of spectral counts	
Position	In vitro	In vivo
T69	10	10
S84	13	70
T89	11	0
S98-105	2	15
S119	7	8
T124-125	16	0
S150-153	28	24
T159	62	0
T164	16	0
S177	23	16
S184	2	3
S234	1	3
S237-242	71	9
S318	120	1
S365-373	378	70

	\checkmark	\downarrow \uparrow \downarrow
Drosophila	EK <mark>SMVMNELALKYL</mark> ROPVDELMKDMRLGASPKSPNPEPLRPI	DNI-GHAQ <mark>SP</mark> NDISNASY <mark>KYLKKY</mark> RLL
Danio	DL <mark>S</mark> LEANAIALKYLSDSQLSRLSLGSQSSSPHSDPSTI-LLRRPAVEK	SNVALSIL <mark>SP</mark> SNM <mark>S</mark> L <mark>A</mark> TC <mark>KY</mark> MKK <mark>Y</mark> GLI
Xenopus	DL <mark>S</mark> MEANAIALKYLNESQLNQLSLSHANKNKQSDSISYNSLLPGTTEK:	SMVGLSLI <mark>SP</mark> SNM <mark>S</mark> F <mark>A</mark> TK <mark>KYMK</mark> RYG <mark>L</mark> I
Homo	DL <mark>S</mark> MEANAIALKYLNENQLSQLSVTRSNQNNC-DPFSLLHINTDR	STVGLSLI <mark>SP</mark> NNM <mark>S</mark> F <mark>A</mark> TK <mark>KY</mark> M <mark>KRY</mark> G <mark>L</mark> L
Gallus	DL <mark>S</mark> MEANAIALKYLSENQLSRLSLSHSGQNPP-TDLCFQDILHSNVEK	SMVGLSLI <mark>SP</mark> NNM <mark>S</mark> F <mark>A</mark> TK <mark>KYMK</mark> RYG <mark>L</mark> I
	: *: * :***** : . : :	. : **:* *: **:*:* *:

Figure 4-7 Alignment of orthologue Ana2 STAN motif sequences highlighting the four conserved Serines phosphorylated by Plk4. Analysis of Ana2/STIL STAN motif sequences of five species; *Drosophila melanogaster, Danio rerio, Xenopus laevis, Homo sapiens* and *Gallus gallus*. Arrows highlighting the Plk4 phosphorylation sites identified in *Drosophila melanogaster,* S318, S365, S370 and S373. Alignment was generated with Clustal Omega ²⁸⁴.



Figure 4-8 MBP-Plk4 phosphorylates Ana2-N (aa1-280) and Ana2-C (aa281-420) *in vitro.* In the presence of ³²P-γ-ATP, GST, GST-Ana2-N and GST-Ana2-C were treated with active MBP-Plk4 in a phosphorylation assay, subjected to SDS-PAGE and autoradiography. GST-Ana2-N and GST-Ana2-C show phosphorylation by MBP-Plk4.

4.2.3 Non-phosphorylatable Ana2 leads to loss of centrosomes; phospho-mimicking Ana2 rescues centriole duplication

4.2.3.1 Ana2 is efficiently depleted by dsRNA against Ana2 CDS and Ana2 UTR

Ana2 is a conserved protein, with the most striking region of homology being a predicted coiled-coil region in the central part of the protein and the conserved STAN motif in the Cterminal part (aa315-384). Ana2 and its homologues (Sas5 in C. elegans, STIL in Homo sapiens) are essential for centriole duplication. I wished to be able to deplete endogenous Ana2 from cultured cells in such a way that I could then express mutant forms of Ana2 in its place. To test the efficiency, I depleted endogenous Ana2 using dsRNA against its UTRs, and asked if I could transfect cells with a rescue construct lacking UTR elements. Depletion of Ana2 with dsRNA against its CDS or UTR and control RNAi was performed over 12 days with 3 dsRNA treatments every 4 days in collaboration with Dr. Dzhindzhev. Cells were fixed and stained to reveal the centrosome marker D-Plp. I then analysed the cells by automated fluorescent microscopy to determine centrosome numbers after depletion of Ana2 or control-GST (Figure 4-9). Over a time course of 4, 8 and 12 days GST RNAi treated cells showed a constant proportion of cells without centrosomes of less than 10%, which is comparable to wild-type Drosophila cell culture. Therefore, GST RNAi does not affect centriole duplication. In contrast, depletion of Ana2 using dsRNA against the CDS, led to an increasing percentage of cells without centrosomes; from 27.2% +/- 2.6% on day 4, to 67.7% +/- 4% on day 8, and 94.3% +/- 0.9% on day 12. When Ana2 was depleted via its UTR regions, the percentage of cells without centrosome increased significantly over the analysed time course; from 24% +/- 2.1% on day 4, to 38.5% +/- 3.3% on day 8, and 67.7% +/- 3.5% on day 12. Therefore, depletion of Ana2, either by its CDS or its UTR, results in loss of centrosomes. Ana2 dsRNA directed against the CDS is more effective in preventing centriole duplication than dsRNA against the UTR. Nevertheless, the effect of dsRNA against Ana2's UTR is substantial (67.7% +/- 3.5% of cells without centrosomes on day 12) compared to the negative GST control (9% +/- 1% of cells without centrosomes on day 12).



Figure 4-9 Depletion of Ana2 using dsRNA against Ana2 CDS or Ana2 UTRs leads to loss of centrosomes. Cultured *Drosophila* cells were depleted of Ana2 by RNAi with dsRNA against Ana2 CDS or dsRNA against Ana2 UTRs, with GST dsRNA as negative control. Centrosome numbers were scored after each round of RNAi on day 4, day 8 and day 12. Loss of Ana2 causes loss of centrosomes. 3x200 cells; error bars represent standard error.

4.2.3.2 Rescue of Ana2 depletion by Ana2-4D but not Ana2-4A

To test the biological significance of the four Plk4-phosphorylation sites in the STAN motif of Ana2, I performed rescue experiments, to study the effect of Ana2-4A and Ana2-4D on centrosome numbers after depletion of endogenous Ana2 in *Drosophila* cell culture. Ana2-4A and Ana2-4D carry mutations at the four identified Plk4-phosphorylation sites S318, S365, S370, and S373; with S to A (Serine to Alanine) mutations for the non-phosphorylatable Ana2-4A and S to D (Serine to Aspartic acid) mutations for the phospho-mimicking Ana2-4D respectively. In collaboration with Dr. Dzhindzhev, stable cell lines expressing pAct5-Ana2-WT, pAct5-Ana2-4A and pAct5-Ana2-4D, were depleted of endogenous Ana2 by RNAi with dsRNA against Ana2 UTR (versus negative control dsRNA

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GST) for 12 days with a depletion round every four days. Cells were fixed and stained to reveal the centrosome markers D-Plp and Asl. DNA was stained with DAPI. Cells were analysed by automated microscopy, to analyse the percentage of cells without centrosomes (Figure 4-10, Figure 4-11). All three cell lines were treated with dsRNA against GST or Ana2 UTR for 12 days respectively, resulting in cells without centrosomes at 4.8% +/- 0.4% versus 11.5% +/- 1% for Ana2-WT expressing cells, 20.8% +/- 0.9% versus 83.5% +/- 0.3% for Ana2-4A expressing cells, and 9.3 % +/- 0.2% versus 22.7% +/- 2.7% for Ana2-4D expressing cells after GST RNAi versus Ana2 UTR RNAi (Figure 4-10). The expression of Ana2-WT and the phospho-mimicking Ana2-4D rescue the depletion of endogenous Ana2 and therefore can fully substitute for the endogenous protein. On the contrary, expression of the transgenic non-phosphorylatable Ana2-4A fails to rescue centrosome numbers, as the percentage of cells without centrosomes is higher after depletion of endogenous Ana2 versus the negative control of GST dsRNA. Additionally, the stable expression of Ana2-4A had a dominant-negative effect on centrosome numbers, with an increase of cells lacking centrosomes in 20.8% +/- 0.9% of cells, compared to 4.8% +/- 0.4% in Ana2-WT expressing cells after control-RNAi (dsRNA GST). Figure 4-11 shows a representative image of cells for each of the three cell lines after depletion of endogenous Ana2 for three rounds over 12 days. In cells expressing Ana2-WT and Ana2-4D, both centrosomal markers D-Plp and Asterless co-localise at the centrosomes whereas the signals for D-Plp and Asterless are greatly lost in the majority of cells expressing Ana2-4A, suggesting loss of centrosomes. Thus, depletion of endogenous Ana2 by its UTR can be rescued by Ana2-WT or Ana2-4D, but not by Ana2-4A. Therefore, the four identified Plk4 phosphorylation sites in the STAN motif of Ana2 (conserved S318, S365, S370, and S373) are functionally necessary to rescue the depletion of endogenous Ana2 and therefore important for centriole duplication.



Figure 4-10 Ana2-WT or Ana2-4D but not Ana2-4A rescue the depletion of endogenous Ana2. Endogenous Ana2 was depleted from *Drosophila* cell cultures overexpressing pAct5c-Ana2-WT, pAct5c-Ana2-4A or pAct5c-Ana2-4D for 3 rounds of dsRNA treatment targeting Ana2 UTRs or control GST. Cells with zero centrosomes were counted on day 12. Error bars represent standard error; 3x200 cells counted.



Figure 4-11 Centrosomal markers D-Plp (red) and Asterless (green), after 12 days of Ana2-UTR RNAi in *Drosophila* cell lines overexpressing Ana2-WT, Ana2-4A or Ana2-4D. Insets show enlarged centrosomes from one pole highlighted by arrows in monochrome for D-Plp and Asterless staining; insets scale bar represent 2µm. DNA was stained with DAPI. Main figure scale bars represent 10µm.

4.2.4 Ana2 can interact with Sas6 after it is phosphorylated by Plk4 *in vitro*

Sas5 and Sas6, the *C. elegans* homologues of *Drosophila* Ana2 and Sas6 respectively, are simultaneously recruited to the procentriole in *C. elegans* ^{53,91}. This raised the question of whether *Drosophila* Ana2 and Sas6 interact with each other. My *in vitro* and *in vivo* studies of direct protein binding (section 4.2.1.1) and mass spectrometry analyses of affinity purified Sas6 or Ana2 from *Drosophila* cell cultures (section 3.2.1.2), did not indicate any interaction between Ana2 and Sas6. However, the finding that Plk4 phosphorylates Ana2 but not Sas6 (section 4.2.2) raised the hypothesis, that in *Drosophila*, Plk4 phosphorylation of Ana2 might be essential for the interaction of Ana2 and Sas6. To analyse this hypothesis, I developed an efficient *in vitro* binding assay to test interactions of Sas6 with pre-phosphorylated Ana2. The final protocol, which was used for the following pre-phosphorylation-binding assays, was established by Dr. Lipinszki (section 2.8.3).

GST-tagged Ana2 and the non-phosphorylatable GST-tagged Ana2-4A were purified from *E. coli* onto resin and treated with active Plk4 (MBP-Plk4) or kinase-dead Plk4 (MBP-Plk4^{KD}) in a phosphorylation assay. Each pre-treated Ana2, Ana2-4A and GST sample (either with active Plk4 or kinase-dead Plk4) was then incubated with ³⁵S-Methionine-labelled Sas6 protein in binding assays, followed by multiple washes of the resin and analysis of the resulting complexes on SDS-PAGE (section 2.8.1). The wash steps remove any free ³⁵S-Methionine-labelled Sas6 from the resin. The SDS-PAGE was then dried and exposed. The resulting autoradiogram shows a signal from ³⁵S-Methionine-labelled Sas6 if it directly bound to a protein on resin (GST, GST-Ana2-WT, GST-Ana2-4A) (left panel of Figure 4-15). Only Plk4-phosphorylated Ana2 binds Sas6 directly *in vitro*, as seen by the detected ³⁵S-Methionine-labelled Sas6 signal in the autoradiogram. Importantly, there is no direct interaction between Ana2 and Sas6, when Ana2 was treated with kinase dead Plk4 (MBP-Plk4^{KD}), confirming the necessity of Plk4-mediated phosphorylation of Ana2, in such that it can interact with Sas6. GST does not interact with Sas6, either when treated with active or kinase dead Plk4. We also found that Ana2-4A, which cannot be phosphorylated by Plk4, Plk4, Plosphorylated Plk4.

cannot interact with Sas6. This indicates that the phosphorylation of Ana2 by Plk4 is necessary to allow Ana2 to interact with Sas6.

The above findings raised the question of whether Plk4 also regulates this interaction of Ana2 with Sas6 *in vivo*. In collaboration with Dr. Lipinszki, Co-IP studies on extracts of *Drosophila* cells confirmed that Ana2 interacts with Sas6, when it is phosphorylated by Plk4 (Figure 4-12). Transiently transfected *Drosophila* cell cultures co-expressing FLAG-Ana2-WT or FLAG-Ana2-4A with firstly, Sas6-Myc and secondly, non-degradable Plk4 (Plk4ND) or kinase dead non-degradable Plk4 (Plk4^{ND-KD}) were FLAG immunoprecipitated, followed by SDS-PAGE and Western Blot analyses. Additionally, inputs were subjected to SDS-PAGE and Western Blot analyses. The input samples confirmed the presence of Plk4ND and Plk4^{ND-KD} by anti-Plk4 antibody staining, Ana2 and Ana2-4D by-FLAG antibody staining, Sas6 by anti-Myc antibody staining and as a control anti- α -tubulin. The Western Blot analyses of the FLAG-IPs of the four samples confirm the presence of Ana2 and Ana2-4D in all the samples by anti-FLAG antibody staining. Sas6 was identified only in the FLAG-IP purification co-expressing FLAG-Ana2 with Sas6-Myc and non-degradable Plk4ND. Hence, Sas6 is able to interact only with Ana2-WT and when Ana2 is phosphorylated by Plk4 *in vivo*. This confirms our previous *in vitro* observations.



Figure 4-12 Plk4 phosphorylation of Ana2 triggers direct interaction of Ana2 and Sas6 *in vivo. Drosophila* cell cultures transiently overexpressing FLAG-Ana2-WT or the four Serine substitution mutant FLAG-Ana2-4A with Sas6-Myc and either the non-degradable degron mutant Plk4ND or the non-degradable kinase dead degron Plk4^{ND-KD} were subjected to FLAG-immunoprecipitation. Inputs of the *Drosophila* cell cultures and the FLAGimmunorecipitations were analysed by SDS-PAGE and Western blotting to reveal the indicated antigens. Experiment and image by Dr. Lipinszki ²⁹⁶.

4.2.4.1 The C-terminus of Ana 2 is nessessary for interaction with Sas6 *in vitro*

In section 4.2.4, I show that Sas6 directly binds Ana2 that was phosphorylated by Plk4, with the four main phosphorylation sites located within the Ana2-C-terminus (Figure 4-6). I wished to explore the possibilities if firstly, Sas6 binds only the Plk4-phosphorylated Ana2-C-terminus, or if secondly, Sas6 binds the Ana2-N-terminus, made accessable due to a confirmation change in Ana2 upon its phosphorylation by Plk4. To answer this question, I tested if Sas6 can directly bind Ana2-N-terminus (aa1-280) or Ana2-C-terminus (aa281-420), after treatment with active or kinase dead Plk4 (Figure 4-13). Together both Ana2 fragments

cover the full length of the Ana2 sequence, with GST-Ana2-C containing only the four identified Plk4-phosphorylated Serine residues of the conserved STAN motif (S318, S365, S370, S373). The phosphorylation-binding-assays (section 2.8.3) confirm that after treatment with active Plk4, the Ana2-C-terminus but not Ana2-N-terminus interacts directly with Sas6. Treatment with kinase-dead Plk4 does not lead to their interaction. Plk4-phosphorylated Ana2-WT and Ana2-C-terminus bind Sas6 equally efficient, determined by equal Sas6 signals on the autoradiogram. In collaboration with Dr. Dzhindzhev, the phosphorylation assay of GST-Ana2-C-WT and GST-Ana2-C-4A treated with active MBP-Plk4 and ³²P-γ-ATP confirms that Ana2-C-terminus is phosphorylated by active Plk4 (Figure 4-14). Thus, the Plk4-phosphorylated Ana2-C-terminus is efficient and sufficient for direct interaction with Sas6.



Figure 4-13 Plk4-phosphorylated Ana2-C (aa281-420) interacts directly with Sas6. GST-Ana2, GST-Ana2-N and GST-Ana2-C were treated with active or kinase dead Plk4 (MBP-Plk4 and MBP-Plk4^{KD} respectively) and incubated with ³⁵S-Methionine-labelled Sas6. The complexes were subjected to SDS-PAGE and autoradiography. SDS-PAGE shows comparable protein levels loaded of each protein sample. The respective autoradiogram shows 1% input of ³⁵S-Methionine-labelled Sas6 and interaction of GST-Ana2 and GST-Ana2-C with ³⁵S-Methionine-labelled Sas6 in a Plk4-phosphorylation dependent manner. GST-Ana2-N does not interact with ³⁵S-Methionine-labelled Sas6, independent of treatment with Plk4.



Figure 4-14 Plk4 phosphorylates GST-Ana2-C (aa281-420) at the four conserved Serines of Ana2-STAN motif. GST-Ana2-C (aa281-420) and GST-Ana2-C-4A (S318A, S365A, S370A, S373A) were incubated with active MBP-Plk4 and ³²P-γ-ATP, then subjected to SDS-PAGE and autoradiography. GST-Ana2-C is phosphorylated by MBP-Plk4. The Serine to Alanine substitution mutant (GST-Ana2-C-4A) is not phosphorylated by Plk4. The four conserved Serine residues in Ana2-STAN in the Ana2-C are necessary for phosphorylation by Plk4.

4.2.5 Plk4 phosphorylation of the four conserved Serines S318, S365, S370 and S373 within the Ana2-STAN motif are necessary for its interaction with Sas6

In section 4.2.4, I showed that Sas6 interacts with Ana2, when Ana2 is phosphorylated by Plk4. On the other hand, Ana2-4A, which has its four main Plk4 phosphorylation Serine residues S318, S365, S370 and S373 mutated to Alanine, cannot be phosphorylated. This raises the question of which of the four Serine residues contributes mainly to the Plk4-mediated phosphorylation of Ana2, that permits this interaction. To address this, I generated, expressed and purified Ana2 with S(erine) to A(lanine) mutations for each individual Serine residue identified as Plk4 phosphorylation residues in the conserved Ana2 STAN motif (section 4.2.4.1), generating GST-Ana2-S318A, GST-Ana2-S365A, GST-Ana2-S370A, and GST-Ana2-S373A. These fusion proteins were bound to resin and subjected to active Plk4 (MBP-Plk4) or kinase dead Plk4 (MBP-Plk4^{KD}) before incubation with ³⁵S-Methionine-labelled Sas6 (section 2.8.3). The samples were then washed and analysed on SDS-PAGE,

followed by autoradiography of the dried gels (Figure 4-15). The autoradiogram shows reduced ³⁵S-Methionine-Sas6 binding with each of the Ana2 single-site mutation proteins, when treated with active Plk4, compared to the interaction with Plk4-phosphorylated Ana2-WT protein. The strongest reduction of the binding of ³⁵S-Methionine-labelled Sas6 to Ana2 can be seen when S373 or S370 are mutated to Alanine, with the latter showing the greatest effect. Control binding assays using kinase dead Plk4 show weak background binding of ³⁵S-Methionine-labelled Sas6 to the Ana2 single-site mutation proteins evident in long exposures.



Figure 4-15 Plk-4 mediated phosphorylation of four conserved Serines within the Ana2-STAN motif is essential for its interaction with Sas6. Alanine substitution mutation of all four conserved Serines within the Ana2-STAN motif is necessary to abolish the Plk4mediated interaction of Ana2 with Sas6. Individual Serine to Alanine substitutions do not fully abolish the interaction. S370A results in the greatest reduction of Sas6 binding to Ana2. GST, GST-Ana2-4A and individual Serine to Alanine mutation GST-Ana2 proteins (GST-Ana2-S318A, GST-Ana2-S365A, GST-Ana2-S370A, GST-Ana2-S373A) were treated with active or kinase dead Plk4 MBP-Plk4 and MBP-Plk4^{KD} respectively, followed by incubation with ³⁵S-Methionine-labelled Sas6. Complexes were subjected to SDS-PAGE and autoradiography. In summary, mutations of individual Serine residues in the conserved STAN motif of Ana2 do not abolish the interaction of Sas6 with phosphorylated Ana2 although mutation of S370 has a significant effect. Together our findings point to the importance of phosphorylation of the four conserved Serine residues in the Ana2-STAN motif for interaction with Sas6 and thus the centriole duplication pathway.

4.2.5.1 Plk4-phosphorylation of all four conserved Serine residues in the STAN motif contribute to the direct interaction of Ana2-C and Sas6

The data provided in section 4.2.5 shows that Plk4-phosphorylation of all four conserved Serine residues in the Ana2-STAN motif, rather than a single site, are necessary for efficient direct interaction with Sas6. In section 4.2.4 and 4.2.4.1 I show that full-length Ana2 and Ana2-C-terminus, both Plk4-phosphorylated, bind Sas6 with equal efficiency. Therefore, I wanted to test if single mutations of the four conserved Serine residues in Ana2-C-terminus behave like their single mutations in full-length Ana2 or if the absence of Ana2-N-terminus might affect interaction with Sas6. I introduced single (S)erine to non-phosphorylatable A(lanine) mutations at S318A, S365A, S370A and S373A in Ana2-C-terminus. Each mutation lowers the efficiency of Ana2-C to bind Sas6 but no single mutation abolishes the interaction with Sas6 completely (Figure 4-16, right panel). The mutation of S373A and particularly S370A reduce the level of Sas6 binding to Plk4-phosphorylated Ana2-C the greatest. The interaction between Ana2-C-terminus and Sas6 can still be seen when only the three most C-terminal of the four Serine residues are mutated to non-phosphorylatable A(lanine) in Ana2-C-3A (S365A, S370A, and S373A). Thus, the findings for Ana2-C are in line with the findings for full-length Ana2 that all four conserved phosphorylation sites in Ana2-STAN contribute to the interaction of Ana2-C/Ana2 with Sas6, but S370 contributes the greatest.

Results



Figure 4-16 Plk-4 mediated phosphorylation of all four conserved Serines within the Ana2-STAN motif is essential for the interaction of GST-Ana2-C-terminus (aa281-420) with Sas6. GST-Ana2-C, GST-Ana2-C-3A, GST-Ana2-C-4A and individual Serine to Alanine mutation GST-Ana2-C proteins (GST-Ana2-C-S318A, GST-Ana2-C-S365A, GST-Ana2-C-S370A, GST-Ana2-C-S373A) were treated with active or kinase dead Plk4 (MBP-Plk4 and MBP-Plk4^{KD} respectively), followed by binding assay with ³⁵S-Methionine-labelled Sas6. Complexes were subjected to SDS-PAGE and autoradiography. Coomassie stainings show protein inputs of GST-Ana2-C constructs on residue. Autoradiogram (left) show abolished interaction between Sas6 and Ana2-C-4A only. Ana2-C-3A alone (S365A, S370A, S373A, left) and individual Ana2-C mutants (right) cannot fully inhibit interaction with Sas6. Importantly, S370A resulting in the greatest reduction of Sas6 binding to Ana2-C. The Alanine substitution mutation of all four conserved Serines within the Ana2-STAN motif is necessary to abolish the Plk4-mediated interaction of Ana2-C with Sas6.

4.2.6 Ana2-4A does not bind Sas6 but Ana2-4D does

As shown in section 4.2.3.2, Ana2-4A causes loss of centrosomes in the absense of wildtype Ana2 and expression of Ana2-4D and Ana2-WT rescues the loss of centrosomes. Ana2, phosphorylated by Plk4, interacts with Sas6 *in vitro* and *in vivo* (section 4.2.4). Nonphosphorylatable Ana2-4A does not interact with Sas6 *in vitro* and phosphorylation of all four Serine residues (S318, S365, S370, S373) is necessary for interaction of Ana2 with Sas6 (section 4.2.4 and 4.2.5). Together, this raises the hypothesis that the observed loss of centrosomes in Ana2-4A expressing cells (section 4.2.3.2) results from lack of interaction of Ana2 with Sas6, due to the non-phosphorylation of the Ana2-STAN motif by Plk4. Therefore, I analysed if the phosphomimick Ana2-4D can interact with Sas6 *in vitro* or if the interaction of Ana2 and Sas6 is otherwise dependent on Plk4 and not alone dependent on the Ana2-STAN motif phosphorylation by Plk4. To this end, I used GST-alone, GST-Ana2, GST-Ana2-4A and GST-Ana2-4D that I treated with active MBP-Plk4 or kinase dead MBP-Plk4^{KD} and then subjected to a binding assay with ³⁵S-Methionine-labelled Sas6 (section 2.8.3). This showed that GST-Ana2 interacts strongly with Sas6 only after treatment with active Plk4 but shows weak background binding for the GST-Ana2 treated with kinase dead Plk4. GST-Ana2-4A does not interact with Sas6 (independent of treatment with active or kinase dead Plk) (Figure 4-17). On the other hand, GST-Ana2-4D which phosphomimicks the phosphorylation of the Ana2-STAN motif by Plk4, shows a strong interaction with ³⁶S-Methionine-labelled Sas6 independent of treatment with active or kinase dead Plk4. Thus the four conserved Serines in the Ana2-STAN motif must be phosphorylated by Plk4 to allow for the specific interaction of Sas6 with Ana2.



Figure 4-17 Ana2-4D interacts with Sas6 independently of Plk4 treatment *in vitro.* GST, GST-Ana2, GST-Ana2-4A and GST-Ana2-4D were treated with active or kinase dead Plk4 (MBP-Plk4 and MBP-Plk4^{KD} respectively) and incubated with ³⁵S-Methionine-labelled Sas6. The complexes were subjected to SDS-PAGE and autoradiography. Interaction of Sas6 with Ana2 is dependent on phosphorylation of the four conserved Serines within the Ana2-STAN motif, with Serine to Alanine mutations (non-phosphorylatable mutant) abolishing interaction, and Serine to Aspartic acid mutations (phospho-mimicking mutant) exhibiting interaction independent of pre-Plk4-treatment of Ana2.

4.2.7 Selective regulation of Ana2 binding by Plk4 phosphorylation

The interaction of Sas6 and Ana2 early on in the assembly of the new daughter centriole during centriole duplication is conserved. In *C. elegans* Spd2 recruits Zyg-1 and then Sas5 and Sas6 assemble to the forming procentriole ^{53,91}. However other screens have identified further proteins involved in the assembly of the daughter centriole, suggesting that other protein interactions might be regulated by Plk4 mediated phosphorylation.

This led me to test whether further centriole duplication proteins interact with Ana2 downstream of its phosphorylation by Plk4. I tested whether Ana1, Bld10, Rcd4 and Sas4 proteins, that are known to be involved in centriole duplication ^{131,288}, might preferentially interact with Plk4-phosphorylated Ana2 (Figure 4-18). I treated GST-Ana2-WT with active or kinase dead Plk4, followed by incubation with ³⁵S-Methionine-labelled protein Ana1, Bld10, Rcd4, Sas4 and Sas6. The complexes were then analysed by SDS-PAGE and autoradiography (Figure 4-18). I found that Ana2 interacts with Sas4 independent of whether treated with active or kinase dead Plk4. Similarly, interaction of Bld10 occurred with phosphorylated and non-phosphorylated Ana2 but the interaction increases significantly when Ana2 is phosphorylated by Plk4. Rcd4 and Ana1 do not show any interaction with phosphorylated or non-phosphorylated Ana2. And as previously shown, Plk4-phosphorylated Ana2 interacts with Sas6 (section 4.2.4). These results show and strengthen the finding of the importance and specificity of the phosphorylation of Ana2 to fully trigger its interaction with Sas6.



Figure 4-18 Interactions of different centriolar proteins with Ana2 following PIk4phosphorylation of Ana2. GST-Ana2 was treated with active or kinase dead PIk4 (MBP-PIk4 and MBP-PIk4^{KD} respectively) and incubated with ³⁵S-Methionine-labelled Sas4, Bld10, Rcd4, Ana1 or Sas6. The complexes were subjected to SDS-PAGE and autoradiography. SDS-PAGE shows representative protein inputs of GST and GST-Ana2. Sas6 interacts with pre-phosphorylated Ana2 (MBP-PIk4 treated) but does not interact with Ana2 when treated with kinase dead PIk4 (MBP-PIk4^{KD}). Sas4 interacts with Ana2 independently of its phosphorylation state. Bld10 shows interaction with Ana2 but PIk4-mdiated phosphorylation of Ana2 increases the interaction. Rcd4 and Ana1 do not show interaction with Ana2, independent of treatment with active or kinase dead PIk4.

4.2.8 Physical interaction of Ana2 and Sas6

4.2.8.1 Plk4-mediated phosphorylation of the conserved Ana2-STAN motif is sufficient for binding of Sas6 to Ana2 *in vitro*

After I determined that the C-terminal Ana2-fragment (aa281-420), which contains the STAN motif and is phosphorylated by Plk4, is sufficient to bind Sas6, I wished to determine the smallest Ana2 region necessary for interaction with Sas6. As we know the signifiance of the STAN motif for Plk4-phosphorylation and as the STAN motif is conserved between species, I focused on this C-terminal Ana2 region. Therefore I generated Ana2-fragments which contain the STAN motif only (aa315-384), and constructs with additional sequence upstream and/or dowstream of the STAN motif (Figure 4-19). The Ana2-STAN constructs I made were: Ana2 aa315-384 (STAN only), Ana2 aa305-394, Ana2 aa295-404 and Ana2 aa315-420 (Figure 4-19), and Ana2 full length and Ana2-C (aa281-420) as controls. I expressed and purified the Ana2-STAN protein samples onto resin (section 2.5.1) and performed Plk4 phosphorylation assays, using active or kinase dead Plk4, followed by binding assays with ³⁵S-Methionine-labelled Sas6 (section 2.8.3). Figure 4-20 shows the coomassie stainings and autoradiograms of the binding assays of ³⁵S-Methionine-labelled Sas6 with the analysed Ana2 fragments, Ana2-FL and Ana2-C as controls. Significantly, when the Ana2 constructs are treated with kinase dead Plk4, none of them interact with ³⁵S-Methionine-labelled Sas6. On the other hand, when these Ana2 constructs are treated with active Plk4 kinase, all interacted with ³⁵S-Methionine-labelled Sas6 but with different efficiencies. Similar binding of ³⁵S-Methionine-labelled Sas6, as observed with Ana2-WT and Ana2-C can be seen for Ana2-STAN (aa315-384) and Ana2-aa315-420. The further two Ana2-STAN constructs analysed (aa295-404 and aa305-394) did not interact as strongly with ³⁵S-Methioninelabelled Sas6. In summary, the Ana2-STAN motif alone interacts as efficiently as Ana2-C with ³⁵S-Methionine-labelled Sas6 when phosphorylated by Plk4.



Figure 4-19 Schematic summary of Ana2-STAN constructs analysed for interaction with Sas6. Four N-terminal GST-tagged Ana2 constructs were generated: the first containing the Ana2-STAN motif only (aa315-384); the second including 10 additional amino acids upstream and downstream of the Ana2-STAN motif (aa305-394); the third including 20 additional amino acids upstream and downstream of the Ana2-SAN motif (aa295-404); and the fourth including the C-terminal part of Ana2 sequence after the STAN motif (aa315-420).





4.2.8.2 The aa276-432 coiled-coil segment of Sas6 interacts with Ana2 that has been phosphorylated by Plk4

From section 4.2.8.1, we know that the C-terminal STAN motif of Ana2 is the smallest Ana2 domain which, after it has been phosphorylated by Plk4, interacts with Sas6. But what is the reciprocal domain within Sas6 that interacts with Ana2? To answer this question I generated Sas6 constructs representing the N-terminal head domain of Sas6 (aa1-180), the majority of the predicted coiled-coil domain of Sas6 (aa181-408), a construct combining these two regions (aa1-408), and a construct representing the whole coiled-coil domain with its most C-terminal unstructured region (aa181-472). The generation of the unstructured C-terminus alone or with additional amino acids from the most C-terminal part of the coiled-coil domain (aa421-472) was not possible, due to the small fragment size of 64aa and the size limitations of the *in vitro* transcription-translation system.

In collaboration with Dr. Lipinszki, these constructs were subjected to binding assays with ³⁵S-Methionine-labelled Ana2 that showed only one constructs was able to interact with Ana2, namely Sas6 aa181-472, which represents the whole coiled-coil and C-terminal unstructured domain of Sas6. Thus, the Sas6 N-terminal head domain alone and the Sas6 head domain together with the majority of the coiled-coil domain (aa1-180 and aa1-408 respectively) do not interact with Ana2. This raises the question of which specific region of Sas6 is necessary for interaction with Ana2. From the initial interaction assays it appeared possible that the regions of Sas6 which may interact with Ana2 are: the whole coiled-coil region, a C-terminal part of the coiled-coil region, the unstructured Sas6-C-terminus, or indeed the unstructured Sas6-C-terminus together with the whole coiled-coil region or together with a C-terminal fragment of the coiled-coil region. To distinguish these possibilities, I generated constructs of Sas6 protein fragments for in vitro transcriptiontranslation, which were truncated N-terminal of the identified Sas6 fragment that interacts with phosphorylated Ana2 (Sas6 aa181-472) or C-terminal of full-length Sas6. Figure 4-21 summarises the constructs I generated and their ability to interact with Plk4-phosphorylated Ana2; dark blue represents a strong interaction, light blue a good interaction and yellow no interaction. I generated ³⁵S-Methionine-labelled Sas6 protein fragments by in vitro transcription-translation reactions and carried out binding assays with GST-Ana2 (pretreated with active or kinase dead Plk4). I then subjected the complexes to SDS-PAGE and exposed dried gels to autoradiography. The constructs with N-terminal truncations were Sas6: aa221-472, aa261-472, aa266-472, aa271-472, aa276-472, aa291-472, aa295-472, aa341-472, aa351-472, aa361-472, aa371-472 and aa381-472. The smallest Sas6 construct that shows good interaction with phosphorylated Ana2 is Sas6 aa276-472 (Figure 4-22). The additional constructs analysed were truncated from the C-terminus of full-length Sas6: aa1-462, aa1-452, aa1-442, aa1-437, aa1-432, aa1-427, aa1-422, aa1-414, and aa1-412. The most truncated Sas6 fragment still showing good interaction with phosphorylated Ana2 was Sas6 aa1-432 (Figure 4-23). In summary, these findings show that Sas6 aa1-432 and Sas6 aa276-472 are the most C- and N-terminal truncated Sas6 fragments respectively, that interact with phosphorylated Ana2 (Figure 4-22, Figure 4-23). This experiment defines the Sas6 domain directly interacting with phosphorylated Ana2 *in vitro* as aa276-432 (Figure 4-21, Figure 4-24). From structural Sas6 protein predictions, this suggests, that it is the Cterminal part of the coiled-coil domain of Sas6 that interacts with Plk4-phosphorylated Ana2.



Figure 4-21 Schematic overview of Sas6 constructs, which were studied in an *in vitro* screen for interaction with Plk4-phosphorylated Ana2, determines Sas6 aa276-432 as the most N- and C-terminal truncated region interacting with Ana2. GST-Ana2 was treated with active or kinase dead Plk4 (MBP-Plk4 or MP-Plk4^{KD} respectively) and incubated with *in vitro* transcribed and translated ³⁵S-Methionine-labelled Sas6 constructs summarised. Complexes were subjected to SDS-PAGE and autoradiography. Green background highlights the smallest Sas6 region directly interacting with Plk4-phosphorylated Ana2 *in vitro*. Sas6 constructs and their individual interaction with Plk4-phosphorylated Ana2 are visualised in yellow (no interaction), light blue (good interaction) and darker blue strong interaction). Red arrows indicating the most N- and C-terminal truncated Sas6 constructs still interacting efficiently with Plk4-phosphorylated Ana2.



Figure 4-22 Most N-terminal truncated Sas6 construct interacting with Plk4phosphorylated Ana2 defined as Sas6 aa276-472. GST-Ana2 was treated in a phosphorylation assay with active MBP-Plk4 or kinase dead MBP-Plk4^{KD} and incubated with different ³⁵S-Methionine-labelled Sas6 constructs truncated from the N-terminus in direct binding assays *in vitro*. Complexes were subjected to SDS-PAGE and autoradiography. The Coomassie stained gel shows GST-Ana2 inputs. The autoradiograms show four of the analysed Sas6 constructs, including the smallest (Sas6 aa276-472) and two larger Sas6 fragments (Sas6 aa271-472 and aa266-472) that interact with Plk4-phosphorylated Ana2, and a smaller Sas6 construct (Sas6 aa291-472) that does not interact with Ana2. Summary of all analysed Sas6 constructs in Figure 4-21.



Figure 4-23 Sas6 construct most truncated from the C-terminus and still interacting with Plk4-phosphorylated Ana2 is Sas6 aa1-432. GST-Ana2 was treated with active MBP-Plk4 or kinase dead MBP-Plk4^{KD} in a phosphorylation assay, and incubated with different ³⁵S-Methionine-labelled Sas6 constructs truncated from the C-terminus in *in vitro* binding assays. Complexes were subjected to SDS-PAGE and autoradiography. Coomassie shows GST-Ana2 protein inputs. Autoradiograms show four of the analysed Sas6 constructs in comparison to full-length Sas6 interacting with Plk4-phosphorylated Ana2. Sas6 aa1-427 lacking interaction with Ana2, and Sas6 aa1-432 and larger fragments (aa1-437, aa1-442) interacting with Plk4-phosphorylated Ana2. Summary of all analysed Sas6 constructs in Figure 4-21.



Figure 4-24 Summary of the findings of *in vitro* interaction studies: The Plk4-phosphorylated Ana2-STAN motif (blue, aa315-384) directly interacts with the Sas6 region aa276-432 (blue).

4.3 Discussion

This chapter focuses on the protein kinase Plk4 and the centriole duplication proteins Ana2 and Sas6. It elucidates their interaction, phosphorylation, dependencies, and strikingly describes their function in the initial steps of procentriole formation. The performed work results in the major centriole duplication related finding, that Plk4-mediated phosphorylation of the conserved STAN motif in Ana2 triggers its interaction with the cartwheel protein Sas6 and enables procentriole formation in *Drosophila*. This new knowledge is one further piece towards understanding the puzzle of the timely link of centriole duplication to only once per cell cycle in order to maintain correct centrosome numbers.

Initial protein interaction studies show that bacterial expressed and purified Plk4 and Ana2 interact directly with the ³⁵S-Methionine-labelled counter protein, expressed in an *in vitro* transcription-translation system, in *in vitro* interaction assays (section 4.2.1.1, Figure 4-1). In contrast, the cartwheel protein Sas6 does not interact with Plk4 or Ana2 in direct in vitro interaction assays (section 4.2.1.1, Figure 4-2). Plk4 is described as the master kinase of centriole duplication, as its overexpression induces centriole duplication in cell culture and de novo centriole formation in Drosophila unfertilized eggs, and depletion of Plk4 causes loss of centrosomes ^{83–85,96,289}. Plk4 is recruited to the centriole by Asterless ⁹² but little is known about Plk4 and its substrates in the centriole duplication process. It is known from C. elegans, that Sas5 and Sas6 are recruited to the centriole after the recruitment of Zyg-1^{53,91}, the Plk4 homologue. This suggests that the Drosophila homologues Ana2 and Sas6 might be recruited in a similar timely manner. The finding in section 4.2.1.1, that Plk4 and Ana2 interact directly with each other in vitro supports this idea. In C. elegans, Sas5 and Sas6 are recruited simultaneously and co-dependently to form the central tube, which then further enlarges with the recruitment of Sas4. But the exact molecular mechanism of the Sas5 and Sas6 interaction is still not fully understood. It is suggested that the C-terminal Sas5 domain (aa390-404) interact with a narrow region in the Sas6 coiled-coil domain (aa275-288) ³⁰². And additionally, that the N-terminal domain of Ana2 (aa82-260) forms a tetramer, which then connects four Sas6 homodimers in two neighbouring rings of the central tube ³⁰⁴ (Figure 4-25). Importantly, the direct and phosphorylation-independent interaction of Zyg-1 with the Sas6 coiled-coil domain results in the recruitment of the Sas6-Sas5 complex to the mother centriole ¹⁵. Both these findings from *C. elegans* differ to the findings observed and described here, where *Drosophila* Sas6 does not directly interact with Plk4 or Ana2 *in vitro* (section 4.2.1.1, Figure 4-2).



Figure 4-25 Schematic model how *C. elegans* Sas5 and Sas6 might interact to form the central hub of the centriole. (A) shows a Sas5 molecule interact with a central region of a Sas6 homodimer. Figure from ³⁰⁴ and as previously reported in ³⁰². (B) shows a model how tetrameric Sas5 could interact with two Sas6 homodimers from two neighbouring rings each in the central hub assembly of *C. elegans*. Figure reproduced with permission from ³⁰⁴.

The analyses of centriole duplication proteins and their possible role as phosphorylation substrates of Plk4 go in line with the direct interaction results. Two versions of Plk4 are used in the performed phosphorylation assays, firstly, an active form of Plk4 (MBP-Plk4-T172E), which has auto-phosphorylation activity, and secondly a kinase dead form of Plk4 (MBP-
Plk4-T172E-K43M). The phosphorylation activity of MBP-Plk4-T172E was shown by bandshift on SDS-PAGE due to auto-phosphorylation of the protein in comparison to the kinase dead Plk4 form (section 4.2.1.2, Figure 4-3). Additionally, treatment of active Plk4 with lambda-phosphatase, which releases phosphate groups from phosphorylated Serine, Threonine and Tyrosine residues, reverses the bandshift to the motility seen by kinase dead Plk4, confirming that MBP-Plk4-T172E is active and can phosphorylate (section 4.2.1.2, Figure 4-3). Phosphorylation assays with N-terminal MBP-tagged Ana2 and Sas6 (section 4.2.1.2, Figure 4-4) and N-terminal GST-tagged Ana2 (section 4.2.1.2, Figure 4-5) show that Plk4 phosphorylates MBP- and GST-N-terminal tagged Ana2 but not MBP-Sas6. The finding of Ana2 phosphorylation by Plk4 but the lack of Sas6 phosphorylation by Plk4 is incomparable to findings in C. elegans and human cells. In C. elegans, the Plk4 homologue Zyg-1 recruits Sas6 in a phosphorylation-independent manner, which in turn is in a preformed complex with Sas5, the Ana2 homologue ¹⁵. However, it was previously described that Sas6 is phosphorylated by Zyg-1 at S123, and that this phosphorylation is crucial for centriole formation *in vivo* and it ensures the maintenance of Sas6 at the procentriole¹¹³. On the other hand, two publications show that the Serine/Threonine protein phosphatase 2A (PP2A) regulates Sas5 recruitment to the centriole. It is suggested that phosphorylation of Sas5 inhibits its recruitment to the procentriole ¹¹⁹ or that phosphorylation of Sas5 promotes its destruction ³⁰⁵. However, neither publication show evidence for which kinase phosphorylates Sas5 in the first instance. It was suggested that Zyg-1 kinase regulates Sas5 association with the centrioles because zyg-1 mutant embryos show normal cytoplasmic levels of Sas5 but lack centriolar localisation of Sas5⁷². In summary, the C. elegans Sas5-Sas6-complex is positively regulated by a combination of PP2A dephosphorylating Sas5 and the Zyg-1 kinase phosphorylating Sas6. Presumably this is also the order of events, as PP2A does not localise to the centriole whereas Zyg-1 does. Additionally, at the time of my experiments, there had been no published evidence about the Plk4 phosphorylation of STIL or Sas6, the human homologues of Ana2 and Sas6. In summary, the phosphorylation of Drosophila Ana2 by Plk4 but on the other hand the lack of Sas6 phosphorylation by Plk4 is an intriguing new observation.

It is important to understand the phosphorylation of Ana2 by Plk4 and the potential role of this phosphorylation in centriole duplication, thus all Plk4 phosphorylation sites were identified by phospho-peptide mapping by mass spectrometry (section 4.2.2, Table 4-1). Samples for analyses were either purified ProteinA-Ana2 from cultured Drosophila cells coexpressing non-degradable Plk4 or in vitro phosphorylated GST-Ana2 protein. The highest spectral counts identified in vitro and in vivo were S318 and S365/S370/S373. Further but weaker Plk4-phosphorylation sites are present in Ana2-N-terminus (section 4.2.2, Figure 4-6). The dominance of phosphorylation sites in the Ana2-C-terminus (aa281-420) is confirmed by the phosphorylation assay (section 4.2.2, Figure 4-8), which shows a stronger phosphorylation signal for C-terminal Ana2 than for N-terminal Ana2 (aa1-280). The significance of the phosphorylation of Ana2 in its C-terminal part suggests an evolutionary conserved region within Ana2. Ana2 does not exhibit a strong sequence homology between species and only recently has Drosophila Ana2 been identified as the functional orthologue of C. elegans Sas5¹¹⁶ and of human STIL. This is despite STIL having been described in connection with T-cell acute lymphoblastic leukaemia as early as 1991 ³⁰⁶ and more recently as being defective in primary microcephaly ³⁰⁷. Structural similarities between Sas5, Ana2 and STIL exist; all proteins have a predicted central coiled-coil domain, a TIM motif at the most C-terminus (aa407-420 in *Drosophila*)¹¹⁷ and most significantly a STAN motif localised in their C-terminal regions. A homology alignment of the STAN motif regions of different species confirms the high significance of the identified Plk4 phosphorylation sites S318, S365, S370 and S/T373 in Figure 4-7, as they are conserved between species. Due to the high spectral count of the four Serine sites in Drosophila Ana2 (section 4.2.2, Table 4-1), the visually high Plk4-phosphorylation of Ana2-C-terminus compared to Ana2-N-terminus in vitro (section 4.2.2, Figure 4-8), and the conservation of these sites throughout different species (section 4.2.2, Figure 4-7), my focus was upon the further characterisation of Ana2 and its Plk4-phosphorylation on S318, S365, S370 and S373 to determine their functional role in centriole duplication.

The role of Ana2/Sas5/STIL in centriole duplication, structure and centrosome numbers is of great interest and its role is starting to emerge. The importance of Ana2 in centriole duplication is confirmed in section 4.2.3.1 (Figure 4-9) because its depletion via RNAinterference in cultured Drosophila cells leads to loss of centrosomes. The experiment shows the effect on centrosome numbers after depletion of Ana2 protein by two different dsRNAs against coding sequence (CDS) of Ana2 and the untranslated regions (UTR) of Ana2. After three rounds of depletion for 4 days each, the cells show a significant loss of centrosomes compared to the negative control (GST RNAi), with approximately 94.3% and 67.7% of cells lacking centrosomes after Ana2 CDS RNAi and Ana2 UTR RNAi respectively. The described inability to duplicate centrioles after Ana2 depletion was also observed in C. elegans 23 and human cells ^{41,117,118}, after depletion of Sas5 and STIL respectively. Interestingly, the loss of centrosomes after Sas5 and STIL depletion is comparable to the observed loss of centrosomes after depletion of Plk4 and Sas6^{85,288}. Additionally, inactivation of Sas5 in C. elegans causes failure of centrosome duplication at the two-cell stage embryos ³⁰⁸, which is also the observed phenotype in embryos deprived of Zyg-1²² or Sas4^{16,20}. Taken together, this confirms the importance of Ana2 in centriole duplication.

Additionally, the results in Figure 4-9 show that Ana2 can be efficiently depleted by its UTR regions. In turn, this allows the specific targeting of endogenous Ana2 in cells expressing transgenic Ana2, with the latter not carrying UTR sequences. This method was applied in section 4.2.3.2, where cultured *Drosophila* cells expressing transient Ana2-4A or Ana2-4D were depleted of endogenous Ana2 by *UTR* RNAi in rescue experiments. Ana2-4A and Ana2-4D carry mutations at aa318, aa365, aa370 and aa373, with a Serine to Alanine mutation or a Serine to Aspartic acid mutation respectively, and represent non-Plk4-phosphorylatable and phospho-mimicking Ana2 constructs respectively. They were used to analyse the importance of the Plk4 phosphorylation of Ana2 at these residues (identified in section 4.2.2, Table 4-1) for centrosome numbers and therefore for centrosome duplication. The expression of transgenic Ana2 with a weak negative effect compared to cells treated with control GST RNAi (section 4.2.3.2, Figure 4-10 and Figure 4-11). This result is similar to that

observed in cells expressing transgenic Ana2-WT after depletion of endogenous Ana2 (section 4.2.3.2, Figure 4-10 and Figure 4-11). On the other hand, cells expressing the transgenic Ana2-4A mutant were not able to rescue centrosome numbers after depletion of endogenous Ana2, as approximately 83.5% of cells exhibit no centrosomes after three rounds of RNAi (section 4.2.3.2, Figure 4-10 and Figure 4-11). The centrosomes were immune-stained using specific antibodies against D-Plp and Asterless, and centrosomes were counted. Cell lines expressing Ana2-WT and Ana2-4D, showed centrosomal colocalisation of Asterless and D-Plp after the depletion of endogenous Ana2 (section 4.2.3.2, Figure 4-11). Whereas cells that expressed transgenic Ana2-4A lacked centrosomal signals of Asterless and D-Plp (section 4.2.3.2, Figure 4-11). In summary, Ana2-4A, the transgenic construct that cannot be phosphorylated by Plk4 at residues aa318, aa365, aa370 and aa373, cannot support centriole duplication. Whereas Ana2-4D, which mimicks Plk4 in phosphorylation, rescues centrosome numbers. In summary, the kinase activity of Plk4 in phosphorylating the four Serine residues in Ana2 (S318, S365, S370, S373) is important in the regulation of centrole duplication.

But how does the Plk4-phosphorylation of Ana2 affect centriole duplication? Is Ana2 phosphorylation directly necessary for its recruitment to the centrosome? Or does it change the accessibility of Ana2 protein for recruitment? And what function does the interaction of Plk4 and Ana2 serve compared to Ana2 phosphorylation? After all, Zyg-1 is recruited by Spd2 as the first protein to the procentriole in *C. elegans*^{53,91}, and it was observed in *Drosophila* that Plk4 is recruited by Asterless⁹², and in human cells by the homologues of Spd2 and Asterless (Cep192 and Cep152 respectively)^{93,294,309}. This raises the question of whether the phosphorylation of Ana2 in fact triggers a more downstream process in centriole duplication? In *C. elegans*, Sas5 and Sas6, the Ana2 and Sas6 homologues, form a Sas5-Sas6 complex before being recruited to the procentriole ¹¹⁴. Therefore, I developed in collaboration with Dr. Lipinszki a phosphorylation and binding assay that enables the direct interaction of Sas6 with Plk4-phosphorylated Ana2 to be tested *in vitro* (section 2.8.3). The difficulties in designing this assay lay in the generation of protein reagents that can be used

in combination but without unspecific binding; and to sustain the Plk4-phosphorylation state of Ana2, but still allow for direct protein interaction assays/pull-downs and washes. The finalised in vitro phosphorylation-binding-assay was then applied to treat GST-Ana2 and GST-Ana2-4A (on resin) with active MBP-Plk4 or kinase-dead MBP-Plk4^{KD}, followed by a direct binding assay with ³⁵S-Methionine-labelled Sas6 protein (section 4.2.4, Figure 4-15 left panel). Excitingly, this identified Sas6 as a direct binding partner of Plk4-phosphorylated Ana2 in vitro. This observation is highly significant in the understanding of the role of Ana2 in the Drosophila centriole duplication process. I previously showed that Sas6 does not interact directly with Ana2 in a direct binding assay in vitro (section 4.2.1.1, Figure 4-2). Moreover, the treatment of GST-Ana2 with kinase-dead Plk4, and GST-Ana2-4A with active and kinase-dead Plk4 in phosphorylation-binding-assays resulted in no interaction of Sas6 with Ana2. Thus, the phosphorylation of GST-Ana2 at S318, S365, S370 and S373 by active Plk4 triggers the interaction of Sas6 with Ana2. A potential physical interaction of Ana2 with Plk4 is not the trigger, as Ana2-4A does not interact with Sas6 independent of treatment with active or kinase-dead Plk4. Thus, the interaction of Sas6 and Ana2 is dependent on Plk4phosphorylation of the four Ana2 Serine residues S318, S365, S370, and S373.

There are multiple hypotheses of how Plk4-phosphorylation of full-length Ana2 permits for its interaction with Sas6. Firstly, the phosphorylation state of the four conserved Serine residues in the Ana2-STAN motif might directly allow Sas6 to bind a region containing these phosphorylation sites. Secondly, phosphorylation of the Ana2-STAN motif might cause a conformational change which makes a more N-terminal Ana2-region accessible for Sas6 to bind. Thirdly, as seen in Table 4⁻¹ and Figure 4-8, the N-terminal region of Ana2 is lightly phosphorylated by Plk4, which could contribute to Sas6 binding to Ana2-C-terminus. Therefore, I wished to know which region of Ana2 interacts with Sas6; and treated N-terminal Ana2 (aa1-280) and C-terminal Ana2 (aa281-420) with active and kinase-dead Plk4 and tested for their direct interaction with Sas6 *in vitro* (section 4.2.4.1, Figure 4-13). Significantly, only the Plk4-phosphorylated Ana2 C-terminal region was able to bind Sas6 directly, as seen for Plk4-phosphorylated full-length Ana2 (Figure 4-15 left panel). The N-terminal part of Ana2 does not appear to contribute to the interaction with Sas6, as it does

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not interact with Sas6 nor does its absence reduce the efficiency of the Plk4-phosphorylated C-terminal part of Ana2 to interact with Sas6.

That the interaction of Plk4-phosphorylated Ana2 and Sas6 is not an artefact observed only *in vitro* is suggested by the complementary co-immunoprecipitation of the two parts from extracts of living cells (section 4.2.4, Figure 4-12, in collaboration with Dr. Lipinszki). Two versions of Ana2 (FLAG-Ana2-WT and FLAG-Ana2-4A) were stably co-expressed with non-degradable or non-degradable kinase-dead Plk4, and transiently expressed Sas6-Myc. FLAG-co-immunoprecipitation revealed that only Plk4-phosphorylated Ana2 was able to interact with Sas6 protein, as observed *in vitro*. This strongly confirms the *in vitro* findings and highlights how important Plk4-mediated phosphorylation of Ana2 is for the very specific and triggered interaction with the cartwheel protein Sas6 and therefore for centriole duplication as a whole. The significance of the above finding is surprising, as nothing similar has been described for their homologues. In *C. elegans*, Sas5 and Sas6 are suggested to be present as individual oligomers, which change confirmation when they form a hetero-Sas5-Sas6-complex and that the interaction between Sas5 and Sas6 is based on synergistic hydrophobic and electrostatic interactions ³⁰².

After identifying that the specific four Serine residues (S318, S365, S370, S373) in the Ana2 STAN motif must be phosphorylated by Plk4 to trigger interaction with Sas6, it raises the question of the importance of each individual Serine residues for Ana2-Sas6 interaction. Is the phosphorylation of a single site efficient to trigger the specific interaction? Or is phosphorylation of all four Serine residues required? The analyses of Sas6's interaction with four individual Ana2 mutant constructs, each carrying a Serine to Alanine mutation at each of the four conserved Serine residues, suggests that all four Serine residues must be phosphorylated by Plk4 to enable a strong interaction of phosphorylated Ana2 with Sas6 (section 4.2.5, Figure 4-15). Significantly, none of the four analysed Ana2 constructs were able to interact as strongly as Ana2-WT with Sas6 but neither did any of the point mutations fully abolish interaction of Ana2 with Sas6. However, the mutation of Ana2-S370A reduces the interaction with Sas6 to a greater extent than the other Ana2 mutants, suggesting that

Plk4-phosphorylation of S370 is of particular significance for the interaction of Ana2 with Sas6. Nevertheless the loss of any one of the four Plk4-phosphorylation sites within the Ana2 STAN motif reduces its efficiency to interact with Sas6; and the interaction does not depend upon any single phosphorylation site.

Similarly, the C-terminal part of Ana2 (aa281-420) binds as efficiently to Sas6 as full-length protein (section 4.2.5.1, Figure 4-16). Significantly, also a triple mutant of Ana2-C-3A, which only retains the phosphorylatable S318 but carries Serine to Alanine mutations for aa365, aa370 and aa373, does not prevent binding of Sas6 fully (section 4.2.5.1, Figure 4-16). But Plk4-phosphorylated Ana2-C-3A shows a more significantly reduced interaction with Sas6 than any of the four individual Serine mutants of Ana2-C. All four conserved Serine residues in the Ana2-STAN motif must be phosphorylated by Plk4 to trigger efficient interaction with Sas6 and mutation in any one reduces but does not abolish binding.

Reciprocally I showed that the Ana2-4D mutant, which mimicks phosphorylation of Ana2 at S318D, S365D, S370D and S373D, interacts with Sas6 independently of treatment with active or kinase dead Plk4 (section 4.2.6, Figure 4-17). The strength of interaction is comparable to the interaction of Plk4-phosphorylated Ana2-WT with Sas6 accounting for the ability of Ana2-4D to rescue centriole duplication after depletion of endogenous Ana2 in *Drosophila* cell culture with similar efficiency as transgenic Ana2-WT (section 4.2.3.2, Figure 4-10 and Figure 4-11). That a phospho-mimicking Ana2 mutant (Ana2-4D) interacts with Sas6 confirms the findings that the four Serine residues in the Ana2-STAN motif are crucial and that their phosphorylation by Plk4 is the trigger for the interaction of Ana2 with the cartwheel protein Sas6.

The identification of a specific phosphorylation mechanism by which Sas6 is recruited raises the question whether Ana2-phosphorylation is also necessary to trigger further downstream interactions with other centrosomal proteins. To address this, I generated ³⁵S-Methionine-labelled proteins known to be found at centrioles, namely Sas4, Bld10, Rcd4 and Ana1

(section 4.2.7, Figure 4-18). The latter two do not interact with Ana2, not in Ana2's Plk4phosphorylated nor non-phosphorylated state, whereas Sas4 interacts strongly with Ana2, and Bld10 increases its interaction when Ana2 is Plk4-phosphorylated.

Rcd4 is a protein identified in a genome-wide RNAi screen for centrosome defects, which localises to the centrosome and was categorised as functioning in centriole duplication and/or efficient PCM recruitment ¹³¹. The *Drosophila* protein does not have any known homologues and to date, there have not been any further published studies on Rcd4.

Ana1 represents one of the three Ana proteins suggested to be involved in centriole duplication. So far, the research undertaken on the protein is limited. But it is known that Bld10, Ana1 and Asterless are recruited sequentially in the centriole-to-centrosome conversion ³⁰ and that after depletion of Plk4, Ana1 no longer localises to the centrosome. Additionally, Ana1 depletion leads to a highly reduced signal of Sas6 at the spindle poles ³¹⁰. This suggests, that Plk4 is required for Ana1 recruitment to centrioles and that Ana1 acts downstream of Plk4. Conversely, Ana1 is recruited to the centriole upstream of Sas6. But Sas6 does not seem required for Ana1 recruitment to centrioles but might play a role in the maintenance of Ana1 at the centriole.

Sas4, a centriole protein essential for microtubule recruitment, interacts strongly with Ana2 independently of Plk4-phosphorylation. That Sas4 interacts with Ana2, regardless of Ana2's phosphorylation state, is in line with the interaction of CPAP and STIL, the human orthologues of Sas4 and Ana2 respectivelly. The analysis of their crystal structure defined their interaction interface to be the STAN motif of STIL and the C-terminal G-box of CPAP, and significantly, mutations within this interface disturbs centriole duplication *in vivo* ^{41,42,44}. Depletion of STIL interfered with CPAP recruitment to the procentriole and centriole elongation, but reciprocal, depletion of CPAP did not affect targeting of STIL to the centriole, suggesting that STIL recruitment to the centriole occurs upstream and is independent of CPAP ⁴¹. Significantly, overexpression of Sas4 causes rapid *de novo* formation of centriole-like structures in approximately 60% of unfertilized *Drosophila* eggs, which normally do not have centrioles ⁹⁶. Moreover, overexpression of Sas4 does not lead to extra centriole-like structures in brain cells nor spermatocytes ⁹⁶. The major role of Sas4 at the centriole is in

recruitment and/or maintenance of microtubules, as depletion of *C. elegans* Sas4 prevents these processes ⁵³. Moreover CPAP overexpression causes very long centrioles ^{38,39}. More research needs to be undertaken to further understand how Sas4 and Ana2 interact with each other and how this affects centriole duplication in *Drosophila*.

Interestingly, Bld10, which is known to maintain centriole structure but is not essential for centriole duplication in Drosophila⁶⁵, interacts with non-phosphorylated Ana2 but this interaction is stronger when Ana2 is Plk4-phosphorylated. The strength of interaction of the latter is comparable to the interaction strength of Sas6 with Plk4-phosphorylated Ana2. Bld10 protein is conserved amongst organisms that have centrioles, and has homologues in C. elegans and human cells; Bld10p and Cep135 respectively ³². Bld10p and Cep135 are essential for centriole formation in Paramecium, Tetrahymena and human cells but not so in Drosophila ^{43,65,73,311,312}. Drosophila mutants that lack Bld10 assemble cartwheels and centrioles, although the cartwheel appears to be wider and unstable ^{32,64–66}. In contrast, Chlamydomonas Bld10 forms the distal part of the cartwheel spoke and contributes to their proper length ⁶². Additionally, Bld10p/Bld10/Cep135 are microtubule-binding proteins ^{43,68}, which suggests they might nucleate and/or stabilize microtubules at the transition zone of cartwheel spokes to microtubules. Details of the molecular interaction of Ana2 and Bld10 and its function is currently unknown but it is possible to speculate that Ana2 might recruit Bld10 to the centriole or that Ana2 could stabilise the cartwheel and microtubules via Bld10. The increase in binding of Bld10 to phosphorylated Ana2 could be a mechanism that times Bld10's association with the centriole or to license Bld10 to interact with other proteins of the cartwheel or centriole.

Structural homology studies of Ana2/STIL reveal that the protein has two conserved C-terminal motifs: the STAN motif and the TIM motif at the very C-terminus ¹¹⁷, with the latter being truncated in microcephaly patients ³⁰⁷. The C-terminal part of Ana2 contains both of these motifs. However, my studies subsequently showed that the STAN motif alone is efficient for phospho-dependent binding to Sas6 which does not depend on the TIM motif (Figure 4-20). This is in line with observations of microcephaly mutants of STIL, which lack

the C-terminal TIM motif and cannot be degraded but remain a normal STIL function ³⁰⁷. It also confirms the high importance of the Ana2-STAN motif in cartwheel assembly and centriole biogenesis.

My phosphorylation and binding assays show that Sas6 aa276-432 is the smallest region able to interact with Ana2 (section 4.2.8.2). We do not know the structure of the entire protein Sas6. However, crystallographic studies of Sas6 homologues have elucidated the 3D structure of the N-terminal head domain and the N-terminal part of the coiled-coil domain ^{63,69,74,75}. These studies show that Sas6 has an N-terminal head domain, which forms the inner cartwheel hub and a coiled-coil domain which dimerises to form the cartwheel spokes, and an unstructured C-terminal end. However, the structure of the whole coiled-coil domain and particularly the C-terminal region, which could be part of the cartwheel spokes that connect microtubules, is not known. It is intriguing that this C-terminal region of Sas6 interacts with Ana2-STAN, as it localises Ana2 function to the outer cartwheel region. This is significant in the light of observations in human cells, where STIL interacts directly with CPAP, and in the case of STIL or Sas6 depletion where CPAP fails to localise to the nascent procentriole⁴¹. The identification of the interacting regions between Ana2 and Sas6 needs further analysis at atomic resolution, to determine the precise structural interaction and how this might affect centriole duplication. This presents a big challenge. To show this, it will be necessary to overcome lack of solubility of the proteins and fragments of the proteins for crystallisation trials; and their stoichiometry, as we know that both proteins form homodimers giving the potential for change in stoichiometry when the proteins interact. To fully understand precisely how Ana2 and Sas6 interact, it will be necessary to overcome these difficulties to gain further insight.

Chapter 5

The novel direct interaction and centrosome localisation of Dragon (CG33052) with the cartwheel protein Sas6

5 The novel direct interaction and centrosome localisation of Dragon (CG33052) with the cartwheel protein Sas6

5.1 Introduction

In this chapter I will explore the interactions of Sas6 with a second protein that we have called Dragon (CG33052) that to date has not been studied in *Drosophila*.

We identified the *Drosophila* homologue Dragon as a partner of the centrosomal protein Sas6 following its affinity purification from *Drosophila* cell culture. My objective in this chapter was to understand its interaction with centriolar proteins and its potential role in centriole duplication. Specifically, I wanted to determine if there is a direct protein-protein interaction between Dragon and the centrosomal cartwheel protein Sas6. If so, what are the structural and interaction characteristics of this potential interaction, where does Dragon localise, and what effect does depletion of Dragon have on centrosome numbers?

5.2 Results

5.2.1 Identification of Dragon, a Golgi protein in complex with the centrosomal protein Sas6

5.2.1.1 *In vivo* purifications of Sas6 reveal the novel Golgi protein Dragon in complex

As part of a study of the interactions made by centrosomal proteins, different centrosomal proteins were purified from Drosophila cell culture and Drosophila syncytial embryos, and subjected to mass spectrometry analyses. My particular interest was in Sas6, which is known to form the inner hub and cartwheel structure of centrioles and is one of the first proteins detected at the site of daughter centriole formation on the mother centriole. In chapter 4, I show phosphorylation of Ana2 by Plk4 at its STAN motif triggers direct interaction of Ana2 with Sas6 and recruitment to the site of procentriole formation. In the analyses of Sas6 assosiated proteins purified from Drosophila cell culture and syncytial embryos, we repeatedly observed the previously uncharacterised protein CG33052 in Drosophila. From here onwards CG33052 will be refered to as Dragon. Table 5-1 summarises the Mascot 'scores' and 'number of peptides' identified by mass spectrometry for Sas6 and Dragon, purified from cultured Drosophila cells and Drosophila syncytial embryos (complete lists in Appendix C). Drosophila cells were stably transformed with pMT-PrA-Sas6 and expression of PrA-Sas6 was induced with 1mM CuSO₄ for 22 hours. As indicated, cells were treated with 25µM MG132 for up to 5 hours to inhibit proteasomal degradation and/or 50nM okadaic acid for 9 to 16 hours to inhibit protein phosphatases. Sas6 was also expressed constitutively in Drosophila syncitial embryos (aged 0-4 hours) derived from poly-Ub-Sas6-GFP expressing flies. During the purification of Sas6, high NaCl (440mM) concentrations and 50nM okadaic acid were included in the elution and wash buffer, as indicated (Table 5-1B).

The Sas6 bait exhibited high Mascot 'scores' and large 'number of identified peptides' in all analysed samples, suggesting successful enrichment of Sas6 protein from *Drosophila* cell cultures and embryos. The samples from cultured *Drosophila* cells consistently revealed Dragon in complex with the bait protein Sas6. Dragon was present with high Mascot scores in the purifications from syncytial embryos, independently of whether okadiac acid treatment was given. A high 440mM NaCl concentration in the elution and wash buffer led to lower Mascot scores of Dragon compared to the samples treated with the usual 150mM NaCl concentration. Control purifications of PrA or GFP expressed alone do not identify Dragon. Purification of Dragon with consistantly high scores when Sas6 was purified from either *Drosophila* cell culture or syncytial embryos suggests that Dragon is a true member of a complex with the centrosomal protein Sas6 *in vivo*.

Table 5-1 Sas6 protein purification and mass spectrometry analyses from *Drosophila* cell culture and *Drosophila* syncytial embryos reveal Dragon protein in a complex with Sas6. Sas6 protein was purified from *Drosophila* cell culture expressing pMT-PrA-Sas6 (treated with and without okadaic acid), and from *Drosophila* syncytial embryos expressing poly-Ubiquitin-Sas6-GFP (treated with and without okadaic acid, high salt equals 440mM), followed by mass spectrometry. The tables summarise the presence of Sas6 and Dragon in complex and their according number of peptides in the samples (*purifications in student projects). OA: okadaic acid. Complete lists in Appendix C.

A Drosophila cell culture

Protein	Score	# of peptides
рМ⊺	Γ-PrA-Sas6; ∣	MG132*
Sas6	4576	281
Dragon	69	5
pMT-PrA-Sas6; OA and MG132*		and MG132*
Sas6	4606	280
Dragon	55	2

B Drosophila syncytial embryos

Protein	Score	# of peptides		
pUb-Sas6-GFP; 0-4h*				
Sas6	13751	272		
Dragon	6514	105		
pUb-Sas6-GFP; 0-4h, high salt*				
Sas6	5900	123		
Dragon	1641	27		
pUb-Sas6-GFP; 0-4h, high salt and OA*				
Sas6	4677	131		
Dragon	1380	27		

5.2.1.2 In vivo purifications of Dragon confirm Sas6 in complex

To further confirm that Sas6 and Dragon form in complex in vivo, I performed the reciprocal experiment; to analyse whether GFP-tagged Dragon co-purifies with Sas6. To this end, I established cell lines for inducible Dragon-GFP and constitutively expressed GFP-Dragon, and affinity purified these proteins from Drosophila. Dragon protein purified from Drosophila cell culture was analysed by mass spectrometry (complete lists in Appendix C). All samples showed high bait Mascot scores for Dragon between 16669 to 61897 (253 to 766 peptides), giving a high protein coverage of 62 to 74%. Sas6 protein was identified as the only centriole duplication protein by mass spectrometry in all analysed purifications (Table 5-2A). But copurified Sas6 seems to be positively affected or stabilised if the Dragon bait is constitutively expressed rather than induced, Dragon is N-terminally tagged rather than C-terminally and the cells were treated with okadaic acid. Significantly, Sas6 was identified as the top scoring protein and the only centriole duplication protein purified with Dragon from syncytial Drosophila embryos (Table 5-2B). Though common contaminants were Heat shock protein cognate 4 CG4264 and Elongation factor 1α48D CG8280 (for full list see Appendix C), which are often found in control purifications. The GFP-trap binding was performed for 2.5 hours to allow for efficient purification of Dragon protein in complexes, including potentially less represented complexes within the sample. Mass spectrometry identified the bait Dragon with a score of 2764 (50 peptides, giving a protein coverage of 71%). On the other hand, Sas6 was identified in complex with Dragon at a score of 752 (18 peptides, 44% protein coverage). Thus, confirming that Dragon and Sas6 co-purify in complex in vivo from cultured Drosophila cells as well as directly from Drosophila syncytial embryos.

Table 5-2 Purifications of Dragon reveal it is in complex with Sas6 *in vivo*. Dragon protein, purified from A) *Drosophila* cell culture expressing poly-Ubiquitin-GFP-Dragon or pMT-Dragon-GFP (treated with and without okadaic acid) and B) from *Drosophila* syncytial embryos expressing poly-Ubiquitin-GFP-Dragon. Mass spectrometry reveals that Sas6 is in complex with Dragon. Number of peptides and the peptide coverage for Dragon and Sas6 are indicated for each sample. Complete lists in Appendix C.

Protein	Score	# of peptides	Coverage
pUb-GFP-Dragon			
Dragon	18036	290	63%
Sas6	159	4	10%
pUb-GFP-Dragon; OA			
Dragon	61897	766	66%
Sas6	1961	37	37%
pMT-Dragon-GFP; 0.5mM CuSO ₄ 24h			
Dragon	16669	253	62%
Sas6	90	2	5%
pMT-Dragon-GFP			
0.5mM CuSO ₄ 24h, 100nM OA 2h			
Dragon	24140	337	74%
Sas6	223	7	10%

A Drosophila cell culture

B Drosophila syncytial embryos

Protein	Score	# of peptides	Coverage
pU	b-GFP-Dra	igon; 2.5hrs bii	nding
Dragon	2764	50	71%
Sas6	752	18	44%

5.2.1.3 *In vivo* purifications of Dragon confirm COPI subunits in complex

In addition to the centrosomal cartwheel protein Sas6 in complex with Dragon (section 5.2.1.2), the majority of the subunits of the Golgi COPI proteins were present in Dragon purifications from *Drosophila* cell culture (Table 5-3). The subunits α COP, β 'COP and ϵ COP of the cage-like subcomplex of COPI and the subunits γ COP and β COP of the adaptor subcomplex of COPI were present in all samples. The ϵ COP subunit of the cage-like

subcomplex was present in all purifications but one. Hence, all three subunits of the cagelike subcomplex (α - β '- ϵ -COPs) are present in the Dragon purifications. On the other hand, the subunits δ COP and ζ COP were not identified. Thus, only two out of the four subunits of the adaptor subcomplex of COPI are present in Dragon purifications. No COPI subunits were found in GFP control purifications or in complex with purified Sas6. Thus COPI subunits appear to associate specifically with the Dragon bait. Additionally, CtBP (C-terminal binding protein), which was suggested to function as a transcriptional co-repressor ^{313–317}, was highly represented in complex with Dragon in all four Dragon purifications from *Drosophila* cell cultures and apparently in higher quantity in cells treated with okadaic acid. This suggests that the inhibition of dephosphorylation by PP2A stabilises CtBP in complex with Dragon.

Table 5-3 Purifications and mass spectrometry analyses reveal subunits of COPI and CtBP in complex with Dragon. Dragon protein, purified from *Drosophila* cell culture expressing poly-Ubiquitin-GFP-Dragon or pMT-Dragon-GFP (treated with (+OA) and without okadaic acid), followed by mass spectrometry show CtBP and five out of seven known COPI subunits in complex with Dragon. Highlighted in pink are the COPI subunits forming the cage-like subcomplex (α - β '- ϵ -COPs), and in blue the COPI subunits forming the adaptor subcomplex (γ - β - δ - ζ -COPs). When present in the purification sample, the Mascot 'scores' and 'number of peptides' are stated for Dragon, CtBP and each subunit of COPI.

	pUb-GFP-Dragon		pUb-GFP-Dragon +OA		pMT-Dragon-GFP		pMT-Dragon-GFP +OA	
Symbol	Score	# of peptides	Score	# of peptides	Score	# of peptides	Score	# of peptides
Dragon	18036	290	61897	766	16669	253	24140	337
αCOP	1106	26	606	13	72	2	329	11
β'COP	322	8	212	3	336	4	441	6
βCOP	1263	19	582	9	259	4	590	12
γCOP	1792	29	1171	22	109	3	488	8
δCOP		-		-		-		-
εCOP	96	2	92	2		-	138	1
ζCOP		_		-		-		-
CtBP	655	11	3502	47	768	22	2262	40

5.2.2 Localisation of Dragon at the centrosome and Golgi

5.2.2.1 Dragon co-localises to the centrosome with Sas6

The human counterpart of Dragon is the protein GoRab that is reported to function at the Golgi and its vesicles ^{202,214-216}. Thus the purification of Dragon in complex with the centrosomal protein Sas6 from Drosophila was unexpected. I therefore asked whether Dragon localises with Sas6 at the centrosome. Therefore, I performed immune localisation studies to determine whether Dragon-GFP or myc-Dragon, stably expressed in cultured Drosophila cells, would allocate with the centrosomal marker D-Plp. This revealed colocalisation of D-Plp with GFP- and myc-Dragon at the centrosome (Figure 5-1), and also GFP- and myc-Dragon at the Golgi structure (this is further explored in section 5.2.2.2). I then set out to determine the position of Dragon related to Sas6 at the centrosome by structured illumination microscopy in collaboration with Dr. Tzolovsky. Drosophila wild-type cells were stained with antibodies against Dragon, Sas6 and D-Plp, followed by imaging and analysis. These images confirmed that Dragon localises to the centrosome and more specifically to zone 1 with the centrosomal cartwheel protein Sas6 within the D-Plp ring (Figure 5-2). D-Plp allows the mother and daughter centriole to be distinguished. D-Plp forms a ring-like structure at the centrosome during the whole cell cycle, and the daughter centriole matures by recruiting D-Plp in a 'horn'-like pattern which develops into a ring-like structure by meta-/anaphase. Sas6 and Dragon co-localise to the inner space of the D-Plp ring (zone 1), corresponding to the mother centriole, throughout the whole cell cycle. Sas6 and Dragon also co-localise as a single dot at the site of procentriole formation. Thus, Sas6 and Dragon co-localise throughout centriole assembly, maturation and separation, and hence are present on both mother and daughter centriole throughout the whole cycle (Figure 5-2). This suggests a simultaneous rather than a sequential recruitment of Sas6 and Dragon.



Figure 5-1 Dragon localises to centrosomes in *Drosophila* **cell culture.** Micrographs show centrosomes revealed by D-Plp and Myc/GFP co-staining in the two *Drosophila* cell lines expressing Act5-Myc-Dragon or pUb-Dragon-GFP; insets show D-Plp and Myc/GFP co-localisation from each pole (indicated by white arrows). Additionally, Myc/GFP stainings reveal Golgi localisation of Dragon in both cell lines (as further explained in Figure 5-3). DNA is stained with DAPI (blue). Scale bars represent 10µm for main image and 1µm for insets.

	Merged	Dragon	Sas6	D-Plp
Interphase				Ø
Prophase		\$	۲	9
Metaphase				Ò
Anaphase	•		•	9
Telophase	2.			2
Cyto/G1	6			0

Figure 5-2 Localisation of endogenous Dragon (green) relative to centrosomal Sas6 (red) and D-Pip (blue) throughout the cell cycle. Structured illumination microscopy of endogenous Dragon, Sas6 and D-Plp throughout cell cycle stages in wild type Drosophila cell culture. Dragon and Sas6 co-localise at the centre of the D-Plp ring at the mother centriole throughout the cell cycle, as well as at the site of procentriole formation and daughter centriole at the periphery of the D-PIp ring. Scale bar 0.25µm. Microscopy and images by Dr. Tzolovsky.

5.2.2.2 Dragon protein localises to the *trans*-Golgi but not the *cis*-Golgi in *Drosophila* cell culture

As the human homologue of Dragon, GoRab, was reported as a *trans*-Golgi protein ²⁰² I wanted to determine whether *Drosophila* Dragon was also a Golgi protein. In collaboration with Miss Chu I studied *Drosophila* cell culture stably expressing FLAG-Dragon to reveal the FLAG-tag, Golgin-245, GM130 and DAPI, to localise Dragon, the *trans*-Golgi, the *cis*-Golgi and DNA respectively (Figure 5-3) ^{318,319}. This identified Dragon at the Golgi, where it co-localises with the *trans*-Golgi marker Golgin-245 but not with the *cis*-Golgi marker GM130. Interestingly, this is similar to observations in human cell culture, where the Dragon homologue GoRab co-localises with the *trans*-Golgi protein Rab6 but not with the *cis*-Golgi matrix marker GM130 ²⁰². Thus Dragon has a dual localisation within cultured *Drosophila* cells; at the *trans*-Golgi and co-localised with Sas6 at the core of the centriole.



Figure 5-3 Localisation of Dragon to the *trans***-Golgi.** Cultured *Drosophila* cells stained to reveal FLAG (Dragon, red), Golgin-245 (green) and GM130 (blue). Dragon co-localises to the *trans*-Golgi with Golgin-245 but not to the *cis*-Golgi with GM130. Scale bar 5µm. Microscopy and images by Miss Chu.

- 5.2.3 Depletion of Dragon in *Drosophila* cell culture causes loss of centrosomes but Golgi structures are not affected
- 5.2.3.1 Depletion of Dragon in *Drosophila* cell culture affects centriole duplication and causes loss of centrosomes



A Drosophila cells, Dragon CDS RNAi

B Drosophila cells, Dragon CDS RNAi 8d

Figure 5-4 Depletion of Dragon by RNAi causes loss of centrosomes in cultured *Drosophila* cells after eight days. A) Numbers of centrosomes per cell are colour coded in the key. (B) Number of cells with zero or with greater and equal than one centrosome per cell after treatment with Dragon dsRNA, GST dsRNA and Plk4 dsRNA. Error bars represent standard error; 3x200 cells counted; significance was calculated by t-test.

As Dragon co-purified and co-localised with Sas6, I wanted to determine whether depletion of Dragon also affected centriole duplication. Therefore, I used RNAi to deplete Dragon from wild-type *Drosophila* cell culture, to study the effect on centrosome numbers. As positive and negative controls, I depleted Plk4 and GST. I performed two 4 day rounds of RNAi and analysed centrosome numbers on day 8. I found that Dragon depletion over this 8 day interval led to loss of centrosomes (Figure 5-4A). The proportion of cells with no centrosomes increased from 6.7% to 46.6%; and with a single centrosome per cell, from 5% to 19.9% after Dragon depletion. This was accompanied by a corresponding decrease in

cells with two centrosomes (from 53.5% to 22.5%); three centrosomes (from 9.3% to 6.3%); and four or more centrosomes (from 25.5% to 4.7%). Dragon depletion was not as effective as Plk4 depletion (46.6% versus 72.2% of cells without centrosomes, Figure 5-4B) but nevertheless suggests a role for Dragon in centriole duplication.

5.2.3.2 Depletion of Dragon does not affect the structure of the Golgi suggesting an alternative role of Dragon at the Golgi

As Dragon co-localises with Golgin-245 at the trans-Golgi (section 5.2.2.1) it raised the question whether the Golgi organisation was affected following Dragon depletion by RNAi. Therefore pilot experiments were performed in collaboration with Miss Chu. Cultured Drosophila cells were treated with dsRNA against Dragon, Sas6, GFP (negative control), and Plk4 (positive control) for three days. Cells were fixed and stained with antibodies against firstly, D-Plp, Dragon and GM130 for *cis*-Golgi or secondly, against D-Plp, GM130 and Golgin-245 for trans-Golgi. These pilot experiments (data not shown) suggest that after control GFP RNAi; D-Plp localised to centrosomes, and Dragon adjacent to the cis-Golgi (GM130). After Sas6 or Plk4 RNAi; the centrosomal D-Plp signal was lost, but Dragon and GM130 remained localised at the Golgi. Dragon RNAi led to reduced or absent D-Plp signals at centrosomes, and loss of Dragon from the Golgi, but localisation of GM130 to the cis-Golgi and Golgin-245 to the trans-Golgi appeared unaffected by Dragon depletion. Thus, the pilot experiments suggest that depletion of centrosomal proteins Sas6 and Plk4 lead to loss of centrosomes without affecting the localisation of Dragon to the Golgi structure. Additionally, it is suggested that the depletion of Dragon led to loss of centrosomes and loss of Dragon from Golgi. However, the localisation of GM130 and therefore the cis-Golgi structure, and Golgin-245 and therefore the trans-Golgi structure do not seem to be structurally affected.

5.2.4 Direct interaction of Dragon and Sas6 confirmed by *in vitro* assays - Identification of binding domains between Dragon and Sas6 *in vitro*

5.2.4.1 The full-length proteins Dragon and Sas6 interact directly with each other *in vitro*

After determining that Dragon and Sas6 exist in a complex *in vivo*; that they co-localise at the centrosome; and that depletion of Dragon protein from *Drosophila* cell culture causes loss of centrosomes, I wished to determine whether Dragon and Sas6 directly interact with each other.

To this end I first expressed full-length GST-tagged Sas6, full-length GST-Dragon and GSTalone in *E. coli.* I purified all of the proteins by binding to Glutathione Sepharose 4B resin via their GST tag (section 2.5.1). Secondly, I synthesised radioactively (³⁵S-Methionine) labelled Sas6 and Dragon protein in coupled transcription-translation reactions. The reactions were performed using the Promega kit TnT® T7 Quick Coupled Transcription/Translation System which contains T7 polymerase and rabbit reticulocyte lysate. For the *in vitro* binding assays, I individually incubated GST-tagged protein or GST-alone bound to resin with ³⁵S-Methioninelabelled protein in binding buffer and at room temperature (section 2.8.1). After allowing a period for binding, I washed the resin samples multiple times and subjected them to SDS-PAGE, transferred the separated proteins to nitrocellulose membrane and exposed them at -80°C using enhancer film. The signal detected on the autoradiogram shows if and to a certain extent how well the ³⁵S-Methionine-labelled protein binds to the protein on resin.

I first analysed whether GST-Dragon immobilised on resin would bind ³⁵S-Methioninelabelled Sas6 protein directly (Figure 5-5A) and secondly, if GST-Sas6 immobilised on resin would bind ³⁵S-Methionine-labelled Dragon protein directly (Figure 5-5B). As a negative control, I used GST-alone bound to resin. ³⁵S-Methionine-labelled Sas6 does not bind to GST alone (lane 2) but shows a strong binding with GST-Dragon. In the reciprocal experimental set up of the *in vitro* binding assays, GST-Sas6 bound to ³⁵S-Methioninelabelled Dragon whereas GST-alone did not (Figure 5-5B).

In summary, the *in* vitro transcription-translation system and binding assay, which contains only the two proteins of interest confirms that Dragon and Sas6 protein bind each other directly *in vitro*, accounting for the co-purification of Sas6 and Dragon in complex from cultured *Drosophila* cells and *Drosophila* syncytial embryos.



Figure 5-5 Sas6 and Dragon interact directly *in vitro.* (A) GST-Dragon was incubated with ³⁵S-Methionine-labelled Sas6 and (B) GST-Sas6 was incubated with ³⁵S-Methionine-labelled Dragon. The complexes were subjected to SDS-PAGE and autoradiography. Both interaction assays confirm that Sas6 and Dragon interact directly with each other *in vitro*. GST (negative control) did not exhibit any interaction with ³⁵S-Methionine-labelled Dragon nor ³⁵S-Methionine-labelled Sas6. * indicates protein sample loaded; ** indicates reticulocyte lysate residue.

5.2.4.2 The C-terminal region of Sas6 binds directly to Dragon in vitro

After I identified full-length Dragon and Sas6 as directly interacting proteins *in vitro*, I wanted to further understand which regions of the proteins were required for the direct protein-protein interaction.

To analyse which region within Sas6 interacts with Dragon *in vitro*, I generated vectors containing fragments of Sas6 downstream of a T7 promotor, to generate protein fragments of Sas6 with the Promega TnT® T7 Quick Coupled Transcription/Translation System for radioactive labelling. I then performed binding assays with these ³⁵S-Methionine-labelled Sas6 fragments and GST-Dragon (full-length) bound to resin (section 2.8.1). The Sas6 fragments I tested in this way are summarised in Figure 5-6 and Figure 5-7.

The first series of Sas6 fragments were designed according to the predicted secondary structure of Sas6 (Figure 5-9). These Sas6 fragments represented the N-terminal head-domain of Sas6 (N, aa1-180); the majority of the coiled-coil domain (CC, aa181-408); the N-terminal head- and majority of the coiled-coil domain together (NC, aa1-408); and the coiled-coiled domain with the unstructured most C-terminal part (CC+C, aa181-472). I carried out binding assays with each of these ³⁵S-Methionine-labelled Sas6 fragments and GST-Dragon before carrying out SDS-PAGE and protein transfer onto nitrocellulose membrane for autoradiography. I observed direct interaction of Dragon only with the Sas6 fragment containing the coiled-coiled and unstructured C-terminal region (CC+C, aa181-472). None of the other analysed Sas6 fragments interacted with Dragon (Figure 5-6, Figure 5-7A).

We know from structural studies that the N-terminal head domain of Sas6 forms the 'inner hub' of the centriole cartwheel and that the N-terminal part of the coiled-coiled domain of Sas6 molecules dimerise and form the cartwheel spokes of the centrioles (Figure 1-8, Figure 1-7). My above described analysis suggests that a region at the C-terminal part of the Sas6 coiled-coil domain and adjacent upstream sequence is important for interaction with Dragon. The coiled-coil region alone (CC) and the N-terminus are not sufficient for binding to Dragon. This suggests an interaction of Dragon with Sas6 in its so far uncharacterised C-terminal coiled-coil region.

To further narrow down the region of Sas6 necessary for binding Dragon, I generated additional Sas6 fragments from within the fragment aa181-472. These constructs are stepwise truncations from the N- or C-terminus of the Sas6 aa181-472 fragment (Figure 5-6). Each of these Sas6 fragments was labelled with ³⁵S-Methionine by coupled transcription-translation reaction and tested for its ability to bind GST-Dragon immobilised on resin. The

most C-terminal truncated Sas6 construct analysed that still exhibits direct binding with Dragon is the Sas6 fragment aa1-462 (Figure 5-6, Figure 5-7C). Sas6 fragments smaller, including aa1-452, do not bind Dragon. Hence, the very C-terminal 10aa of Sas6, which represent the unstructured C-terminus of the protein according to secondary structure prediction in Figure 5-9, are not essential for binding with Dragon. Removal of N-terminal sequence from Sas6 did not prevent interaction with Dragon until residue 351 (construct aa351-472; Figure 5-6, Figure 5-7B).

Taken together, Sas6 protein fragments aa1-462 and aa351-472 are respectively the most C- and N-terminal truncated protein fragments which are still able to directly interact with Dragon *in vitro*. Thus the Sas6 protein region 351-462aa is necessary for interaction with Dragon. Interestingly, this region of Sas6 shows conservation between species (Figure 5-8).



Figure 5-6 Schematic diagram of interactions of Sas6 protein fragments with Dragon *in vitro.* Sas6 fragments are shown relative to secondary structure features of Sas6 (N-term, coiled-coil, C-terminal coiled-coil and unstructured region). 19 Sas6 fragments were analysed corresponding to the indicated numbers of amino acids. Blue, Sas6 fragments that interact with Dragon *in vitro*. Yellow, Sas6 fragments that do not interact with Dragon *in vitro*. Units of the interacting region are identified by red arrows and pink shading.



Figure 5-7 Autoradiograms of Sas6 fragments and their interaction with full-length **Dragon.** (A) Sas6 segment aa181-472 interacts with Dragon. (B) Testing for the smallest Sas6 fragment with stepwise N-terminal truncations within aa181-472 that interacts with Dragon reveals aa351-472. (C) Testing for the most C-terminal truncation within Sas6 that allows for interaction with Dragon reveals aa1-462. Complementary to Figure 5-6. Shown is 1% input of ³⁵S-Methionine-labelled Sas6 constructs and their interaction with GST (negative control) or GST-Dragon. Autoradiograms in (C) were cropped from the same exposure, original film in Appendix D.

Drosophila	AEKKILHTKRQALEMA <mark>SEEISKANQIIVK</mark> QSQELLN <mark>L</mark> KKTIAWRTE <mark>VALQQEK</mark> AVQAKES
Danio	SKQLQISKLESTVKSL <mark>SEELIKANGIIKK</mark> LQADLKA <mark>L</mark> LGKIKVKNS <mark>V</mark> TVP <mark>QEK</mark> ILQETSD
Xenopus	OKOVOTGKLETTVKSL <mark>SEELIKANEIIKK</mark> LOTDMKKLMEKIKLKNA <mark>VTMOOEK</mark> LLGEKEO
Homo	KNOVOLGKLEATIKSL <mark>SAELLKANEIIKK</mark> LOGDLKTLMGKLKLKNTVTIO <mark>OEK</mark> LLAEKEE
Mus	KNŐIŐLGKLEATIKSL <mark>SAELLKANEIIKK</mark> LŐGDLKTLMGKLKLKNT <mark>V</mark> TIŐ <mark>ŐEK</mark> LLAEKEE
Drosophila	LLSLRENELREARITIEKLREEIPOOLOSMRNFAOGLEOKY <mark>SKOIL</mark> ILKERL
Drosophila Danio	LLSLRENELREARITIEKLREEIPQQLQSMRNFAQGLEQKY <mark>SKQIL</mark> ILKERL KLOROORELODTOORLSLKEEEAAKLKEOLEATVOKLDESREVLKTNENV
Drosophila Danio Xenopus	LLSLRENELREARITIEKLREEIPQQLQSMRNFAQGLEQKY <mark>SKQIL</mark> ILKERL KLQRQQRELQDTQQRLSLKEEEAAKLKEQLEATVQKLDESREVLKTNENV TLOKEKLELTNIKHTLKMKEEEMLKLKEOLDSTTEKLEESKOLLKTNENV
Drosophila Danio <u>Xenopus</u> Homo	LLSLRENELREARITTEKLREEIPQQLQSMRNFAQGLEQKY <mark>SKQIL</mark> ILKERL KLQRQQRELQDTQQRLSLKEEEAAKLKEQLEATVQKLDESREVLKTNENV TLQKEKLELTNIKHTLKMKEEEMLKLKEQLDSTTEKLEESKQLLKTNENV KLOKEOKELODVGOSLRIKEOEVCKLOEOLEATVKKLEESKOLLKNNEKL
Drosophila Danio Xenopus Homo Mus	LLSLRENELREARITTEKLREEIPQQLQSMRNFAQGLEQKY <mark>SKQIL</mark> ILKERL KLQRQQRELQDTQQRLSLKEEEAAKLKEQLEATVQKLDESREVLKTNENV TLQKEKLELTNIKHTLKMKEEEMLKLKEQLDSTTEKLEESKQLLKTNENV KLQKEQKELQDVGQSLRIKEQEVCKLQEQLEATVKKLEESKQLLKNNEKL MLOKERKESODAGOFLRAKEOEVCRLOEOLETTVOKLEESKOLLKNNEKL
Drosophila Danio <u>Xenopus</u> Homo Mus	LLSLRENELREARITTEKLREEIPQQLQSMRNFAQGLEQKYSKQILILKERL KLQRQQRELQDTQQRLSLKEEEAAKLKEQLEATVQKLDESREVLKTNENV TLQKEKLELTNIKHTLKMKEEEMLKLKEQLDSTTEKLEESKQLLKTNENV KLQKEQKELQDVGQSLRIKEQEVCKLQEQLEATVKKLEESKQLLKNNEKL MLQKERKESQDAGQFLRAKEQEVCRLQEQLETTVQKLEESKQLLKNNEKL

Figure 5-8 Alignment of the Dragon interacting region of *Drosophila melanogaster* **Sas6 (aa351-462) shows that it is highly conserved.** The five aligned species are: *Drosophila melanogaster, Danio rerio, Xenopus laevis, Homo sapiens* and *Mus musculus.* Pink background highlights amino acids conserved between species; grey background highlights similar amino acid groups between species, with dark grey background highlighting the amino acid for *Drosophila melanogaster*. Alignment generated with Clustal Omega ²⁸⁴.



Figure 5-9 Secondary structure prediction shows that Dragon-interacting domain of Sas6 (aa351-462) is the C-terminal part of a predicted coiled-coil domain. Sas6 fulllength secondary structure prediction shows the N-terminal head domain between residues 1 and 180, followed by a predicted coiled-coil domain and a small C-terminal unstructured region. Windows described in ²⁸⁶; the higher the window number, the better is the distinction between coiled-coil and other regions. Analysing software: coils server ²⁸⁶.

5.2.4.3 The C-terminal coiled-coiled region of Dragon interacts directly with Sas6 *in vitro*

After I identified the Sas6 region aa351-462 within its coiled-coiled domain to interact directly with Dragon in vitro, I wanted to determine which part of Dragon binds directly to Sas6. To this end I constructed recombinant DNAs containing a T7 promotor and fragments of the Dragon DNA sequence, which I used to generate ³⁵S-Methionine-labelled Dragon protein fragments by coupled transcription-translation. I divided the Dragon protein fragments into Nand C-terminal parts (aa1-171 and aa172-339 respectively), and approximate thirds (aa1-113, aa114-243 and aa244-339 respectively) (Figure 5-10). I then performed binding assays with these ³⁵S-Methionine-labelled Dragon protein fragments and GST-Sas6 immobilised on resin (section 2.8.1). The fragments aa1-113, aa1-171 and aa114-243 did not interact with Sas6 whereas the fragment aa172-339 bound efficiently. The smaller C-terminal Dragon fragment, aa244-339, interacted with Sas6 but more weakly. I then expressed a Dragon fragment, aa191-318, designed to cover the predicted C-terminal coiled-coil domain of the protein (Figure 5-12). This fragment of Dragon (aa191-318) interacted with Sas6 as efficiently as full-length Dragon (Figure 5-11). This coiled-coil region of Dragon exhibits a high homology with Danio rerio, Mus musculus and Homo sapiens, Xenopus (Silurana) tropicalis and Chrysemys picta bellii (Figure 5-13).

In summary, the *in vitro* binding assays identified aa191-318 of Dragon as the binding domain for Sas6 protein, which corresponds to a predicted and conserved coiled-coil domain. I also showed that the aa351-462 segment of Sas6 interacts directly with Dragon (Figure 5-14).

Results



Figure 5-10 Schematic image of Dragon protein fragments that were tested for direct interaction with full-length Sas6 *in vitro.* The binding assays identified the C-terminal Dragon aa191-318 domain as the smallest fragment to strongly interact with Sas6. Blue, interaction; blue stripes, weak interaction; yellow, no interaction of Dragon fragment and Sas6 *in vitro*.



Figure 5-11 Autoradiograms showing binding of Sas6 with Dragon full-length and Dragon aa191-318. In contrast the comparably weak interaction with the smaller Dragon aa244-339 fragment. GST and GST-Sas6 immobilised on resin were incubated with ³⁵S-Methionine-labelled Dragon full length (aa1-339), aa191-318 or aa244-339. 1% input of the ³⁵S-Methionine-labelled Dragon constructs and the resin complexes were then subjected to SDS-PAGE and autoradiography. Complementary to Figure 5-10.



Figure 5-12 Secondary structure prediction of Dragon aa191-318, identified as interacting directly with Sas6 *in vitro*. This region of Dragon is predicted to be the main coiled-coil structure (right, pink) within the protein. Analysing software: coils server (left) ²⁸⁶ and Psipred (right) ²⁸⁵.

Drosophila Danio Xenopus Chrysemys Homo Mus	ISLKDFEQHRRMIEEQNKQKKQMLYQAIEQHTQKTAAESRKIEEIRHELSKLESDLAVDVALLRKQ NRLQQLQWEQRIMEEKNKKRKALLTKTIAEKSKQTQAEAIKLKKIQRELQVLDDSVSSDIGVLRKL SRLDQLQMEQRLMEEKNKRKKALLAKAIAERSKKTQAEAVKLNRIQKQLQALDDLVSTDIGILRNR SRWEVLQQEQRLMEEKNKRKKALLAKAIAERSKRTQAETVKLKRIQKELQALDDMVSADIGILRNR SRWEVLQQEQRLMEEKNKRKKALLAKAIAERSKRTQAETMKLKRIQKELQALDDMVSADIGILRNR SRWEVLQQEQRLMEEKNKRKKALLAKAIAERSKRTQAETMKLKRIQKELQALDDMVSADIGILRNR SRWEVLQQEQRLMEEKNKRKKALLAKAIAERSKRTQAETIKLKRIQKELQALDDMVSADIGILRNR
Drosophila Danio Xenopus Chrysemys Homo Mus	IDNACIHFAN <mark>V</mark> EKQYVKIEAQELRAKIELHN <mark>A</mark> SEKKELLTEHLCTVIAHNEDRKAQKLTELMQKV IEQSSMDYSLAWKRFEKAEAEYVAAKMDLHRKTEVKEQLTEHLCAIIQQNELRKARKLEELMLQL IDQACMEFSQAKKRYDKAEAEYILAKVDLHKKTELKEQLTEHLCTIIQQNEARKAKKLEELMQQL IDQASMDYSFARKRYDKAESEYVAAKLDFQRKTEIKERLTEHLCTIIQQNELRKAKKLEELMKQL IDQASLDYSYARKRFDRAEAEYIAAKLDIQRKTEIKEQLTEHLCTIIQQNELRKAKKLEELMQQL IDQASLEYSYARKRFDRAEAEYITAKLDLQRKTETKEQLTEHLCTIIQQNELRKAKKLEELMQQL *:::::::::::::::::::::::::::::::::::

Figure 5-13 Alignment of *Drosophila melanogaster* **Dragon aa190-320 with other species reveals conservation of the coiled-coil domain.** The five aligned species are: *Drosophila melanogaster, Danio rerio, Xenopus laevis, Chrysemys picta bellii, Homo sapiens* and *Mus musculus*. Pink, amino acids conserved between all analysed species; grey, similar amino acid groups between species; dark grey, the single divergent amino acid within the analysed species; and yellow, a single divergent amino acid in *Drosophila* compared to all other analysed species. Alignment generated with Clustal Omega²⁸⁴.



Figure 5-14 Summary figure of *in vitro* **direct interaction assays.** The C-terminal Sas6 aa351-462 (light blue) interacts directly with C-terminal Dragon aa191-318 (light blue) *in vitro*. Pink, Dragon interaction motif aa260-286 (as described in section 5.2.5).

5.2.4.4 Dragon interacts with itself in vitro

Sas6 molecules are known to dimerise via their coiled-coil regions and assemble into 9-fold cartwheel structures via their N-terminal head domains. This led me to consider whether Dragon, like Sas6, might oligomerise. I applied the *in vitro* direct binding assay used in previous sections to answer this question. I incubated full-length GST-Dragon bound to resin with full-length ³⁵S-Methionine-labelled Dragon in a binding assay, washed the resin to remove any unbound ³⁵S-Methionine-labelled Dragon, and subjected aliquots to SDS-PAGE and transferred the separated proteins onto nitrocellulose membrane for autoradiography. This showed that full-length Dragon molecules interact directly with each other. To characterise which region of Dragon enables oligomerisation, I carried out binding assays with the previously described ³⁵S-Methionine-labelled Dragon fragments and GST-Dragon (full-length) and GST-alone control (Figure 5-15). This revealed the C-terminal third of Dragon (aa244-339) as the smallest analysed Dragon fragment which can efficiently bind full-length Dragon directly (Figure 5-16). This region overlaps with the region that interacts with Sas6 (aa191-318; section 5.2.4.3). Significantly, the aa244-339 segment of Dragon was not able to bind Sas6 protein as efficient as aa191-318 (section 5.2.4.3). The analysis of the

smallest protein region necessary for oligomerisation of Dragon still needs to be analysed further.



Figure 5-15 *In vitro* interaction analysis shows that Dragon interacts with itself at its **C-terminus.** Five Dragon fragments representing thirds and halves of the protein show that Dragon C-terminus is important for potential oligomerisation, with the most narrow analysed fragment covering aa244-339.



Figure 5-16 Dragon C-terminus (aa244-339) interacts with Dragon full-length *in vitro.* Protein coomassie gel and autoradiography show that ³⁵S-Methionine-labelled Dragon aa244-339 directly interacts with Dragon full-length protein. * protein sample loaded; ** reticulocyte lysate residue.
5.2.5 Identification of the interaction motif (IM) in Dragons' C-terminal binding domain which is essential for interaction with Sas6

5.2.5.1 *In vitro* direct interaction screen of Dragon mutants, to identify a Dragon interaction motif necessary for the binding of Sas6

In section 5.2.4.3, I described a region of 128aa within the C-terminus of Dragon aa191-318 as able to bind Sas6. To narrow down the binding region I made small deletions within the conserved binding domain (Dragon aa191-318) by site-directed mutagenesis of grouped conserved amino acids. These mutants are summarised in Figure 5-17. These mutant constructs were used to generate ³⁵S-Methionine-labelled proteins *in vitro* that were used in binding assays with GST-Sas6. The outcome of these experiments is summarised in Figure 5-17. It can be seen that the smallest deletion which abolishes Dragon's binding to Sas6 is aa260-286. Interestingly, three independent and smaller deletions within the region of Dragon (aa260-266, aa267-281 and aa282-286) are still able to bind Sas6 (Figure 5-18). Two further but larger deletion mutants, which include the 260-286aa deletion, also abolish binding of Sas6, namely deletions aa220-286 and aa220-318. This confirms the importance of aa260-286 of Dragon, in its interaction with Sas6. All other tested Dragon-mutants that carry a deletion outside of aa260-286 bind Sas6 efficiently *in vitro*.



Figure 5-17 Dragon deletion mutants used to identify interaction motif (IM) for binding to Sas6 as aa260-286. 11 Dragon mutants were generated in full-length Dragon protein by site-directed mutagenesis, with deletions indicated. ³⁵S-Methionine-labelled mutant proteins were used in direct *in vitro* interaction assays with Sas6. +, *in vitro* interaction of Sas6 with Dragon mutant. -, no *in vitro* interaction of Sas6 with Dragon mutant.



Figure 5-18 The mutant Dragon^{ΔIM} (DragonΔaa260-286) is unable to interact with Sas6 in vitro. Autoradiography of Sas6 interaction with ³⁵S-Methionine-labelled Dragon FL, DragonΔaa267-281 and Dragon^{ΔIM} (Δaa260-286); confirming interaction of the full-length proteins Sas6 and Dragon but that deletion of aa260-286 within Dragon abolishes this interaction. A smaller deletion in DragonΔaa267-281 still allows for interaction with Sas6. Short and long exposures confirm the lost direct interaction between Dragon^{ΔIM} and Sas6.

5.2.5.2 Purification of GFP-Dragon constructs from *Drosophila* cell culture, transiently transfected with Sas6 and Dragon variants, confirms that the Dragon-IM region is essential for interaction with Sas6 *in vivo*

Having identified a Dragon deletion (Δ aa260-286) that fails to bind Sas6, I wished to determine the consequences of expressing this protein *in vivo*. Therefore, I transiently transfected *Drosophila* cell culture with myc-Sas6 and GFP; myc-Sas6 and GFP-Dragon; and myc-Sas6 and GFP-Dragon^{Δ IM} and performed GFP-purifications with extracts of each of the three transiently transfected cell culture samples. I then determined by Western Blotting and antibody staining, which Dragon construct could interact with Sas6 (Figure 5-19). I used antibodies against GFP, myc and α -tubulin to detect GFP/GFP-Dragon/GFP-Dragon^{Δ IM}, myc-

Sas6 and α -tubulin (control) respectively. Figure 5-19 shows the according Western Blots of the GFP-purifications and inputs/cell lysates. The inputs confirm that each combination of transient transfection was efficient, as anti-GFP detects GFP, GFP-Dragon and GFP-Dragon^{ΔIM}, anti-myc detects myc-Sas6, and α -tubulin is detected in all three samples. The Western Blots of the GFP-purifications confirm that GFP, GFP-Dragon and GFP-Dragon^{ΔIM} are present in the respective cell samples. Significantly, I could only detect myc-Sas6 associated with GFP-Dragon. I could not detect myc-Sas6 with GFP only or with GFP-Dragon^{ΔIM}. Thus the deletion of aa260-286 in otherwise full-length Dragon abolishes the interaction with Sas6 *in vivo*, confirming my *in vitro* findings.



Figure 5-19 Co-IP confirms *in vivo* that Dragon^{Δ IM} cannot interact with Sas6. *Drosophila* cell cultures were transiently transfected with myc-Sas6 and GFP-Dragon^{Δ IM}, GFP-Dragon or GFP, followed by GFP-IP. Western Blot and anti-myc staining shows loss of interaction between Sas6 and GFP-Dragon^{Δ IM}, whereas interaction occurs between Sas6 and Dragon. Anti-GFP stains for GFP, GFP-Dragon and GFP-Dragon^{Δ IM}. Anti- α -tubulin control and anti-myc signals detected in the input samples.

5.2.5.3 GFP-Dragon^{∆IM} and its effect on centrosome numbers compared to GFP-Dragon and *Drosophila* WT cells

I then wished to determine whether the Dragon^{ΔIM} mutant could rescue loss of centriole depletion resulting from Dragon depletion (section 5.2.3.1). This experiment necessitated that I deplete Dragon efficiently with dsRNA against its UTR sequence so that I could utilise the mutant gene that does not carry the UTR sequences. To determine whether UTR mediated RNAi had similar effect on centriole duplication as observed with RNAi using Dragon CDS I carried out three 4 day rounds of RNAi directed against GST (control), Dragon CDS and Dragon UTRs (Figure 5-20). The loss of centrosomes was significant in a comparison between GST (control) and both Dragon depletions (CDS and UTRs). There is also a significant difference in cells without centrosomes when RNAi against Dragon CDS is compared to Dragon UTRs. But this difference is less significant compared to the GST control. Thus, depletion of Dragon by dsRNA CDS and UTRs are efficient and have a significant effect on centriole duplication, causing loss of centrosomes.



Figure 5-20 Depletion of Dragon using dsRNA against Dragon CDS or Dragon UTRs both lead to loss of centrosomes. *Drosophila* cell culture was depleted of Dragon by RNAi (dsRNA CDS or dsRNA UTRs) versus GST control RNAi. Centrosome numbers were scored on day 12, after three rounds of depletion. Error bars represent standard error; 3x200 cells counted; significance was calculated by t-test.

Having identified conditions for efficient depletion of Dragon by RNAi directed against its UTRs, I generated a cell line stably expressing GFP-Dragon^{ΔIM} from the constitutively active promotor poly-Ubiquitin. RNAi directed against Dragon UTR in control cells resulted in an increase of cells lacking centrosomes, from 13.3% to 26.7%. A similar result was seen for GFP-Dragon^{ΔIM} expressing cells where cells without centrosomes increase from 6.8% to 15.2%. But GFP-Dragon expressing cells show only a slight increase of cells without centrosomes, from 14.8% to 21.2%. The ratio of cells without centrosomes after GST RNAi versus Dragon UTRs RNAi is 1:2 in control cells, 1:2.2 in GFP-Dragon^{ΔIM} expressing cells, and 1:1.4 in cells expressing GFP-Dragon. Hence, Dragon^{ΔIM} fails to rescue the depletion of endogenous Dragon (Figure 5-21). The Western Blot in Figure 5-22 shows the complete depletion of endogenous Dragon after RNAi of Dragon UTRs and the expression of constitutively expressed GFP-Dragon and GFP-Dragon^{ΔIM}.







Figure 5-22 Endogenous Dragon is fully depleted from wild-type *Drosophila* cells and cells stably expressing GFP-Dragon or GFP-Dragon^{ΔIM} after two rounds of RNAi against Dragon UTRs over 8 days. Constitutively expressed GFP-Dragon and GFP-Dragon^{ΔIM}, and endogenous Dragon are revealed by anti-DragonN antibody staining after Western Blot.

5.2.6 Study of the human homologues GoRab and HsSas6, in relation to the findings for *Drosophila* Dragon and Sas6

5.2.6.1 The human homologues GoRab and HsSas6 interact directly *in vitro*

As human cells have homologues for both proteins Dragon and Sas6, namely GoRab and HsSas6 respectively, I wished to analyse if these human homologues also interacted directly. The human homologue GoRab has two functional isoforms, variant 1 and variant 3. The first isoform represents the full-length protein (395aa) and the latter is a shorter version (247aa), which lacks the C-terminal extension of variant 1. When comparing these two variants with *Drosophila* Dragon by homology, it is evident, that only GoRab variant 1 contains the region homologous to *Drosophila* Dragon-IM (aa260-286) and the full *Drosophila* Sas6-binding domain (aa191-318). GoRab variant 3 contains only aa191-247, which corresponds to the N-terminal region of the *Drosophila* Dragon for Sas6 binding (aa191-246) upstream of *Drosophila* Dragon-IM (aa260-286) (Figure 5-23, Figure 5-24). To

study if human GoRab and HsSas6 interact directly with each other, I expressed GST-HsSas6 in *E. coli* and bound it to Glutathione Sepharose 4B resin via the GST tag (section 2.5.1). I generated ³⁵S-Methionine-labelled GoRab variant 1 and variant 3 by coupled *in vitro* transcription-translation reaction. I then performed *in vitro* binding assays (section 2.8.3) with GST-HsSas6 and ³⁵S-Methionine-labelled GoRab variant 1 or variant 3, subjected the proteins to SDS-page and transferred the separated proteins onto nitrocellulose membrane for autoradiography. The autoradiograms show that GoRab variant 1 directly interacts with HsSas6 but not the negative control GST-alone (Figure 5-25A). In contrast, ³⁵S-Methionine-labelled GoRab variant 3 interacts similarly with the negative control GST and GST-HsSas6, indicative of background binding and not due to the interaction of ³⁵S-Methionine-labelled GoRab variant 3 with HsSas6.

In summary the human counterparts of Dragon and Sas6, GoRab variant 1 and HsSas6, also interact directly with each other *in vitro*. A second isoform of the human homologue, GoRab variant 3, which is a shorter C-terminal truncated isoform of variant 1, does not interact directly with HsSas6 *in vitro*.



Figure 5-23 Homology between *Drosophila* Dragon and *Homo sapiens* GoRab variant **1** and variant **3**. *Drosophila* Dragon aa191-318 (green) is the Sas6 binding domain identified by direct *in vitro* binding assays, and aa260-286 (purple) is the Dragon-IM that is necessary for Sas6 to bind Dragon. GoRab variant 1 includes the full and according homologous region of Dragon aa190-318, whereas GoRab variant 3 is a shorter isoform which only contains the most N-terminal homologous region and lacks the homologous Dragon-IM and the upstream sequence.

Results



Figure 5-24 Alignment of *Drosophila* **Dragon aa185-338 and** *Homo sapiens*** GoRab variant 1 and variant 3.** GoRab variant 1 and variant 3 share the same sequence of amino acids but differ in length. Highlighted are the same amino acids that are identical between Dragon and GoRab (pink) or similar (grey). Alignment generated with Clustal Omega²⁸⁴.



Figure 5-25 Only the long isoform of GoRab variant 1 directly interacts with HsSas6 *in vitro*, **confirming findings for** *Drosophila* **Dragon and Sas6**. ³⁵S-Methionine-labelled GoRab variant 1 and variant 3 were individually assessed for binding to HsSas6 *in vitro*. Coomassie stainings show protein inputs for GST and GST-HsSas6. Autoradiograms show direct interaction of GoRab variant 1 with HsSas6 but lacks specific interaction for GoRab variant 3 with HsSas6.

5.2.6.2 Centrosome numbers are reduced in U2OS cells following GoRab RNAi

After I determined that HsSas6 and GoRab variant 1 could interact directly with each other *in vitro* (section 5.2.6.1), I wished to know whether depletion of GoRab in human cell culture

would reduce centrosome numbers, as observed after depletion of Dragon in *Drosophila* cell culture in section 5.2.3.1.



Figure 5-26 Depletion of GoRab in U2Os cells negatively affects centriole duplication. U2Os cells that are arrested in S-phase by Aphidicolin (A) and HydroxyUrea (HU) treatment and under control GFP siRNA conditions show a significant increase in cells with \geq 4 centrosomes per cell. Treatment of U2Os cells with GoRab siRNA prevents an increase in cells with \geq 4 centrosomes per cell, suggesting a negative effect on centriole duplication. Error bars represent standard error; 3x100 cells counted.

To address this question, I depleted GoRab via siRNA from U2OS cells and blocked the cells in S-phase 24 hours after transfection with Aphidicolin and Hydroxyurea before assessing centrosome numbers; GFP siRNA was used as a negative control (section 2.9.4). When U2OS cells are blocked in S-phase by Aphidicolin and Hydroxyurea, DNA duplication and therefore cell division is prohibited, but centriole duplication still occurs as normal leading to an increase in the number of centrosomes within each cell. Accordingly, cells treated with control RNAi and blocked in S-phase show an increase from 2.7% to 19.7% of

cells having \geq 4 centrosomes per cell. By contrast, U2OS cells treated with GoRab siRNA alone exhibited just 4% of cells with \geq 4 centrosomes per cell, which is comparable to the 3% of U2OS cells showing \geq 4 centrosomes per cell after treatment with GoRab siRNA and being blocked in S-phase. This shows that duplication of centrosomes in S-phase blocked U2OS cells is prevented after depletion of GoRab. Thus, the homologues Dragon and GoRab appear to have roles in centriole duplication in *Drosophila* and human cells respectively.

5.3 Discussion

5.3.1 Dragon and the centrosome

It is curious why purification of Sas6 from cultured cells do not show other centriole duplication proteins. But most interestingly, the uncharacterised Dragon was present in all Sas6 purifications (Table 5-1). Indeed, Dragon and Sas6 appear to be in complex *in vivo*, when either is overexpressed in *Drosophila* cell cultures, or in *Drosophila* syncytial embryos overexpressing Dragon (Table 5-1 and Table 5-2). The levels/'number of peptides' of Dragon were increased when purified Sas6 is constitutively expressed in *Drosophila* syncytial embryos compared to induced overexpression of Sas6 in *Drosophila* cell culture. On the other hand treatment with okadaic acid to inhibit dephosphorylation by PP2A and treatment with MG132 to inhibit proteasomal degradation did not seem to affect the ratio of Sas6:Dragon. Thus, Dragon seems to associate with Sas6 in a phosphorylation independent manner. On the other hand, the constitutive expression of Dragon results in a higher number of Sas6 peptides in complex compared to the induced expression of Dragon, which can be due to constitutive versus induced expression. Alternatively, complex formation could be affected by the tag on the N- or C-terminus of Dragon. It is possible that the GFP-tag at the C-terminus interferes with the ability of Sas6 to be in complex with Dragon.

Dragon localises with Sas6 to the mother and procentriole/daughter centriole (Figure 5-2). Its presence at procentriole formation could indicate that it supports the process of daughter centriole formation ²⁹⁶. An indication for a potential structural role of Dragon at the centriole is its localisation not only at the procentriole/daughter centriole but that it also remains co-localised with Sas6 at the mother centriole. Additionally, depletion of Dragon causes loss of centrosomes (Figure 5-4). To further understand the recruitment of Sas6 and Dragon to the centriole, additional structural illumination microscopy needs to be performed to study the interdependency of Dragon and Sas6 at the centriole when one or the other protein is depleted. This will shed light on their recruitment hierarchy to the site of procentriole

formation to determine whether this occurs sequentially, together, or interdependent, and the consequences of their depletion upon the centrosome structure.

5.3.2 Dragon and the Golgi

Dragon also localises to the Golgi (Figure 5-1), in accordance with previous observations with the human homologue GoRab²⁰². Specifically it co-localises with Golgin-245 at the trans-Golgi (Figure 5-3), as was observed for the human homologue GoRab²⁰², and the GoRab interacting partner Rab6³²⁰. Dragon's function at the *trans*-Golgi is not known but indications from mass spectrometry analyses of its complexes suggest a potential role in dependency to COPI. This is because five out of seven subunits of COPI were identified by mass spectrometry as co-purifying with Dragon from cultured Drosophila cells. Interestingly, COPI is one of three types of vesicles at the Golgi, in addition to COPII and clathrin-coated vesicles. These proteins are vesicle coat proteins with a diverse set of functions at the Golgi, representing division of the Golgi into three stages of maturation from the cisternal assembly stage to the carbohydrate synthesis stage and carrier formation (Figure 1-13) ^{321,322}. The three types of Golgi coat proteins function in direct protein and membrane trafficking, by selecting specific cargo proteins in different Golgi compartments. Proteins synthesized in the Endoplasmic Reticulum (ER) are selectively exported by COPII vesicles, which in turn then bud to form new cis-Golgi cisterna ³²³. On the other hand, COPI vesicles function in the transfer of Golgi proteins between medial- and trans-Golgi cisternae, and additionally recycle proteins from the *cis*-Golgi to the ER³²³⁻³²⁶. The third vesicle type, clathrin-coated vesicles, are cargo carriers that form during cisterna disintegration at the trans-Golgi-network (TGN) and apparently recycle proteins from mature to newly formed TGN cisternae ³²⁷⁻³²⁹. It is known that COPI protein forms two subcomplexes; the adaptor subcomplex made up of γ-βδ-ζ-COPs and the cage-like subcomplex of α -β'-ε-COPs ^{330–334}. The mass spectrometry data shows that all subunits of the latter are present in the Dragon purifications from Drosophila cell culture (Table 5-3). Thus, suggesting a COPI specific function of Dragon at the Golgi.

That the subunits of COPI and COPII are not present in the Dragon complexes purified from Drosophila syncytial embryos most likely reflects the timing of the biosynthesis of the Golgi. The Golgi apparatus consists of small fragments in syncytial and gastrulating Drosophila embryos ^{335–338} but it mainly develops later to have small vesicles and tubules in early thirdinstar larvae (72 hours after fertilisation). Larger clusters of Golgi marked with GM130, p115, and Fringe appear in late third-instar larvae, and only at the pupa state do Golgi stacks appear (120 hours after fertilisation) ^{339,340}. Additional support for the hypothesis that Drosophila Dragon functions in the secretory pathway comes from the known interaction of the human homologue GoRab with Rab6 ²⁰². Rab6 functions in the recruitment of motor proteins and the retrograde transport from endosomes to the Golgi apparatus ^{341,342}. The absence of Rab proteins in complex with the purified Dragon from Drosophila cell culture is therefore surprising but may reflect the stability of this association. I was unable to reveal a function of Dragon at the Golgi because the attempted depletion of Dragon did not show any changes in the co-localisation with the trans-Golgi marker Golgin-245 or localisation of the cis-Golgi marker GM130 by fluorescent microscopy (data not shown, collaboration with Miss Chu). Several explanations are possible: either the RNAi was inefficient at depleting Dragon to a sufficient degree to see a Golgi phenotype; that the assay used was inadequate for deleting Dragon's Golgi function; or that indeed Dragon has no Golgi function. An interesting finding for more study is C-terminal binding protein (CtBP) that is present in complex with Dragon (Table 5-3). CtBP is required for the G2-mitotic checkpoint that leads to fission of the Golgi ribbon into separate Golgi stacks in mammalian cells ³⁴³, followed by further fragmentation and disassembly ³⁴⁴. The specific function or the mechanism behind the disassembly of the mammalian Golgi is not understood but suggestions include that the process could be necessary for the correct division of the Golgi into the two daughter cells by the mitotic spindle during cell division ³⁴⁵ or that the Golgi disassembly might release proteins that are important for chromosome segregation or cytokinesis. Importantly and in contrast to mammalian Golgi, Drosophila Golgi stacks are not connected by a ribbon ¹⁸³ and they do not fragment or disassemble ³⁴⁶. But we know that Dragon exhibits dual localisation to the Golgi and the centrosome (section 5.2.2), and that the Golgi is associated with microtubules and the centrosome ^{184,345}. Initial pilot experiments of *in vitro* binding assay failed to indicate direct protein interaction of CtBP with Dragon or Sas6 (data not shown). Could therefore CtBP function be part of a signalling pathway linking the Golgi and the centrosome or cilia for centricle biogenesis or cilia absorption; for the progress of the cell into mitosis; or the correct division of the Golgi into the two daughter cells during cell division? These speculations also go hand in hand with the finding that the centrosomal Dragon signal increases in interphase and adjusts to the levels of its interacting partner Sas6 thereafter (Figure 5-2). Additionally, the mammalian homologue CtBP is targeted by Pak1 kinase ³⁴⁷, which is required for mitotic entry ³⁴⁸; and the function of CtBP in mitotic entry could be conserved in *Drosophila*. Dragon's specific function at the Golgi was not the focus in this study and further studies need to be performed to understand its potential role in secretion and signalling pathways.

5.3.3 Physical interaction of Dragon and Sas6

My findings demonstrate that Dragon and Sas6 interact directly with each other *in vitro* (section 5.2.4.1). It is Sas6 fragments that contain the C-terminal region of the coiled-coil domain that interact with Dragon *in vitro* (schematic in Figure 5-6). Significantly, this region was not described previously. On the other hand, the N-terminal head domain of Sas6 form the cartwheel hub of centrioles, and the N-terminal regions of the coiled-coil domains of two Sas6 molecules dimerise and form a spoke of the centriole cartwheel. The most truncated protein fragments of Sas6 that still interact strongly with Dragon are the segments aa351-472 and Sas6 aa1-462 (Figure 5-6, Figure 5-7). The latter is potentially truncated by the majority of the predicted unstructured C-terminal domain of Sas6. Figure 5-9 suggests that the predicted coiled-coil domain ends around aa450 and a closer analysis of the homology alignment of Sas6 from multiple species in Figure 5-8 shows a two amino acids insertion (QK: Glutamine and Lysine respectively) only in *Drosophila* at aa449-450 and could potentially be the site of transition from coiled-coil to unstructured protein sequence. The homology alignment of Sas6 (Figure 5-8) shows conserved regions but it does not identify a specifically and highly conserved domain in the C-terminal region of the coiled-coil domain.

The structural features of *Drosophila* Dragon protein are uncharacterised. It has a predicted C-terminal coiled-coil domain (aa191-318, Figure 5-12) that interacts directly with Sas6 *in vitro* (Figure 5-10, Figure 5-11). Significantly, the C-terminal third fragment of Dragon (aa244-339), which is smaller and misses the N-terminal part of the coiled-coil domain, interacts only weakly with Sas6. This suggests a specific interaction of the whole coiled-coil domain of Dragon with Sas6. This notion is supported by the alignment studies of *Drosophila* Dragon aa190-320 with other species, which confirms that the coiled-coil domain is highly conserved between species (Figure 5-13). On the other hand, sequences N- and C-terminal to the coiled-coil region show almost no conserved residues, apart from a short 12 amino acid stretch in the N-terminus (aa5-16 in *Drosophila*, not shown). Thus, the coiled-coil domain is likely to play an important role that is conserved throughout species. The C-terminus of Dragon interacts with Sas6, making it likely that a C-terminally tagged Dragon is less efficient at interacting with Sas6, highlighting the importance of the accessibility of Dragon's C-terminally coiled-coil domain (section 5.2.4.3).

That Dragon interacts with C-terminal Sas6 suggests that it localises to the ends of the centriole cartwheel spokes. Potential functions could be stabilising the cartwheel endings; aiding and guiding Sas6 self-assembly abilities as a distance spacer between Sas6 cartwheel spokes; determining the 9-fold symmetry of the centriole; or supporting the transition zone between the cartwheel and microtubules. The specificity of Dragon interaction and co-localisation with Sas6 is intriguing as Dragon was not observed in other purifications of centriole duplication proteins. Preliminary attempts were made in collaboration with Dr. Gang Dong (Vienna) to address the stoichiometry of the Dragon and Sas6 interaction with the potential to purify an affinity complex for crystallisation trials. However the expression of Dragon resulted in low purification yields, and increasing concentrations led to aggregate formation. On the other hand, a smaller fragment of Dragon (aa172-339) proved unstable and degraded during purification and aggregation have not allowed to date for the measurement of exact binding affinities. Thus, it was not possible to

advance further structural examination of Dragon or its interaction with Sas6. Further studies will be required to precisely characterise Dragon's structure and function at the centrosome.

A region of potential Dragon self-interaction was found in the Dragon C-terminal third (aa244-339) that overlaps with the region that interacts directly with Sas6 (section 5.2.4.4, Figure 5-10, Figure 5-15). The potential of competition between Dragon oligomerisation and its interaction with Sas6 presents regulatory possibilities that should be studied further.

Protein phosphorylation plays a critical role in centriole duplication. Hennies *et al.* highlight that GoRab protein has many predicted phosphorylation sites (Figure 5-27A) ²⁰², but Dragon has potentially many fold more possibilities of potential phosphorylation (Figure 5-27B). Remarkably there are clusters of predicted phosphorylation sites at Dragon aa79-94 and aa113-191, which are located directly upstream of the Sas6 binding site (aa191-318). This further fuels the idea that the phosphorylation of Dragon by an unknown kinase might be necessary for its function at the centrosome or Golgi. To gain a better understanding of Dragon's function at both the centrosome and Golgi, it will be important to identify and characterise other interacting proteins of Dragon and the phosphodependence of their interactions. Additionally, this might further our understanding of the microtubule nucleation functions of the centrosome and the Golgi, and a potential link between the two processes.



Figure 5-27 Predicted generic phosphorylation sites in the homologous GoRab (A) and Dragon (B). Analyses performed with NetPhos 2.0 Server ³⁴⁹ over the whole protein sequences of GoRab and Dragon. The sequence position of potential phosphorylation sites (in amino acids) are blotted against their phosphorylation potential (with 0 to 1 equalling 'unlikely' to 'very likely', and the threshold in red at 0.5). Pictured are predicted phosphorylation sites for Serine (green), Threonine (blue) and Tyrosine (pink). The closer the phosphorylation potential towards 1, the more 'very likely' is the predicted phosphorylation site a true phosphorylation site.

To study the cellular effect of loss of interaction between Dragon and Sas6 at the centrosome, I further analysed which smaller site in Dragon aa191-318 was essential for interaction with Sas6. A mutant that lacks the region aa260-286 cannot interact with Sas6 *in vitro* (section 5.2.5.1). This interaction motif (IM) could be the necessary site for direct protein-protein interaction between Dragon and Sas6 or it could function as a "spacer" within

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Dragon that leads to a secondary structure formation of Dragon that allows for physical interaction with Sas6. If this "spacer" was deleted, as for the Dragon^{Δ IM} mutant, it could change the secondary structure of Dragon and consequently its physical and structural ability to bind Sas6. The Dragon^{Δ IM} mutant cannot rescue the loss of centrosomes after the depletion of endogenous Dragon (section 5.2.5.3). Whether the loss of centrosomes after loss of interaction between Dragon and Sas6 is directly due to failed co-recruitment of Dragon and Sas6 to the procentriole or a missing protein interaction at the centrosome itself requires further study by immune fluorescence and especially high resolution structured illumination microscopy. This will shed light on the dependency of the interaction of Dragon and Sas6 on recruitment and localisation of the two proteins to the centrosome. Both possibilities are likely and yet it is surprising that Dragon has not been described previously in screens for *Drosophila* centriole duplication structurally by interacting with the cartwheel protein Sas6.

5.3.4 The human homologue GoRab and centriole duplication

The human homologue of Dragon, GoRab, has been described in relation to the disease Gerodermia osteodysplastica but a centrosomal connection has not been published. But alignments of Dragon and GoRab from different species, including *Drosophila* and *Homo sapiens*, show that the C-terminal domain of *Drosophila* aa191-318 is highly conserved (Figure 5-13, Figure 5-24). The identification of the novel direct interaction of Sas6 and Dragon and its effects on centriole duplication when Dragon is depleted or cannot interact with Sas6 raises the question if this function is conserved in the human homologue GoRab (section 5.2.6). Two functional isoforms of GoRab are known, GoRab variant 1 and GoRab variant 3, which share the same amino acid sequence but variant 3 is truncated at the C-terminus (Figure 5-22). A closer analysis of the isoforms with the homology alignment reveals that GoRab variant 3 does not align to the full Dragon region that interacts with Sas6

(aa191-318); it only contains most of the N-terminal region downstream of Dragon-IM (aa260-286). On the other hand, GoRab variant 1 aligns along the whole *Drosophila* Dragon sequence. The study of these two GoRab isoforms and their direct interaction with HsSas6 *in vitro* shows that only GoRab variant 1 is able to directly interact with HsSas6. Thus, as observed in *Drosophila*, also the human homologous GoRab and HsSas6 interact directly *in vitro* and the highly conserved C-terminal domain is necessary to allow for this interaction. The conserved interaction between GoRab and HsSas6 raises the question of whether there is a conserved functional role in centriole duplication in human cell culture. Performed siRNA experiments on U2Os cells revealed that the depletion of GoRab protein does result in failure of centriole duplication (Figure 5-26). This is in line with loss of centrosomes observed after Dragon depletion in *Drosophila* cell culture and the failure of Dragon^{ΔIM} to rescue centriole duplication.

Together the data presented in this chapter indicated that the novel direct interaction of Dragon/GoRab with Sas6 has a significant function in centriole duplication. Dragon and Sas6 interact within their C-terminal protein domains and have potential functions for both centriole duplication and structure. The roles of Dragon at the Golgi are less certain and further research will be necessary to further understand the role and specific function of Dragon in vesicle trafficking.

Chapter 6

Final discussion

6 Final discussion

This thesis focuses how the core proteins of the centriole interact with each other as a network, with a specific focus on the structural and functional interaction of Sas6 with Ana2 and Sas6 with Dragon in the process of centriole duplication.

In Chapter 3 I studied the interactions of centriole duplication proteins identified by mass spectrometric analysis of protein complexes purified using affinity tagged centriole duplication proteins in cultured *Drosophila* cells (section 3.2.1). I also performed protein-protein binding assays *in vitro* to test for direct protein interactions (section 3.2.2) and studied direct protein interactions *in vivo* by yeast-2-hybrid assays (section 3.2.3). Together this allowed me to build a protein network of potentially interacting centriole duplication proteins in relation to their localisation within the five zones of the centrosome ^{24,30}. Each of these three methods can be strong and reliable but in my hands they have proven to be a guide for further studies rather than giving conclusive results.

In Chapter 4 I focused on the core centriole duplication proteins Ana2 and Sas6, which were identified as centriole duplication proteins in two genome wide dsRNAi screens in *D. melanogaster* cell culture ^{131,288}. Moreover Sas6 was shown to be a major component of the centriole cartwheel ^{63,69,74,75}. In summary, I show that Plk4 and Ana2 interact directly with each other but that neither shows direct interaction with Sas6 using *in vitro* binding assays (section 4.2.1). Similarly, Plk4 phosphorylates Ana2 but not Sas6 *in vitro* (section 4.2.1.1). Phospho-peptide mapping by mass spectrometry identified that the residues S318, S365, S370 and S373 in the conserved Ana2-STAN motif are phosphorylated by Plk4 (section 4.2.2). Importantly, an Ana2-4A mutant that cannot be phosphorylated by Plk4 leads to loss of centrosomes, which in turn can be rescued by the phospho-mimicking Ana2-4D mutant (section 4.2.3). This suggests an essential downstream event of Ana2 phosphorylation for

centriole duplication. *In vitro* and *in vivo* studies showed that Plk4-phosphorylation of Ana2 mediates the interaction of the centriole cartwheel protein Sas6 with Ana2 (section 4.2.4). Structurally, the Plk4-phosphorylated Ana2-C-terminus is sufficient for the interaction with Sas6 (section 4.2.4.1); and specifically the four Serine residues within the Ana2-STAN motif (S318, S365, S370, S373) need to be phosphorylated by Plk4 for the interaction of Sas6 with Ana2-C-terminus to occur (section 4.2.5). Accordingly, the non-phosphorylatable Ana2-4A mutant does not interact with Sas6 *in vitro*, whereas the phospho-mimicking Ana2-4D does (section 4.2.6). Further *in vitro* interaction studies revealed that the Plk4-phosphorylated Ana2-STAN motif alone is sufficient for interaction with Sas6 and that the Sas6 aa276-432 coiled-coil segment is efficient in binding Ana2 (section 4.2.8).

In Chapter 5 I report the identification and initial characterisation of a novel protein Dragon (CG33052) that associates with centrosomes and the Golgi. Dragon was identified by mass spectrometry analysis of Sas6-complexes purified from cultured Drosophila cells (section 6.2.1.1). Reciprocal purifications of Dragon from cultured Drosophila cells identified the centrosomal cartwheel protein Sas6 and subunits of the Golgi COPI protein in complex with Dragon (section 6.2.1.2 and section 6.2.1.3). Dragon is a novel protein that exhibits dual localisation at the trans-Golgi and the centrosome in Drosophila cell culture. Dragon colocalises with the cartwheel protein Sas6 at the centriole throughout its duplication cycle (section 6.2.2). In vitro binding assays confirmed that Dragon interacts directly with Sas6 (section 6.2.4). Specifically, the segment of Sas6 between aa351-462 interacts directly with the conserved Dragon C-terminal coiled-coil domain (aa191-318) within which the sequence between aa260-286 is necessary for interaction with Sas6. The human homologues of Dragon and Sas6, GoRab variant 1 and HsSas6 respectively, also interact directly in vitro (section 6.2.6.1). Depletion of Dragon/GoRab causes loss of centrosomes in Drosophila cell culture and human U2Os cells (section 6.2.3 and section 6.2.6.2 respectively). Moreover a Dragon^{ΔIM} mutant that does not interact with Sas6 in vitro or in vivo fails to rescue centriole duplication in Drosophila cell culture (section 6.2.5). Thus Dragon appears necessary for centriole duplication. In contrast, the precise function of Dragon at the Golgi and potentially in secretory pathways is uncertain.

The relationship between Plk4, Ana2 and Sas6 and their role in procentriole formation was further characterised by examining loading dependencies in vivo using structured illumination microscopy to assess loading (expertise of Dr. Tzolovsky, RNAi by Dr. Dzhindzhev). These studies support the *in vitro* findings²⁹⁶. Together this establishes the loading dependencies of Ana2 and Sas6 and characterises their interaction in relation to their localisation at the centriole. In wild-type Drosophila cells, endogenous Sas6 and Ana2 localise to the mother and the daughter centriole as two independent dots throughout the cell cycle (the outer centriolar marker D-Plp allows mother and daughter centrioles to be distinguished; Figure 6-1). In interphase and prometaphase, Sas6 and Ana2 localise to the centre of the mother centriole and D-Plp ring, and to the daughter centriole which has yet to develop its D-Plp ring. The daughter centriole matures by recruiting D-Plp in a "horn" like pattern around the centriole and completes its ring structure by meta-/anaphase. This is followed by disengagement of the mother and daughter centriole in anaphase. In late ana-/telophase, each of the separated centrioles shows a new dot for Ana2 and Sas6 at the periphery of the mother D-Plp ring. This characterises the site of the nascent procentriole, which is already determined at telophase and not after cytokinesis in G1, as previously believed.

Significantly, the depletion of Sas6 by RNAi does not have an effect on the above described centriole localisation of Ana2 in the majority of analysed *Drosophila* cells, with the majority of interphase cells exhibiting two dots of Ana2, of which one is in the centre and one on the periphery of the D-Plp ring, the mother centriole and the site of procentriole formation respectively (Figure 6-2). This suggests that Ana2 localises to the centriole independently of Sas6. Therefore, Ana2 maintenance at the mother centriole and Ana2 recruitment to the site of procentriole formation does not depend on Sas6. On the contrary, depletion of Ana2 or Plk4 by RNAi causes Sas6 to localise to a single dot at the mother centriole in the centre of the D-Plp ring. Localisation of Sas6 to a second dot at the periphery of the D-Plp ring and

therefore to the site of procentriole formation does not occur in the majority of Ana2 depleted interphase cells (Figure 6-3A). Thus individually depleting Ana2 or Plk4 does not allow for Sas6 to be recruited to the site of procentriole formation but they do not interfere with maintenance of Sas6 at the mother centriole. In other words, the loading of Sas6 and consequential the formation of the procentriole are dependent on Ana2. The lack of Sas6 recruitment could be due to the lack of Plk4 or Ana2 protein after their depletion thus preventing potential physical interactions between Sas6 and Ana2.



Figure 6-1 Localisation of endogenous Ana2 and Sas6 relative to D-Plp throughout the cell cycle. Structured illumination microscopy of endogenous Ana2, Sas6 and D-Plp throughout cell cycle stages in cultured *Drosophila* cells. Ana2 and Sas6 localise to the mother centriole at the centre of the D-Plp ring throughout the cell cycle. At mitotic entry, Ana2 and Sas6 localise as a second dot to the periphery of the D-Plp ring of the mother centriole, the site of procentriole formation. The second dot matures a D-Plp ring until meta-/anaphase, followed by disengagement of mother and daughter centriole. At late ana-/telophase, each of the two centrioles acquires a new dot of Ana2 and Sas6 at the new site of procentriole formation. Scale bar: 0.5µm. Images by Dr. Tzolovsky ²⁹⁶.

	D-Plp	Ana2	GST RNAi	Sas6 RNAi
Category 1	a	•	3	3
Category 2	G	-	27	19

Figure 6-2 Ana2 localisation to the centriole is independent of Sas6. Structural illumination microscopy and categories of Ana2 in interphase *Drosophila* cells after Sas6 or control RNAi. Numbers on the right indicate how many centrioles were observed in each category. Ana2 localisation relative to the outer centriole marker D-Plp. The majority of cells exhibit a two dot localisation of Ana2 at the mother and procentriole. Scale bar: 0.5µm. Images by Dr. Tzolovsky ²⁹⁶.

Together with the described in vitro findings that Plk4 phosphorylates Ana2, to allow for Sas6 to interact with the phosphorylated Ana2 (section 4.2.4), this suggests that Sas6 localisation to the site of procentriole formation depends on the upstream event of Ana2 phosphorylation by Plk4. When endogenous Ana2 was depleted (by UTRs directed RNAi) from transgenic cells expressing Ana2-WT or Ana2-4A the majority of Ana2-WT cells exhibited the previously described double dot localisation of Ana2 and Sas6 to the centre and the periphery of the mother centriole D-Plp ring (Figure 6-1), whereas the majority of Ana2-4A expressing cells showed correct Ana2 localisation and the localisation of Sas6 is limited to the centre of the mother centrioles (Figure 6-4B). This resembles the findings of Sas6 localisation in wild-type Drosophila cells after RNAi of Ana2 or Plk4 (Figure 6-3). In summary, this confirms that the lack of Sas6 protein at the site of procentriole formation is due to the lack of Plk4phosphorylated Ana2 and is therefore in line with the in vitro finding that Plk4phosphorylation of Ana2 triggers its interaction with Sas6 (section 4.2.4). Additionally, this confirms that Ana2 is recruited to the centriole independently of its phosphorylation in the STAN motif by Plk4; and that Ana2 and Sas6 do not have to form a complex to allow for Ana2 recruitment to the centriole. This is in line with findings in human cells, where STIL and Sas6 have not been detected in a stable complex ¹¹⁷, nor using protein fragments in yeast-2hybrid assays 41 . This contrasts to Sas5 and Sas6 that form a complex and are recruited codependently to the procentriole in *C. elegans* 72 .



Figure 6-3 Ana2 and Plk4 are essential for centriolar loading of Sas6. Structured illumination microscopy of Sas6 and D-Plp in *Drosophila* cells after Ana2, Plk4 or control RNAi. Sas6 (green) localisation relative to the outer centriole marker D-Plp (red). (A) Categories of Sas6 localisation at the centriole as one or two dots and relative to number of times observed after Ana2, Plk4 or control RNAi. (B) Localisation of Sas6 relative to D-Plp throughout cell cycle stages after Ana2 or control RNAi. Cells depleted of endogenous Ana2 fail to load Sas6. (C) Localisation of Sas6 relative to D-Plp throughout cell cycle stages after Plk4 or control RNAi. Cells depleted of endogenous Plk4 or Ana2 fail to load Sas6. Scale bar: 0.5µm. Images by Dr. Tzolovsky ²⁹⁶.



Figure 6-4 PIk4-mediated phosphorylation of S318, S365, S370 and S373 in the Ana2-STAN motif is essential for Sas6 recruitment to centrioles. Structured illumination microscopy of Ana2, Sas6 and D-PIp in interphase *Drosophila* cells expressing Ana2-WT (A) or Ana2-4A (B) after depletion of endogenous Ana2. Number of centrioles observed indicated on the right. (A) The majority of interphase cells expressing transgenic Ana2-WT exhibit co-localisation of Ana2 and Sas6 as two dots at the centre and the periphery of the D-PIp ring, the mother centriole and the site of procentriole initiation respectively. (B) The majority of interphase cells expressing transgenic Ana2-4A, a non-PIk4-phosphorylatable mutant at four Serine residues in the Ana2-STAN motif, which are essential for interaction with Sas6, has normal Ana2 localisation at the mother centriole and is recruited to the site of procentriole formation (two dots of Ana2, comparable to Ana2 localisation in Figure 6-4A). Sas6 only localises as one dot to the mother centriole and is not recruited to the site of procentriole formation. Scale bar: 0.5µm. Images by Dr. Tzolovsky²⁹⁶.

It has also been suggested that the direct binding of Plk4 to STIL activates its kinase activity by promoting auto-phosphorylation of the activation loop in the kinase domain. This would provide a timely mechanism for Plk4 activity in centriole duplication because human Plk4 localises to the centriole throughout the cell cycle ²⁶ whereas STIL only accumulates from late G_1 -/early S-phase and is then degraded after anaphase onset in human cells ^{41,117,120}. Thus STIL could be a regulating protein for Plk4 and not only a target substrate. However, human Plk4 becomes localised to a single site of procentriole formation at the beginning of S-phase ^{93–95}. So far, it is only known that depletion of STIL prevents this localisation of Plk4 to a single site ⁹⁵ but the precise molecular basis of this remains unknown. How Ana2/STIL is recruited and how Plk4 is activated at a single site in the process are questions that remain to be answered. I have shown that Plk4-phosphorylation of the Ana2 STAN motif is necessary to allow Sas6 to bind to the single site and initiate procentriole formation. Similar findings have been made in human cells, where STIL S1108 and S1116 are phosphorylated by Plk4 and these phosphorylations are necessary for efficient targeting of STIL and Sas6 binding to the centriole ³⁰⁰. We have shown that Ana2 does not require Plk4 phosphorylation at its STAN motif for centriole localisation. However in human cells, it has been suggested by Moyer et al. that the efficient targeting of STIL depends on STAN-phosphorylation by Plk4 but the actual interaction between the two proteins does not ³⁰⁰. On the other hand Kratz et al. suggested that Plk4-phosphorylation of STIL is not mandatory for its interaction with Plk4 nor its localisation to the centriole but it is required to allow centriole duplication ¹²³. Significantly, the residue S1116, identified in human cells ^{123,300} corresponds to Drosophila S370^{95,296}, thus confirming the conserved importance of this Plk4-phosphorylation site within the STIL/Ana2-STAN motif for centriole duplication. Interestingly, it is not the loss of the STAN motif but the loss of the central coiled-coil domain of STIL that strongly reduces its localisation to the centriole, as this was observed to be necessary for interaction with Plk4 95. A significant difference between Drosophila and human cells is seen in the recruitment of Sas6. Whereas Sas6 is recruited directly to the site of procentriole formation in Drosophila, the human Sas6 homologue is transiently recruited to the lumen of the mother centriole in early S-phase and then relocates to the outer wall in a process dependent upon Plk4 and STIL. This is followed by cartwheel and procentriole assembly ³⁵⁰, and then the cartwheel structure is lost again during daughter-to-mother centriole transitions in mitosis ¹²⁰. This occurs with the loss of centrosomal STIL by Cdk1, followed by loss of Sas6 from the centriole ¹²⁰; suggesting that dephosphorylation of STIL could potentially cause dissociation of Sas6 from the centriole.

It is remarkable that Sas6 does not interact with non-phosphorylated Ana2 at all. Therefore, phosphorylation of Ana2 must be tightly regulated, to guarantee its phosphorylation only occurs when recruitment of Sas6 and procentriole formation must be initiated. It is known from *C. elegans* that Sas5 and Sas6 are present as homodimers, before an unknown process allows them to form a complex ^{15,114,302,304}. However, the structural differences in the organisation of the core centriole and the arrangement of Sas6 in the two species may indicate a requirement for different regulatory steps. Further structural and molecular information on Ana2 and Sas6 complexes is needed, to fully understand the difference between their recruitment to the site of procentriole formation in *C. elegans* and *Drosophila* that reflect the structural character of tube and cartwheel respectively. How the structural arrangement of Ana2 and Sas6 correlates on a molecular basis with the phosphorylation state of Ana2 still needs to be answered.

Together, my results demonstrate that Ana2 and Plk4 are interacting proteins and that Plk4mediated phosphorylation of Ana2 brings about the interaction of Sas6 with Ana2. Structured illumination microscopy by Dr. Tzolovsky additionally shows that Ana2 localises to the procentriole independently of its phosphorylation state by Plk4 and that Sas6 is recruited to the procentriole only when Ana2 is phosphorylated by Plk4. These results further our understanding of the molecular and functional processes during centriole duplication. For further directions, it is of utmost interest how Ana2 is recruited to the centriole, how it localises to a single site for procentriole formation and what regulates its timely recruitment. It is of interest to understand the structural complex between Ana2 and Sas6 as this will further our understanding of the instructural arrangements during procentriole formation.

The identification of the uncharacterised protein Dragon; its co-localisation with Sas6 at the centriole; and the finding that Dragon and Sas6 interact directly with each other is of particular interest. Dragon's human homologue GoRab localises to the *trans*-Golgi²⁰² and a null mutant has been identified in patients exhibiting gerodermia osteodysplastica²⁰².

Despite this knowledge the precise function of GoRab is unknown. Similarly, Dragon localises to the trans-Golgi and could function in signalling pathways as well as in connection with COPI transport vesicles because subunits of COPI were identified in complex with Dragon by mass spectrometry. However, the precise function of Dragon at the Golgi remains unknown. Dragon protein participates in centriole duplication because its depletion leads to loss of centrosomes. However, Dragon's precise molecular function at the centriole remains unknown. Additionally, I show that the conserved C-terminal coiled-coil domain of Dragon (aa191-318) interacts with the C-terminal part of the Sas6 coiled-coil domain (aa351-462). The latter region was not described in structural studies for the formation of the centriole cartwheel by Sas6. Thus Dragons could be important in the assembly of the procentriole or in the transition from the cartwheel assembly to interactions with microtubules. Dragon could structurally support the 9-fold symmetry of the centriole or directly connect proteins in the centriole assembly process. Importantly Dragon co-localises with Sas6 throughout the cellcycle, suggesting it has a cartwheel related function or participates in another unidentified process that occurs with similar timing as Sas6 recruitment. From here onwards, studies of the interdependency between Dragon and Sas6 in their roles in centriole duplication and maturation need to be studied in greater detail. Additional structural knowledge of Dragon and Sas6 or their interacting regions in complex would lead to further understanding of the arrangement of these proteins at the centriole and what roles they might have on the cartwheel of the centriole as a whole in guaranty of 9-fold symmetry. Once these questions have been answered and we have more knowledge about the function of Dragon at the centriole, we can determine the relationship between the centriole and the Golgi mediated by Dragon or its isoforms. Additional studies of Dragon at Drosophila spermatocytes and the basal body of the sperm are needed to elucidate its function at these sites.

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Appendix

Appendix

Appendix A: Mass spectrometry results from purifications of centriole duplication proteins from cultured *Drosophila* cells.

Tables show the full list of hits identified from the stated purification; indicating CG numbers, Mascot scores, Number of peptides (#pep), and the Full name of the protein if available. Tables are supplementary to Table 3-1 and Table 3-2.

CG #	Score	#pep	Full name
CG7186	3411	118	Plk4
CG9277	1532	55	beta-Tubulin at 56D
CG4264	1051	37	Heat shock protein cognate 4
CG3401	935	35	beta-Tubulin at 60D
CG1913	895	30	alpha-Tubulin at 84B
CG4821	808	20	Tequila
CC2010	626	25	Asterlass
CG2919	529	23	Asteriess 25D
CG14025	538	15	Blastoderm-specific gene 25D
CG33957	460	19	cp309
CG4147	447	15	Heat shock protein cognate 3
CG7439	368	12	Argonaute 2
CG7808	358	8	Ribosomal protein S8
CG5502	352	11	Ribosomal protein L4
CG7490	337	13	Ribosomal protein LP0
CG9795	314	9	CG9795
CG6453	302	8	Glucosidase 2 ß subunit
CG7123	298	6	Laminin B1
CG31022	290	8	prolyl-4-bydroyylase-alpha FEB
CG2100	280	6	CG2100
CG2199	280	0	CG2199
CG4087	279	/	Ribosomal protein LP1
CG16858	268	8	viking
CG3412	261	10	supernumerary limbs
CG13800	259	8	CG13800
CG4832	257	9	centrosomin
CG5436	251	8	Heat shock protein 68
CG3992	240	6	serpent
CG14792	233	7	stubarista
CG11100	232	5	Mes2
CG1119	230	7	Germ line transcription factor 1
CG6253	220	5	Ribosomal protein I 14
CG2168	206	9	Ribosomal protein £14
CC6750	200	5	Ribosomai protein 35A
CG6/59	200	3	cdc16
	200	n 1	Ninchan
007212		0	Nipshap
CG5504	200	4	lethal (2) tumorous imaginal discs
CG5504 CG7283	200 196	4	lethal (2) tumorous imaginal discs Ribosomal protein L10Ab
CG5504 CG7283 CG7450	200 196	4 4 4	lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element
CG5504 CG7283 CG7450	200 196 194	4 4 4	lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A
CG5504 CG7283 CG7450 CG5920	200 196 194 184	4 4 4 4	lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A string of pearls
CG5504 CG7283 CG7450 CG5920 CG7434	200 196 194 184 181	4 4 4 4 5	lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A string of pearls Ribosomal protein L22
CG5204 CG7283 CG7450 CG7450 CG5920 CG7434 CG16983	200 196 194 184 181 180		lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A string of pearls Ribosomal protein L22 skpA
CG5204 CG5504 CG7283 CG7450 CG5920 CG7434 CG16983 CG15220	200 196 194 184 181 180 170		lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A string of pearls Ribosomal protein L22 skpA Replication protein A3
CG52112 CG5504 CG7283 CG7450 CG5920 CG7434 CG16983 CG15220 CG5119	200 196 194 184 181 180 170 168		lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A string of pearls Ribosomal protein L22 skpA Replication protein A3 polyA-binding protein
CG5204 CG5504 CG7283 CG7450 CG5920 CG7434 CG16983 CG15220 CG5119 CG13624	200 196 194 184 181 180 170 168 165		lethal (2) tumorous imaginal discs Ribosomal protein L10Ab Cyclic-AMP response element binding protein A string of pearls Ribosomal protein L22 skpA Replication protein A3 polyA-binding protein Repressed by TOR
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	-	CG10652	117	2	Ribosomal protein L30
e 25D		CG2/46	117	4	Ribosomal protein L19
		CG31650	116	3	CG31650
nate 3	↓ ⊢	CG4863	115	3	Ribosomal protein L3
		CG6779	114	4	Ribosomal protein S3
8		CG31012	112	3	CIN85 and CD2AP orthologue
A		CG11276	112	5	Ribosomal protein S4
P0		CG10377	109	3	Heterogeneous nuclear ribonucleoprotein at 27C
nit		CG14999	108	4	Replication-factor-C 40kD subunit
19 FFB		CG10305	104	3	Ribosomal protein S26
ia Li D		CG12163	104	3	CG12163
P1		CG8280	103	4	Elongation factor 1alpha48D
		CG4463	100	2	Heat shock protein 23
		CG8610	100	2	Cdc27
18		CG17489	99	3	Ribosomal protein L5
		CG14648	98	3	lost
10		CG1821	98	3	Ribosomal protein I 31
08		CG5654	95	2	vnsilon schachtel
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al discs	. ⊢	CG7622	92	2	Ribosomal protein L36
)Ab	-	CG9484	91	2	hyperplastic discs
ement		CG2508	90	3	cdc23
		CG8715	90	2	lingerer
		CG9198	88	1	shattered
22		CG31160	87	2	CG31160
		CG3203	86	1	Ribosomal protein L17
43		CG3589	86	1	CG3589
in		CG17870	84	1	14-3-3zeta
		CG12233	83	4	lethal (1) G0156
12		CG10811	82	1	Eukaryotic-initiation-factor-4G
.7		CG3379	80	3	Histone H4 replacement
	1	CG14476	79	1	Glucosidase 2 a subunit
18		CG15784	79	1	CG15784
24		CG7323	79	1	CG7323
50		CG8055	78	2	shrub
		CG33956	78	1	kayak
		CG10473	77	1	Acinus
uffs P2		CG6241	76	1	TATA box-binding protein- associated factor RNA
24	-				polymerase I subunit B
	1 _	CG7977	76	4	Ribosomal protein L23A
	1 –	CG7726	75	1	Ribosomal protein L11
		CG4399	75	1	enhanced adult sensory threshold
23		CG7111	73	2	Receptor of activated protein kinase C 1
18	1 [CG6258	72	1	Replication factor C 38kD subunit
	1 [CG31992	71	1	gawky
	1 [CG10712	70	1	Chromator
6	1 [CG2998	69	2	Ribosomal protein S28b
	1	CG14617	69	2	CP110
	1 F	CG17521	69	1	Om

A.1 Act5-PrA-Plk4 purification from Drosophila cells

CG1341	69	1	Rpt1
CG3395	69	4	Ribosomal protein S9
CG6904	68	1	CG6904
CG12740	68	2	Ribosomal protein L28
CG11522	67	1	Ribosomal protein L6
CG1344	67	1	CG1344
CG3548	66	1	CG3548
CG17520	66	1	Casein kinase II alpha subunit
CG11271	65	1	Ribosomal protein S12
CG3917	65	1	gamma-tubulin ring protein 84
CG15437	65	1	modifier of rpr and grim, ubiquitously expressed
CG18001	64	1	Ribosomal protein L38
CG3008	64	1	CG3008
CG4145	64	2	Collagen type IV
CG8947	63	1	26-29kD-proteinase
CG14066	63	1	La related protein
CG3661	62	1	Ribosomal protein L23
CG8987	61	1	tamas
CG7863	61	1	dream
CG17437	61	1	will die slowly
CG32435	59	1	chromosome bows
CG1242	59	1	Heat shock protein 83
CG3361	57	2	martik
CG12775	57	1	Ribosomal protein L21
CG3061	57	1	CG3061
CG18495	56	1	Proteasome alpha6 subunit
CG6141	56	1	Ribosomal protein L9
CG5575	56	1	ken and barbie
CG3060	55	1	morula
CG15697	54	1	Ribosomal protein S30
CG5313	54	1	RfC3
CG10423	54	1	Ribosomal protein S27
CG7110	53	1	CG7110
CG3074	53	1	Secreted Wg-interacting molecule
CG17286	53	1	spindle defective 2
CG10289	52	1	CG10289
CG7337	52	1	CG7337
CG13780	51	1	PDGF- and VEGF-related factor 2
CG15442	51	1	Ribosomal protein L27A
CG4573	51	1	Glutamyl-tRNA synthetase,

		I	mitochondrial
CG6846	50	1	Ribosomal protein L26
CG2960	50	1	Ribosomal protein L40
CG4460	50	1	Heat shock protein 22
CG3422	49	1	Proteasome 28kD subunit 1
CG9641	49	1	CG9641
CG18572	49	1	rudimentary
CG5499	49	1	Histone H2A variant
CG7627	48	2	CG7627
CG5726	48	1	CG5726
CG3157	47	1	gamma-Tubulin at 23C
CG12179	47	1	CG12179
CG12052	47	1	longitudinals lacking
CG5827	47	1	Ribosomal protein L37A
CG9633	46	1	Replication Protein A 70
CG4046	46	1	Ribosomal protein S16
CG6831	46	1	rhea
CG5336	46	1	Ced-12
CG6742	46	1	centaurin beta 1A
CG17342	45	1	Lk6
CG12275	45	1	Ribosomal protein S10a
CG9273	45	1	Replication protein A2
CG18811	45	1	Caprin
CG8857	45	1	Ribosomal protein S11
CG5378	44	1	Rpn7
CG33087	44	1	LDL receptor protein 1
CG3647	44	1	shuttle craft
CG1399	44	1	Leucine-rich repeat
CG4759	44	1	Ribosomal protein L27
CG6692	44	1	Cysteine proteinase-1
CG32491	43	1	modifier of mdg4
CG12157	43	1	Translocase of outer membrane 40
CG1263	43	1	Ribosomal protein L8
CG5690	43	1	Centrobin
CG6439	43	2	CG6439
CG12437	42	1	raw
CG4785	42	1	Integrator 14

A.2 pMT-PrA-Plk4 +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG16901	48679	842	squid
CG1913	11462	224	α-Tubulin at 84B
CG9277	8869	252	β-Tubulin at 56D
CG7186	8544	205	Plk4
CG15792	4434	83	zipper
CG2919	3542	148	asterless
CG3401	1730	37	β-Tubulin at 60D
CG4264	1707	64	Heat shock protein cognate 4
CG7185	692	12	CG7185
CG4147	641	19	Heat shock protein cognate 3
CG5178	515	22	Actin 88F
CG5119	505	14	polyA-binding protein
CG4145	503	13	Collagen type IV
CG16858	500	11	viking
CG4027	494	21	Actin 5C
CG3201	470	12	Myosin light chain cytoplasmic
CG14648	470	17	growl
CG33957	468	13	cp309
CG4463	405	13	Heat shock protein 23
CG18743	402	14	Heat-shock-protein-70Ab
CG6450	398	9	lava lamp
CG5834	396	14	Hsp70Bbb
CG12101	389	9	Heat shock protein 60
CG8280	378	11	Elongation factor 1a48D
CG4183	365	13	Heat shock protein 26
CG5654	362	12	vpsilon schachtel
CG4466	327	8	Heat shock protein 27
CG31618	325	5	His2A:CG31618
CG7581	322	9	Bub3
CG9748	318	8	belle
CG7439	311	13	Argonaute 2
CG15784	308	4	CG15784
CG5436	296	11	Heat shock protein 68
CG10811	296	6	eukaryotic translation initiation factor 4G
CG1528	282	6	Coat Protein (coatomer) v
CG10578	263	9	DnaJ-like-1
CG14066	259	4	La related protein
CG12233	249	7	lethal (1) G0156
CG1691	239	11	IGF-II mRNA-binding protein
CG1341	229	5	Rpt1
CG3455	213	3	Rpt4
CG3412	212	8	supernumerary limbs
CG1489	211	6	Pros45
CG1883	205	8	Ribosomal protein S7
CG6181	198	8	Ge-1
CG3689	184	4	CG3689
202007			00000

CG3612	176	5	bellwether
CG4832	176	4	centrosomin
CG3218	175	3	female sterile (1) K10
CG5934	171	2	CG5934
CG17347	171	3	lethal (2) 37Ce
CG31022	165	7	prolyl-4-hydroxylase-alpha EFB
CG6631	160	4	anastral spindle 1
CG4211	159	3	no on or off transient A
CG5726	156	2	CG5726
CG10360	153	5	refractory to sigma P
CG9212	147	5	Nipsnap
CG3981	144	2	Unc-76
CG8994	143	2	exuperantia
CG10596	143	2	Msr-110
CG17081	143	3	Cep135
CG4394	140	2	TNF-receptor-associated factor-like
CG10938	139	2	Proteasome α5 subunit
CG16916	138	2	Rpt3
CG32626	138	2	AMP deaminase
CG8472	134	3	Calmodulin
CG11984	131	2	CG11984
CG7769	131	2	piccolo
CG3595	130	3	spaghetti squash
CG10230	130	4	Rpn9
CG10732	126	3	combover
CG3379	125	3	Histone H4 replacement
		-	Myelodysplasia/myeloid leukemia
CG8295	123	2	factor
CG6831	121	3	rhea
CG3322	120	2	Laminin B2
CG4266	118	2	CG4266
CG8597	114	6	lark
CG1524	109	4	Ribosomal protein S14a
CG7961	105	2	Coat Protein (coatomer) a
CG31012	105	1	CIN85 and CD2AP orthologue
CG11198	104	1	Acetyl-CoA carboxylase
CG1242	102	3	Heat shock protein 83
0010752	100		Small ribonucleoprotein particle
CG10/53	100	2	protein SmD1
CG7915	99	2	Ect4
CG3157	97	3	γ-Tubulin at 23C
CG13277	96	2	CG13277
CG5378	94	2	Rpn7
CG3210	92	2	Dynamin related protein 1
CG2186	89	3	CG2186
CG10922	88	1	La autoantigen-like
CG33554	88	2	Nipped-A
CG8900	87	2	Ribosomal protein S18
CG3422	85	2	Proteasome 28kD subunit 1

CG14472	84	3	purity of essence
CG2025	84	3	CG2025
CG13849	84	2	Nop56
CG5374	82	1	Tcp1-like
CG9282	82	1	Ribosomal protein L24
CG5604	81	2	CG5604
CG2508	81	2	cdc23
CG2910	76	2	spenito
CG2960	75	4	Ribosomal protein L40
CG16940	75	2	CG16940
CG8578	73	1	CG8578
CC7400	73	1	Dibacamal matrix LD0
CG/490	71	1	Clatheir harmachair
CG9012	/1	2	Clathrin heavy chain
CG2216	/1	1	Ferritin 1 heavy chain homologue
CG6203	71	1	Fmr1
CG12264	71	1	CG12264
CG8426	71	1	lethal (2) NC136
CG5208	60	2	Protein associated with topo II related
005208	0)	2	- 1
CG14207	69	2	HspB8
CG5502	68	2	Ribosomal protein L4
CG10289	68	1	CG10289
CG6815	67	2	belphegor
CG17158	66	2	capping protein beta
CG17291	66	1	Protein phosphatase 2A at 29B
CG6866	65	1	loguacious
200000	05		Mitochondrial trifunctional protein a
CG4389	64	1	cubunit
CG7224	64	1	CG7224
CG1324	64	1	CG/324
CG1/838	63	2	Syncrip
CG9206	62	1	Glued
CG7726	61	1	Ribosomal protein L11
CG18495	61	1	Proteasome a1 subunit
CG8055	61	1	shrub
CG7831	60	2	non-claret disjunctional
CG6223	60	2	Coat Protein (coatomer) B
0017010	60	2	Bub3 interacting GLEBS and Zinc
CG1/912	60	2	finger domain protein
CG6439	59	3	CG6439
			Heterogeneous nuclear
CG10377	58	1	ribonucleoprotein at 27C
CG8715	55	1	lingerer
CG10061	53	2	Sas-4
CG14812	52	1	Cost Protein (costomer) &
CC9962	52	1	Dra Lika 2
CG8865	52	1	DhaJ-like-2
CG10/01	51	1	Moesin
CG2168	51	2	Ribosomal protein S3A
CG18174	50	1	Rpn11
CG10232	50	1	CG10232
CG18572	49	2	rudimentary
CG2033	49	1	Ribosomal protein S15Aa
CG3024	49	1	torp4a
CG10535	48	1	Elongator complex protein 1
CG5316	47	1	CG5316
CG6253	46	1	Ribosomal protein L14
CG9589	46	2	CG9589
CG1484	40	3	flightless I
CC4460	45	2	Hast sheal metain 22
CG4400	43	2	Dumain beauty abain at 26C
0000020	44	1	Dynem neavy chain at 30C
CG6610	44	1	CG6610
CG1345	44	1	Glutamine:fructose-6-phosphate
			aminotransferase 2
CG6692	43	1	Cysteine proteinase-1
CG10149	43	1	Proteasome p44.5 subunit
CG9684	43	1	CG9684
CG10305	42	1	Ribosomal protein S26
CG15427	42	1	modifier of rpr and grim, ubiquitously
CG15457	42	1	expressed
CG15697	42	1	Ribosomal protein S30
CG2684	41	3	lodestar
CG5753	41	1	staufen
CG10851	41	2	B52
CG4164	41	1	CG4164
CG10423	41	2	Ribosomal protein S27
CG2637	40	1	Female sterile (2) Kotol
CG4808	40	2	Tronomyosin 1
CC7507	20	2 1	Dynain boowy show 64C
CG/30/	20	1	Dynem neavy chain 64C
CG1821	39	1	KIDOSOMAI protein L31
CG11963	59	1	skpA associated protein
CG10370	38	1	I at-binding protein-1
CG9795	38	1	CG9795
CG6779	37	1	Ribosomal protein S3
CG32138	37	1	CG32138
CG8571	35	1	smallminded
CG8588	35	1	pastrel
CG6987	35	1	SF2
CG7123	34	1	Laminin B1
CG9888	34	2	Fibrillarin
CG6509	34	2	Discs large 5
CG0760	3/	1	CG0760
CG1683	33	4	Adenine nucleotide translocase 2
CC01005	22	2	
CC12240	22	1	LU0100 Regulatory resticle non ATD 12
007615	35	1	Regulatory particle non-ATPase 13
CG/945	33	1	CG/945
CG11888	32	1	Rpn2
			005000

	32	1	sponge
CG33309	32	1	CG33309
CG7033	31	1	CG7033
CG6617	31	1	CG6617
CG17768	31	1	CG17768
CG14647	31	1	CG14647
CG4569	30	1	Proteasome 28kD subunit 1B
CG17286	30	1	spindle defective 2
CG8415	30	1	Ribosomal protein S23
CG5144	30	1	CG5144
CG8542	29	1	Heat snock protein cognate 5
CG3481	29	1	Ieak
CG4033	29	1	RNA polymerase I 135kD subunit
CG1850	29	1	CG1850
CG10102	29	1	CG10102
CG6684	29	2	Ribosomal protein S25
CG4904	28	1	Proteasome 35kD subunit
CG9450	28	1	tudor
CG4252	28	2	meiotic 41
CG13185	28	1	CG13185
CG1925	27	1	mutagen-sensitive 205
CG16944	27	3	stress-sensitive B
CG14616	27	1	Chetathiana Stransformer E12
CG16936	27	1	Glutatnione S transferase E12
CG9940	27	1	CG9940
CG8332	27	1	ATD symthese asymptics for the C 11
CG1202/	27	1	ATP synthase, coupling factor 6-like
CG18176	27	1	deflated
CG0451	21	1	Diuestreak
CG4220	26	1	elbow B
CG3395	26	1	Kibosomal protein S9
CG4257	26	1	transcription protoin at 02E
			Small ribonucleonrotein marticle
CG1249	26	1	protein SmD2
CG4038	25	1	CG4038
CG17484	25	1	Adherens junction protein p120
CG2244	25	2	MTA1-like
CG15678	25		noor Imd response upon knock-in
CG5902	25	1	CG5902
CG32046	25	2	CG32046
CG2714	23	1	cramped
CG16983	24	1	skn A
CG5004	24	1	CG5004
CG4704	24	1	CG4704
CG9506	24	1	slow as molasses
CG12878	24	1	harentsz
CG31617	24	1	His1:CG31617
CG4097	23	1	Proteasome 26kD subunit
CG4651	23	1	Ribosomal protein L13
CG3333	23	1	Nucleolar protein at 60B
CG5888	23	1	CG5888
CG13742	23	1	CG13742
CG6327	23	1	CG6327
CG3711	23	1	CG3711
CG5154	23	1	Imaginal disc growth factor 5
-	22	1	Ribosomal protein L23A
CG7977	22	1	Rpn1
CG7977 CG7762	22	1	
CG7977 CG7762 CG30490	22 22 22	1 1	CG30490
CG7977 CG7762 CG30490 CG33093	22 22 22 22	1 1 2	CG30490 CG33093
CG7977 CG7762 CG30490 CG33093 CG8923	22 22 22 22 21	1 1 2 2	CG30490 CG33093 meiotic 218
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949	22 22 22 22 21 21	$ \begin{array}{c} 1\\ 1\\ 2\\ 2\\ 2\\ \end{array} $	CG30490 CG33093 meiotic 218 coracle
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258	22 22 22 21 21 21 21	$ \begin{array}{c} 1\\ 1\\ 2\\ 2\\ 1\\ 1 \end{array} $	CG30490 CG33093 meiotic 218 coracle dribble
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012	22 22 22 21 21 21 21 21		CG30490 CG33093 meiotic 218 coracle dribble genghis khan
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144	22 22 22 21 21 21 21 21 21 21		CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174	22 22 22 21 21 21 21 21 21 21	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{array} $	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174
CG7977 CG7762 CG30490 CG3093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG3382	22 22 22 21 21 21 21 21 21 21 21 21		CG30490 CG33093 meiotic 218 coracle dribble <u>genghis khan</u> lysine ketoglutarate reductase CG5174 Organic anion transporting
CG7977 CG7762 CG30490 CG30490 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382	22 22 22 21 21 21 21 21 21 21 21 21 21 2	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 1 \\ $	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG3382 CG11261	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261
CG7977 CG7762 CG30490 CG33093 CG8923 CG1949 CG4258 CG4012 CG7144 CG5174 CG3382 CG11261 CG33106	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble <u>genghis khan</u> lysine ketoghtarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG5174 CG51762 CG707 CG70	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble <u>genghis khan</u> lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Harchimen 4
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382 CG11261 CG33106 CG3001 CG3001	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Debe2
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG2163 CG2163	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 nitchourga
CG7977 CG77762 CG30490 CG33093 CG1949 CG4258 CG11949 CG4258 CG7144 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG8047	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoghtaratte reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD.prostainase
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG8947 CG4557	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble <u>genghis khan</u> lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382 CG11261 CG33106 CG33001 CG2163 CG6375 CG8947 CG4557 CG8947 CG4557 CG10778	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557 CG10778
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG8947 CG4557 CG8947 CG4577 CG10778 CG10778	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitichoune 26-29kD-proteinase CG4557 CG10778 CG10747
CG7977 CG7762 CG30490 CG33093 CG1949 CG4258 CG11949 CG4258 CG7144 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG8947 CG4557 CG40778 CG10347	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoghtarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557 CG10347 Vacuolar protein sortine 52
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG8947 CG4557 CG10778 CG10778 CG10778	22 22 21 21 21 21 21 21 21 21 21 21 21 2	I 1 2 2 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557 CG10778 CG10347 Vacuolar protein sorting 52 CG9316
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG5174 CG3382 CG11261 CG33106 CG33001 CG2163 CG6375 CG8947 CG4557 CG8947 CG4557 CG10778 CG10377 CG10778 CG10371 CG9316	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557 CG10778 CG10778 CG10347 Vacuolar protein sorting 52 CG9316
CG7977 CG77762 CG30490 CG33093 CG11949 CG4258 CG4012 CG7144 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG8947 CG4557 CG10347 CG4557 CG10347 CG7371 CG9316	22 22 22 21 21 21 21 21 21 21 21 21 21 2	1 1 2 2 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoghtarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557 CG10778 CG10778 CG10347 Vacuolar protein sorting 52 CG9316 Corepressor of Pangolin CG32164
CG7977 CG7762 CG30490 CG33093 CG8923 CG11949 CG4258 CG4012 CG7144 CG5174 CG3382 CG11261 CG33106 CG3001 CG2163 CG6375 CG6375 CG6947 CG4557 CG10347 CG4557 CG10347 CG7311 CG7316 CG32164 CG32164 CG32164	22 22 22 21 21 21 21 21 21 21 21 21 21 2	I 1 2 2 1	CG30490 CG33093 meiotic 218 coracle dribble genghis khan lysine ketoglutarate reductase CG5174 Organic anion transporting polypeptide 58Db CG11261 multiple ankyrin repeats single KH domain Hexokinase A Pabp2 pitchoune 26-29kD-proteinase CG4557 CG10347 Vacuolar protein sorting 52 CG9316 Corepressor of Pangolin CG32164 Extracellularly regulated kinase 7
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A.3 pMT-PrA-Plk4 +OA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG33957	4029	116	cp309
CG15792	3481	76	zipper
CG1913	31/3	69	α-1ubulin at 84B
CG/186	3011	70	PIK4 9 Tubulin at 56D
CG4264	2923	80	Heat shock protein cognate 4
CG2919	1778	53	asterless
CG6631	1776	55	anastral spindle 1
CG4147	1246	32	Heat shock protein cognate 3
CG3401	1189	32	B-Tubulin at 60D
CG17081	1107	33	Cep135
CG4027	1062	36	Actin 5C
CG18743	983	26	Heat-shock-protein-70Ab
CG5834	962	25	Hsp70Bbb
CG4463	946	27	Heat shock protein 23
CG4832	927	22	centrosomin
CG8014	785	20	Receptor mediated endocytosis 8
CG16901	780	14	squid
CG12101	710	13	Heat shock protein 60
CG10067	659	27	Actin 57B
CG5436	611	17	Heat shock protein 68
CG8280	600	21	Elongation factor 1α48D
CG16896	507	17	CG16896
CG16858	480	11	viking
CG10370	434	12	Tat-binding protein-1
CG3201	422	9	Myosin light chain cytoplasmic
CG10061	409	19	Sas-4
CG4183	3/8	15	Heat shock protein 26
CG16015	257	10	Det 2
CG3505	357	7	rpspatti sauseb
CG12222	352	10	lethal (1) G0156
CG8472	347	9	Calmodulin
CG10230	328	6	Rpn9
CG1341	320	9	Rpt1
CG4466	301	7	Heat shock protein 27
CG10360	290	7	refractory to sigma P
CG3422	274	7	Proteasome 28kD subunit 1
005200	244	-	Proteasome 26S subunit subunit 4
CG5289	266	6	ATPase
CG1548	263	4	cathD
CG10938	251	7	Proteasome a5 subunit
CG1242	243	8	Heat shock protein 83
CG18572	243	7	rudimentary
CG3455	237	4	Rpt4
CC17520	231	5	casein kinase IIa
CG17520	201	5	
CG10811	226	4	eukaryotic translation initiation factor
CG10811	226	4	eukaryotic translation initiation factor 4G
CG10811 CG18495	226 226	4	eukaryotic translation initiation factor 4G Proteasome al subunit
CG10811 CG18495 CG4145	226 226 224	4 7 6	eukaryotic translation initiation factor 4G Proteasome α1 subunit Collagen type IV
CG17320 CG10811 CG18495 CG4145 CG5261	226 226 224 203	4 7 6 8	eukaryotic translation initiation factor 4G Proteasome αl subunit Collagen type IV midline uncoordinated
CG17320 CG10811 CG18495 CG4145 CG5261 CG31022	226 226 224 203 202	4 7 6 8 5	eukaryotic translation initiation factor 4G Proteasome αl subunit Collagen type IV midline uncoordinated prolyl-4-hydroxylase-alpha EFB
CG17320 CG10811 CG18495 CG4145 CG5261 CG31022 CG4460 CG7762	226 226 224 203 202 200	4 7 6 8 5 5 8	eukaryotic translation initiation factor 4G Proteasome α1 subunit Collagen type IV midline uncoordinated prolyl-4-hydroxylase-alpha EFB Heat shock protein 22 Paral
CG17320 CG10811 CG18495 CG4145 CG5261 CG31022 CG4460 CG7762 CG11899	226 226 224 203 202 200 197	4 7 6 8 5 5 5 8	eukaryotic translation initiation factor 4G Proteasome α1 subunit Collagen type IV midline uncoordinated prolyl-4-hydroxylase-alpha EFB Heat shock protein 22 Rpn1 Pm2
CG17320 CG10811 CG18495 CG4145 CG5261 CG31022 CG4460 CG7762 CG11888 CG4904	226 226 224 203 202 200 197 191 183	4 7 6 8 5 5 5 8 9 5	eukaryotic translation initiation factor 4G Proteasome al subunit Collagen type IV midline uncoordinated prolyl-4-hydroxylase-alpha EFB Heat shock protein 22 Rpn1 Rpn2 Proteasome 35tD subursit
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CG11320 CG10811 CG18495 CG4145 CG31022 CG4460 CG7762 CG11888 CG4904 CG12000 CG5378	226 226 224 203 202 200 197 191 183 179 176	4 7 6 8 5 5 8 9 5 3 5	eukaryotic translation initiation factor 4G Proteasome α1 subunit Collagen type IV midline uncoordinated prolyl-4-hydroxylase-alpha EFB Heat shock protein 22 Rpn1 Rpn1 Proteasome 35kD subunit Proteasome β7 subunit Rn7
CG11320 CG10811 CG18495 CG4145 CG5261 CG31022 CG4460 CG7762 CG11888 CG4904 CG12000 CG5378 CG13162	226 226 224 203 202 200 197 191 183 179 176 175	4 7 6 8 5 5 5 8 9 5 3 5 3	eukaryotic translation initiation factor 4G Proteasome α1 subunit Collagen type IV midline uncoordinated prolyl-4-hydroxylase-alpha EFB Heat shock protein 22 Rpn1 Rpn2 Proteasome β7 subunit Proteasome β7 subunit Rpn7 angstral spindle 3
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CG3612	102	2	bellwether
CG5119	101	3	polyA-binding protein
CG7581	100	2	Bub3
CG5330	97	1	Nucleosome assembly protein 1
CG14750	96	2	Vacuolar protein sorting 25
CG5174	93	2	CG51/4
CG4157	91	2	Rpn12
CG13349	91	2	AMD doomingoo
CG32626	88	1	AMP deaminase
CG12184	86	4	CGI2184
CG2216	85	1	Ferritin I heavy chain homologue
CG315/	83	3	γ -Tubulin at 23C
CG12323	82	3	Proteasome \$5 subunit
CG1/949	82	1	His2B:CG1/949
CG/185	81	1	CG/185
CG31196	80	2	14-3-38
CG3662	/8	1	CG3662
CG9748	72	3	belle
CG1528	72	3	Coat Protein (coatomer) y
CG11981	71	1	Proteasome \$3 subunit
CG8055	71	2	shrub
CG1683	70	1	Adenine nucleotide translocase 2
CG3981	70	1	Unc-76
CG6617	69	1	CG6617
CG10632	67	1	sosondowah
CG16983	65	2	skpA
CG6840	64	1	Rpb11
CG8368	63	1	CG8368
CG5266	61	2	Proteasome 25kD subunit
CG7033	61	1	CG7033
CG8478	61	1	CG8478
CG5825	60	1	Histone H3.3A
CG7945	60	1	CG7945
CG9281	59	1	CG9281
CG17498	59	1	mad2
CG1977	58	1	a Spectrin
CG2152	58	1	Protein-L-isoaspartate (D-aspartate)
			O-methyltransferase
CG5092	57	1	Target of rapamycin
CG1569	56	1	rough deal
CG2025	56	1	CG2025
CG31764	56	1	virus-induced RNA I
CG31012	55	1	CIN85 and CD2AP orthologue
CG32138	55	1	CG32138
CG1/291	55	1	Protein phosphatase 2A at 29B
CG1524	54	1	Ribosomal protein S14a
CG1/158	53	1	capping protein beta
CG14648	53	1	growl
	54	1	CG5934
CG5934	55	- 1	
CG5934 CG6692	52	1	Cysteine proteinase-1
CG5934 CG6692 CG4581	53 52 52	1 2	Thiolase
CG5934 CG6692 CG4581 CG8947	52 52 51	1 2 2	Thiolase 26-29kD-proteinase
CG5934 CG6692 CG4581 CG8947 CG4164	53 52 52 51 51	1 2 2 1	Cysteine proteinase-1 Thiolase 26-29kD-proteinase CG4164
CG5934 CG6692 CG4581 CG8947 CG4164 CG1883	53 52 52 51 51 51	1 2 1 1	Cysteme proteinase-1 Thiolase 26-29kD-proteinase CG4164 Ribosomal protein S7
CG5934 CG6692 CG4581 CG8947 CG4164 CG1883 CG5374	53 52 52 51 51 51 50 50	1 2 1 1 1 2	Cysteme proteinase-1 Thiolase 26-29kD-proteinase CG4164 Ribosomal protein S7 TCp1-like
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CG5954 CG6692 CG4581 CG8947 CG4164 CG1883 CG5374 CG6223 CG12019 CG7619 CG7619	53 52 52 51 51 51 50 50 50 50 40 40	1 2 1 1 2 1 2 1 2	Cysteme proteinase-1 Thiolase 26-29kD-proteinase CG4164 Ribosomal protein S7 Tcp1-like Coat Protein (coatomer) β Cdc37 Proteasome 54kD subunit communication matrix 24
CG5934 CG6692 CG4581 CG8947 CG4164 CG1883 CG5374 CG6223 CG12019 CG7619 CG7619 CG3917	53 52 52 51 51 51 50 50 50 50 50 49	1 2 1 1 2 1 2 1 2 1	Cysteme proteinase-1 Thiolase 26-29kD-proteinase CG4164 Ribosomal protein S7 Tcp1-like Coat Protein (coatomer) β Cdc37 Proteasome 54kD subunit gamma-tubulin ring protein 84 Proteasome 64 fe urbunit
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CG2534	31	1	canoe
CG9155	31	1	Myosin 61F
CG5366	31	1	Cullin-associated and neddylation- dissociated 1
CG13284	31	1	CG13284
CG33694	31	1	CENP-ana
CG8194	30	1	Ribonuclease X25
CG6988	30	1	Protein disulfide isomerase
CG10975	30	1	Protein tyrosine phosphatase 69D
CG11929	30	2	CG11929
CG4003	30	1	pontin
CG30477	30	1	CG30477
CG1484	29	1	flightless I
CG5474	29	1	Signal sequence receptor β
CG5094	29	1	small glutamine-rich tetratricopeptide containing protein
CG31426	29	1	ligatin
CG7507	29	1	Dynein heavy chain 64C

CG7595	28	2	crinkled
CG7935	28	1	moleskin
CG13091	28	1	CG13091
CG10546	28	1	Cellular retinaldehyde binding protein
CG7837	28	1	CG7837
CG7439	28	1	Argonaute 2
CG1703	27	1	CG1703
CG3610	27	1	CG3610
CG14792	26	1	stubarista
CG30388	26	1	Magi
CG31149	26	1	CG31149
CG3431	25	1	Ubiquitin C-terminal hydrolase
CG16742	25	1	CG16742
CG2139	24	1	aralar1
CG8008	24	1	CG8008
CG3799	24	1	Ephexin

A.4 Act5-PrA-Asl purification from Drosophila cells

CG #	Score	#рер	Full name
CG6450	4816	186	lava lamp
CG16858	4302	176	viking
CG4145	3761	137	Collagen type IV
CG2919	2736	138	Asterless
CG6988	1327	150	Protein disulfide isomerase
CG4147	1247	50	Heat shock protein cognate 3
CG21022	1247	52	prolyl 4 hydroxylasa alpha EEP
CC2074	1040	52	Secreted We interacting malacula
0022057	1040	30	Secreted wg-interacting molecule
CG33957	112	29	cp309
CG2512	610	18	alpha-Tubulin at 84D
CG6199	597	26	procollagen lysyl hydroxylase
CG4264	581	25	Heat shock protein cognate 4
CG6944	540	23	Lamin
CG9282	322	7	Ribosomal protein L24
CG9277	291	21	beta-Tubulin at 56D
CG8014	259	8	Receptor mediated endocytosis 8
CG6631	229	11	anastral spindle 1
CG7808	189	3	Ribosomal protein S8
CG15792	182	5	zipper
CG8983	146	6	ERp60
CG3751	124	3	Ribosomal protein S24
CG10652	123	3	Ribosomal protein L30
CG17081	123	5	CG17081
CG4918	123	2	Ribosomal protein LP2
CG7622	122	2	Ribosomal protein L 26
CG5726	121	2	CC5726
CC1921	111	2	Bibasamal matain L 21
CG1821	111	2	Dibasanal protein L31
00(252	100	3	Ribosoniai protein 57
CG6253	108	2	Ribosomai protein L14
CG/490	105	4	Ribosomai protein LPO
CG12184	102	4	CG12184
CG17520	99	2	Casein kinase II alpha subunit
CG17286	97	3	spindle defective 2
CG8900	94	4	Ribosomal protein S18
CG2216	94	2	Ferritin 1 heavy chain homologue
CG8922	92	2	Ribosomal protein S5a
CG5920	90	1	string of pearls
CG3203	90	2	Ribosomal protein L17
CG4897	89	4	Ribosomal protein L7
CG2168	88	4	Ribosomal protein S3A
CG12101	82	2	Heat shock protein 60
CG14792	80	1	stubarista
CG3201	74	1	Myosin light chain cytoplasmic
CG7726	70	1	Ribosomal protein L11
CG1524	66	1	Ribosomal protein S14a
			Succinate dehydrogenase, subunit A
CG5718	65	3	(flavoprotein)-like
CG33102	64	2	Hey_t1
CG10732	60	2	combover
CG8507	60		CG8507
CC5502	57	2	Dihasamal matain L 4
CG5502	57	2	Ribosomai protein L4
CG4087	57	1	Ribosomal protein LP1

CG3195	56	1	Ribosomal protein L12			
CG16896	55	2	CG16896			
CG32031	53	2	Arginine kinase			
CG8280	53	2	Elongation factor 1alpha48D			
CG2998	53	2	Ribosomal protein S28b			
CG10061	52	1	lethal (3) s2214			
CG11271	50	1	Ribosomal protein S12			
CG5178	49	1	Actin 88F			
CG8281	49	1	CG8281			
CG7186	49	2	Plk4			
CG5168	48	1	CG5168			
CG3092	47	1	CG3092			
CG17177	47	1	CG17177			
CG5809	47	1	CaBP1			
CG15207	46	1	CG15207			
CG7603	46	1	QIL1			
CG7434	45	1	Ribosomal protein L22			
CG4744	45	1	CG4744			
CG8200	45	1	flotillin			
CG6019	44	1	mutagen-sensitive 308			
CG33554	44	1	Nipped-A			
CG10272	44	1	grappa			
CG18076	44	1 short stop				
CG6779	44	1 Ribosomal protein S3				
CG3157	44	1 gamma-Tubulin at 23C				
CG11276	43	1 Ribosomal protein S4				
CG31195	43	1 CG31195				
CG12010	43	1 CG12010				
CG16833	42	1	CG16833			
CG17836	42	1	CG17836			
CG18102	42	1	shibire			
CG31159	42	1	Elongation Factor G2			
CG10423	42	1	Ribosomal protein S27			
CG3314	42	1	Ribosomal protein L7A			
CG8472	41	1	Calmodulin			
CG33301	41	1	CG33301			
CG12233	41	1	lethal (1) G0156			
CG15844	40	1	Kinesin-like protein at 54D			
CG4337	40	1	mitochondrial single stranded DNA-			
0.000			binding protein			
CG8379	39	I	CG8379			
CG8930	38	I	rickets			
CG4078	38	1	CG4078			
CG15442	5/	1	Kibosomal protein L2/A			
CG3356	3/	1	CG3356			
CG41466	23	1	cp309			
CG18625	0	1	CG18625			
CG10107	0	1	veloren			

A.5 Act5-AsI-PrA purification from Drosophila cells

CG #	Score	#pep	Full name
CG2919	10717	465	CG2919
CG16858	2421	82	viking
CG4145	1798	60	Collagen type IV
CG6450	1099	39	lava lamp
CG17498	875	26	mad2
CG33957	798	24	cp309
CG9277	769	43	beta-Tubulin at 56D
CG4264	736	33	Heat shock protein cognate 4
CG6631	628	26	anastral spindle 1
CG4147	597	19	Heat shock protein cognate 3
CG2512	555	19	alpha-Tubulin at 84D

CG31022	462	9	prolyl-4-hydroxylase-alpha EFB			
CG3401	394	25	beta-Tubulin at 60D			
CG3074	300	11	Secreted Wg-interacting molecule			
CG7186	224	9	Plk4			
CG6944	178	6	Lamin			
CG17081	174	6	Cep135			
CG6988	144	5	Protein disulfide isomerase			
CG5062	125	6	CG5062			
CG6199	124	3	procollagen lysyl hydroxylase			
CG2960	122	4	Ribosomal protein L40			
CG13800	111	3	CG13800			
CG10346	108	5	Grip71			

CG5718	104	7	Succinate dehydrogenase, subunit A (flavoprotein)-like			
CG17286	87	4	spindle defective 2			
CG9795	83	2	CG9795			
CG9900	78	2	mitotic 15			
CG8280	77	3	Elongation factor 1alpha48D			
CG4918	74	1	Ribosomal protein LP2			
CG8962	73	4	Platelet-activating factor acetylhydrolase alpha			
CG10061	71	1	lethal (3) s2214			
CG3203	69	1	Ribosomal protein L17			
CG8983	68	2	ERp60			
CG15792	66	2	zipper			
CG31012	64	1	CIN85 and CD2AP orthologue			
CG4744	63	3	CG4744			
CG10652	61	2	Ribosomal protein L30			
CG7808	60	1	Ribosomal protein S8			
CG9699	60	2	Septin 4			
CG4897	58	2	Ribosomal protein L7			
CG33554	56	1	Nipped-A			
CG11522	54	1	Ribosomal protein L6			
CG9282	53	1	Ribosomal protein L24			
CG33555	53	1	bitesize			
CG1683	52	2	Adenine nucleotide translocase 2			
CG17520	49	2	Casein kinase II alpha subunit			
CG8605	48	1	RINT1 ortholog			
CG6785	47	1	CG6785			
CG7603	47	1	QIL1			

CG40500	47	2	CG40500	
CG12129	47	1	CG12129	
CG31045	46	1	Myosin heavy chain-like	
CG9924	46	1	roadkill	
CG12753	46	1	endosomal maturation defective	
CG16896	46	1	CG16896	
CG31374	45	1	sarcomere length short	
CG15828	45	1	Apolipoprotein lipid transfer particle	
CG11999	45	1	CG11999	
CG1104	44	1	CG1104	
CG13359	44	1	CG13359	
CG6692	43	1	Cysteine proteinase-1	
CG11282	43	1	capricious	
CG14025	42	1	Blastoderm-specific gene 25D	
CG8900	42	 Ribosomal protein S18 		
CG17927	41	1	Myosin heavy chain	
CG3902	41	1	CG3902	
CG18255	41	1	Stretchin-Mlck	
CG6667	40	1	dorsal	
CG32031	40	1	Arginine kinase	
CG17839	40	1	CG17839	
CG4585	40	1	CG4585	
CG18572	31	1	rudimentary	
CG2762	0	1	u-shaped	
CG13772	0	1	neuroligin	

A.6 Act5-Asl (531-994aa)-PrA purification from Drosophila cells

CG #	Score	#pep	Full name	L	CC
CG2919	3340	152	Asterless		CG
CG9277	1964	72	beta-Tubulin at 56D		CG
CG4264	1333	47	Heat shock protein cognate 4		CC
CG3401	1075	46	beta-Tubulin at 60D		cc
CG33957	1057	29	cp309	_	cc
CG2512	942	34	alpha-Tubulin at 84D	_	CG
CG17286	616	23	spindle defective 2		CG
CG4147	437	16	Heat shock protein cognate 3	_	CC
CG7808	361	7	Ribosomal protein S8		CC
CG17498	306	8	mad2		CC
CG5436	272	11	Heat shock protein 68		CG
CG6631	248	11	anastral spindle 1		CG
CG4832	237	7	centrosomin		CC
CG7490	230	9	Ribosomal protein LP0		CC
CG10732	217	5	combover		CC
CG6253	197	4	Ribosomal protein L14		CC
CG8947	193	4	26-29kD-proteinase		CG
CG10652	189	3	Ribosomal protein L30		CC
CG13800	189	5	CG13800		CG
CG3195	187	5	Ribosomal protein L12	[CC
CG8280	183	7	Elongation factor 1alpha48D	[CG
CG7622	179	4	Ribosomal protein L36		CG
CG7977	170	6	Ribosomal protein L23A		CC
CG17081	165	3	CG17081		CC
CG14206	163	4	Ribosomal protein S10b		CC
CG5502	163	7	Ribosomal protein L4		CG
CG6779	155	4	Ribosomal protein S3		CC
CG3751	155	4	Ribosomal protein S24		CC
CG4918	150	2	Ribosomal protein LP2		CC
CG9282	149	2	Ribosomal protein L24		CC
CG31022	145	4	prolyl-4-hydroxylase-alpha EFB		CG
CG1821	142	3	Ribosomal protein L31		CC
CG10944	137	4	Ribosomal protein S6		CG
CG1548	132	2	cathD		CG
CG6453	128	4	Glucosidase 2 ß subunit	_	CC
CG7111	126	5	Receptor of activated protein kinase C 1	_	CC
CG1883	124	3	Ribosomal protein S7	_	CG
CG3661	123	4	Ribosomal protein L23	_	CC
CG8900	123	4	Ribosomal protein S18		CG
CG14792	121	3	stubarista	l L	CG
CG8615	120	2	Ribosomal protein L18	l L	CG
CG3157	118	3	gamma-Tubulin at 23C	l L	CC
CG4863	117	4	Ribosomal protein L3	1	CC
CG2960	116	4	Ribosomal protein L40	1	CG
CG4087	111	3	Ribosomal protein LP1		CC
CG2168	108	2	Ribosomal protein S3A	1 F	
CG6692	102	2	Cysteine proteinase-1	1	CG
CG11271	101	2	Ribosomal protein S12	1	CG
CG7939	101	2	Ribosomal protein L32	1 -	00
CG16858	100	2	viking	4 -	CG
CG1263	100	2	Ribosomal protein L8	4 -	CG
CG7283	94	2	Ribosomal protein L10Ab	1 -	0
CG12163	94	2	CG12163	1 -	0
CG1524	94	3	Ribosomal protein S14a		<u> </u>
CG2216	93	1	Ferritin 1 heavy chain homologue		6
CG7726	92	1	Ribosomal protein L11		<u> </u>
CG7014	92	1	Ribosomal protein S5b		<u> </u>
CG1489	91	2	Pros45	1 F	<u></u>
CG5119	80	2	polyA-binding protein	4 -	
CG2746	77	2	Ribosomal protein L19		u

CG9795	76	2	CG9795
CG16944	76	2	stress-sensitive B
CG16896	75	2	CG16896
CG6510	74	2	Ribosomal protein L18A
CC 5290	70	1	Proteasome 26S subunit subunit 4
CG3289	12	1	ATPase
CG11579	71	1	armadillo
CG17489	69	1	Ribosomal protein L5
CG4897	69	3	Ribosomal protein L7
CG2998	68	2	Ribosomal protein S28b
CG3314	67	2	Ribosomal protein L7A
CG32031	67	4	Arginine kinase
CG12184	64	2	CG12184
CG7434	64	2	Ribosomal protein L22
CG6846	63	1	Ribosomal protein L26
CG2411	63	2	patched
CG8415	62	1	Ribosomal protein S23
CG10305	61	1	Ribosomal protein S26
CG3074	60	2	Secreted Wg-interacting molecule
CG17520	60	1	Casein kinase II alpha subunit
CG2772	59	2	CG2772
CG32626	58	1	AMP deaminase
CG15697	57	1	Ribosomal protein S30
CG4525	52	1	CG4525
CG8472	52	2	Calmodulin
CG1633	51	1	thioredoxin peroxidase 1
CG12385	50	1	thetaTrypsin
CG8857	50	1	Ribosomal protein S11
CG4651	50	2	Ribosomal protein L13
CG2033	50	1	Ribosomal protein S15Aa
CG6141	49	1	Ribosomal protein L9
CG18001	49	2	Ribosomal protein L38
CG9117	49	1	CG9117
CG31915	49	1	CG31915
CG11963	48	1	skpA associated protein
CG8055	47	1	shrub
CG5920	47	1	string of pearls
CG11276	47	1	Ribosomal protein S4
CG5467	46	1	scribbled
CG10061	46	1	lethal (3) s2214
CG12233	46	1	lethal (1) G0156
CG13389	46	1	Ribosomal protein S13
CG6303	45	1	Bruce
CG3429	45	1	swallow
CG15442	44	1	Ribosomal protein L 27A
2013442		1	Glycosylphosphatidylinositol anchor
CG3033	44	1	attachment 1 ortholo
CG15548	44	1	CG15548
CG12775	44	1	Ribosomal protein L21
CG5462	44	1	scribbled
CG14304	44	1	CG14304
CG33555	44	1	bitesize
CG2928	43	1	Rhythmically expressed gene 5
CG6383	43	1	crumbs
CG8815	42	1	Sin34
CG40500	42	1	CG40500
CG9761	42	1	Nenrilysin 2
CG/300	41	1	anhanced adult sensory threshold
CG2509	41	1	ede22
CG1695	41	1	CG1695
CG1095	41	1	Ribosomal protain \$0
CC21045	41	1	Muosin kaareeskeise Ulee
CG31045	41	1	Myosin heavy chain-like

Appendix

CG6355 CG6684

CG6355 Ribosomal protein S25 40 40

CG10967 CG13762

40 39

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Autophagy-specific gene 1 brivido-3

A.7 pMT-Ana2-PrA +MG132 purification from Drosophila cells

CC #	G		E-B	CC10044	41	1 2	Dihasamal matain S6
CG #	Score	#pep	Full name	CG2612	41	2	kibosomai protein So
CG15792	6625	131	zipper	CC3012	40	1	CC7085
CG8262	4562	80	anastrai spindle 2	CG/985	39	1	CG/985
CG4264	3244	61	Heat shock protein cognate 4	CG6509	39	2	Discs large 5
CG4027	1900	54	Actin 5C	CG/490	5/	1	Kibosomal protein LPU
CG10067	1487	47	Actin 57B	CG/581	5/	2	Bub3
CG9277	1339	33	β-Tubulin at 56D	CG5119	35	1	polyA-binding protein
CG3201	883	14	Myosin light chain cytoplasmic	CG/003	34	2	Msh6
CG1913	701	19	α-Tubulin at 84B	CG10370	32	1	Tat-binding protein-1
CG18743	657	14	Heat-shock-protein-70Ab	CG1633	32	1	thioredoxin peroxidase 1
CG4147	637	24	Heat shock protein cognate 3	CG8978	31	1	Suppressor of profilin 2
CG5834	631	14	Hsp70Bbb	CG9155	31	2	Myosin 61F
CG5450	543	11	Cytoplasmic dynein light chain 2	CG17209	31	1	CG17209
CG3401	524	18	β-Tubulin at 60D	CG14996	31	1	Chd64
CG3595	523	12	spaghetti squash	CG3996	30	2	CG3996
CG8937	472	11	Heat shock protein cognate 1	CG1539	30	1	tropomodulin
CG5436	412	9	Heat shock protein 68	CG2168	29	1	Ribosomal protein S3A
CG12101	409	7	Heat shock protein 60	CG1683	29	2	Adenine nucleotide translocase 2
CG4463	397	10	Heat shock protein 23	CG6428	29	1	CG6428
CG10641	282	6	Swiprosin-1	CG8578	29	1	CG8578
CG8472	267	7	Calmodulin	CG5502	28	1	Ribosomal protein L4
CG8280	265	9	Elongation factor 1a48D	CG10277	20	1	Heterogeneous nuclear ribonucleoprotein at
CG4183	173	3	Heat shock protein 26	010377	20	1	27C
CG7438	173	3	Myosin 31DF	CG14040	28	1	senju
CG31618	146	2	His2A:CG31618	CG3074	28	1	Secreted Wg-interacting molecule
CG9086	140	6	Ubr1 ubiquitin ligase	CG3382	28	1	Organic anion transporting polypeptide 58Db
CG10465	137	5	CG10465	CG7434	27	1	Ribosomal protein L22
CG1106	124	4	Gelsolin	000407	07		Small ribonucleoprotein particle protein
CG14637	124	3	abstrakt	CG8427	27	1	SmD3
CG4145	111	4	Collagen type IV	CG7961	26	1	Coat Protein (coatomer) a
CG12750	100		nucampholin	CG11522	26	1	Ribosomal protein L6
CG4808	109	2	Tropomyosin 1	CG7595	25	1	crinkled
CC0040	108	2	CC0040	CG10071	25	1	Ribosomal protein L29
CC17159	108	2	CG9940	CG1484	22	1	flightless I
CG17138	103	2	capping protein beta	CG2692	24	1	gooseberry-neuro
CG31022	104	3	protyt-4-itydroxytase-aiplia EFB	CG10061	24	1	Sas-4
CG10340	101	3	Capping protein alpha	CG1403	24	1	Septin-1
CG4087	93	2	Ribosomal protein LP1	CG2941	24	1	CG2941
CG5499	89	1	Histone H2A variant	CG10353	24	1	CG10353
CG6988	89	2	Protein disulfide isomerase	CG1810	24	1	mPNA_copping_enzyme
CG5934	86	1	CG5934	CG0777	24	1	CC0777
CG/283	81	1	Ribosomal protein L10Ab	CG7210	24	1	Sermin 29D
CG8947	78	1	26-29kD-proteinase	CC2711	24	1	CC2711
CG9282	77	1	Ribosomal protein L24	CC17040	24	1	Uis2B-CC17040
CG11999	77	1	CG11999	CG1/949	24	1	HIS2B:CG17949
CG8542	74	3	Heat shock protein cognate 5	CG3830	23	1	stonewall
CG2146	74	4	dilute class unconventional myosin	CG10855	23	1	0002772
CG5695	72	2	jaguar	CG2/6/	23	1	CG2/6/
CG6341	66	1	Elongation factor 1 β	CG13609	23	1	CG13609
CG1548	63	1	cathD	CG3432	23	1	CG5432
CG9684	62	3	CG9684	CG3/51	23	1	Ribosomal protein S24
CG31712	61	3	CG31712	CG10851	22	1	B52
CG11276	60	1	Ribosomal protein S4	CG4063	22	1	ebi
CG6253	60	1	Ribosomal protein L14	CG5214	22	1	CG5214
CG1826	60	4	BTB (POZ) domain containing 9 ortholog	CG18408	21	1	CAP
CG18572	54	1	rudimentary	CG7999	21	1	Mediator complex subunit 24
CG2960	54	1	Ribosomal protein L40	CG32365	20	1	CG32365
CG9581	54	1	CG9581	CG11274	18	1	SRm160
CG1516	47	1	Pyruvate carboxylase	CG10986	17	1	garnet
CG7808	44	1	Ribosomal protein S8				
CG7791	43	1	CG7791				
CG10663	43	3	CG10663				
CG7144	42	2	lysine ketoglutarate reductase				
CG18174	42	1	Rpn11				
CG12233	41	1	lethal (1) G0156				
CG10546	41	1	Cellular retinaldehyde binding protein				
010540	41	1	Central retiliardenyde binding protein				

A.8 pMT-Ana2-PrA +OA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name			
CG8262	11127	177	anastral spindle 2			
CG4264	4392	98	Heat shock protein cognate 4			
CG9277	1234	32	β-Tubulin at 56D			
CG18743	1106	23	Heat-shock-protein-70Ab			
CG6998	1065	22	cut up			
CG5834	1043	21	Hsp70Bbb			
CG3401	945	28	β-Tubulin at 60D			
CG4147	789	21 Heat shock protein cognate 3				
CG5436	781	15	Heat shock protein 68			
CG1913	724	20	α-Tubulin at 84B			
CG12051	681	22	Actin 42A			
CG4027	678	22	Actin 5C			
CG10465	599	18	CG10465			
CG15792	461	13	zipper			
CG10067	434	16	Actin 57B			

000000	070	10	E1 (6 (1.40D
CG8280	3/3	10	Elongation factor 1048D
CG3201	364	8	Myosin light chain cytoplasmic
CG14996	274	7	Chd64
CG12101	248	4	Heat shock protein 60
CG4463	243	5	Heat shock protein 23
CG6988	239	7	Protein disulfide isomerase
CG31022	234	6	prolyl-4-hydroxylase-alpha EFB
CG31618	210	2	His2A:CG31618
CG4183	181	3	Heat shock protein 26
CG1548	179	4	cathD
0010277	149	2	Heterogeneous nuclear
CG105//			ribonucleoprotein at 27C
CG14637	133	4	abstrakt
CG18572	129	4	rudimentary
CG1826	128	5	BTB (POZ) domain containing 9 ortholog

CG2960	113	3	Ribosomal protein L40
CG3937	103	2	cheerio
CG9086	87	3	Ubr1 ubiquitin ligase
CG6521	86	1	Signal transducing adaptor molecule
CG17498	85	1	mad2
CG10938	83	2	Proteasome a5 subunit
CG11143	76	3	Inos
CG5499	74	1	Histone H2A variant
CG12750	73	1	nucampholin
CG3265	69	1	Eb1
CG2050	67	1	modulo
CG5170	67	2	Dodeca-satellite-binding protein 1
CG9940	65	2	CG9940
CG1528	64	2	Coat Protein (coatomer) v
CG31712	63	3	CG31712
CG4466	62	2	Haat shock protein 27
CG3595	60	2	spaghetti squash
CG11274	59	2	SPm160
CC0748	55	2	halla
CG9/48	33	3	Delle Folosovicio initiation fostan 2 o 40
CG9124	53	1	Eukaryotic initiation factor 3 p40 subunit
CG10191	53	2	Proteome of centrioles 1
CG8947	53	1	26-29kD-proteinase
CG17291	52	1	Protein phosphatase 2A at 29B
CG4145	51	1	Collagen type IV
CG8542	51	2	Heat shock protein cognate 5
CG1977	50	1	a Spectrin
CG9684	/0	2	CG9684
CG7985	47	1	CG7085
CG5174	44	1	CG5174
CG1516	44	1	Burnwete cerboxylase
CG10546	43	1	Callular ratinaldabuda binding protain
C010540	41	1	Small rikerwalaonnatain portiala matain
CG10753	39	1	Sman ribonucleoprotein particle protein SmD1
CG11276	38	1	Ribosomal protein S4
CG7961	38	2	Coat Protein (coatomer) a
CG10230	38	1	Rpn9
CG4904	37	1	Proteasome 35kD subunit
CG6223	37	1	Coat Protein (coatomer) B
CG6453	37	1	Glucosidase 2 β subunit
CG10663	37	2	CG10663
CG18811	37	1	Caprin
CG1683	36	3	Adenine nucleotide translocase 2
CG4087	35	1	Ribosomal protein LP1
CG6509	35	1	Discs large 5
CG10851	34	2	B52
CG6773	32	1	sec13
CG7581	32	1	Bub3
CG1341	32	1	Rnt1
CG6602	31	1	Cysteine proteinase-1
CG3370	31	1	Histone H4 replacement
CG17769	31	1	CG17768
CG1072	20	1	
CG1510	20	1	yata Protoscomo g7 subunit
COIDIA	29	1	rioteasome a/ subunit

CG6428	29	1	CG6428
CG17209	29	1	CG17209
CG1633	29	1	thioredoxin peroxidase 1
CG7595	28	1	crinkled
CG6699	28	1	Coat Protein (coatomer) B'
CG17949	28	1	His2B:CG17949
CG2168	27	1	Ribosomal protein S3A
CG4898	26	1	Tropomyosin 1
CG17870	26	1	14-3-35
CG11198	26	1	Acetyl-CoA carboxylase
CG13609	26	1	CG13609
CG9750	26	1	reptin
CG3711	26	1	CG3711
CG4063	25	1	ebi
CG1591	25	1	REG
CG2692	24	1	gooseberry-neuro
CG7144	24	1	lysine ketoglutarate reductase
CG14040	24	1	senju
CG7219	24	2	Serpin 28D
CG9934	24	1	CG9934
CG8857	24	1	Ribosomal protein S11
CG11963	24	1	skpA associated protein
CG34130	24	2	CG34130
CG6631	24	1	anastral spindle 1
CG5825	23	1	Histone H3.3A
CG2488	23	1	(6-4)-photolyase
CG6230	23	1	CG6230
CG31370	23	1	CG31370
CG6850	22	1	UDP-glucose-glycoprotein
000000			glucosyltransferase
CG18408	22	1	CAP
CG5195	22	1	artichoke
CG5406	22	1	still life
CG6944	21	1	Lamin
CG9581	21	1	CG9581
CG7434	20	1	Ribosomal protein L22
CG5708	20	2	CG5708
CG13345	20	1	RacGAP50C
CG9888	19	1	Fibrillarin
CG3836	19	1	stonewall
CG9191	19	1	Kinesin-like protein at 61F
CG8427	19	1	Small ribonucleoprotein particle protein SmD3
CG10712	19	1	Chromator
CG10986	18	1	garnet
CG10333	18	1	CG10333
CG6781	18	1	sepia
CG3382	17	1	Organic anion transporting polypeptide 58Db

A.9 pAct5-PrA-Ana2 + pMT-Plk4 +OA

CG #	Score	#pep	Full name
CG8262	7098	138	anastral spindle 2
CG15792	1987	42	zipper
CG4027	1342	39	Actin 5C
CG4264	896	21	Heat shock protein cognate 4
CG10686	846	16	trailer hitch
CG5450	662	22	Cytoplasmic dynein light chain 2
CG8280	512	15	Elongation factor 1a48D
CG11183	444	11	Decapping protein 1
CG4147	430	8	Heat shock protein cognate 3
CG5436	345	8	Heat shock protein 68
CG4063	340	9	ebi
CG5834	338	8	Hsp70Bbb
CG3201	287	5	Myosin light chain cytoplasmic
CG3595	169	6	spaghetti squash
CG9277	136	4	β-Tubulin at 56D
CG4013	130	2	Smrter
CG17002	116	3	CG17002
CG6995	115	1	Scaffold attachment factor B
CG4087	93	1	Ribosomal protein LP1
CG16858	92	1	viking
CG31022	89	1	prolyl-4-hydroxylase-alpha EFB
CG11901	78	2	Eflγ
CG4145	74	2	Collagen type IV
CG9412	72	1	rasputin
CG1913	69	1	α-Tubulin at 84B
CG10984	69	1	CG10984
CG3195	58	1	Ribosomal protein L12
CG14648	56	1	growl
CG7434	54	1	Ribosomal protein L22
CG3922	51	1	Ribosomal protein S17

CG3821	49	1	Aspartyl-tRNA synthetase
CG1524	49	1	Ribosomal protein S14a
CG2746	47	1	Ribosomal protein L19
CG14206	47	1	Ribosomal protein S10b
CG30084	47	1	Z band alternatively spliced PDZ-motif protein 52
CG3937	44	1	cheerio
CG3661	43	1	Ribosomal protein L23
CG7622	41	1	Ribosomal protein L36
CG12306	41	1	polo
CG3314	41	1	Ribosomal protein L7A
CG17489	41	1	Ribosomal protein L5
CG17158	38	1	capping protein beta
CG4046	38	1	Ribosomal protein S16
CG2098	37	1	ferrochelatase
CG10576	37	1	CG10576
CG7985	36	1	CG7985
CG11276	35	1	Ribosomal protein S4
CG6253	35	1	Ribosomal protein L14
CG10161	34	1	Eukaryotic initiation factor 3 p66 subunit
CG5920	33	1	Ribosomal protein S2
CG6684	33	1	Ribosomal protein S25
CG7186	32	1	Plk4
CG6509	32	1	Discs large 5
CG7878	32	1	CG7878
CG9155	31	1	Myosin 61F
CG8274	31	1	Megator
CG6148	31	1	Putative Achaete Scute Target 1

A.10 pMT-Sas4-PrA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG10061	39977	1290	Sas-4
CG9277	10982	296	β-Tubulin at 56D
CG4264	7674	292	Heat shock protein cognate 4
CG3401	4606	106	β-Tubulin at 60D
CG4463	3894	120	Heat shock protein 23
CG4164	3130	/4	α-1ubulin at 84B
CG5436	1/37	35	Heat shock protein 68
CG18743	1427	47	Heat-shock-protein-70Ab
CG5502	1228	32	Ribosomal protein L4
CG5834	1199	36	Hsp70Bbb
CG9748	1084	30	belle
CG11999	995	35	CG11999
CG4147	982	33	Heat shock protein cognate 3
CG4183	863	29	Heat shock protein 26
CG8478	713	22	CG8478
CG12233	676	22	lethal (1) G0156
CG6815	566	14	belphegor
CG8280	562	22	Elongation factor 1a48D
CG7831	516	12	non-claret disjunctional
CG11451	492	15	Spc105-related
CG1883	490	15	Ribosomal protein S7
CG4027	464	14	Actin 5C
CG7478	439	13	Actin 79B
CG3981	378	9	Unc-76
CG31618	321	7	His2A:CG31618
CG3203	306	8	Ribosomal protein L17
CG4466	298	6	Heat shock protein 27
CG7915	297	11	Ect4
CG14207	296	7	HspB8
CG7439	294	11	Argonaute 2
CG5119	290	12	polyA-binding protein
CG8900	283	6	Ribosomal protein S18
CG1427	200	9 7	CINOS and CD2AP orthologue
CG1427	257	/	UG142/
CG5029	230	0	ypsiion schachtel
CG5330	249	5	Nucleosome assembly protein 1
CG6143	240	3	Protein on ecdysone puffs
CG4897	247	12	Ribosomal protein L 7
CG31022	240	5	prolyl-4-hydroxylase-alpha FFB
CG7863	239	8	dream
CG16858	233	4	viking
CG14648	232	8	growl
			eukaryotic translation initiation factor
CG10811	227	4	4G
CG4087	219	7	Ribosomal protein LP1
CG14792	219	5	stubarista
CG4460	218	5	Heat shock protein 22
CG5174	213	6	CG5174
CG10578	212	10	DnaJ-like-1
CG6779	202	8	Ribosomal protein S3
CG8332	202	6	Ribosomal protein S15
CG7323	201	3	CG7323
CG1489	199	3	Pros45
CG1242	197	7	Heat shock protein 83
CG9281	195	8	CG9281
CG15/84	191	3	CG15/84
CG10220	1//	5	Ribosomai protein S8
CG16072	1/0	4	rpn9 misshanan
CG2169	108	5	Ribosomal protein \$2.4
CG1/206	167	5	Ribosomal protein \$10b
CG3612	166	5	hellwether
CG11522	164	3	Ribosomal protein L 6
CG11276	161	7	Ribosomal protein S4
CG3455	157	3	Rpt4
CG9188	145	3	septin interacting protein 2
CG8947	144	4	26-29kD-proteinase
CG3201	141	5	Myosin light chain cytoplasmic
CG4145	140	4	Collagen type IV
CG3379	140	5	Histone H4 replacement
CG2746	135	1	Ribosomal protein L19
CG16944	131	5	stress-sensitive B
CG12775	131	7	Ribosomal protein L21
CG9282	130	2	Ribosomal protein L24
CG3922	129	3	Ribosomal protein S17
CG32626	129	2	AMP deaminase
CG7977	128	5	Ribosomal protein L23A
CG8922	127	2	Ribosomal protein S5a
CG9325	127	3	hu li tai shao
CG3395	123	6	Ribosomal protein S9
CG4464	122	5	Ribosomal protein S19a
CG3422	121	3	Proteasome 28kD subunit 1
CG/283	120	3	Ribosomal protein L10Ab
CG16916	118	2	Rpt3
CG5499	116	2	Histone H2A variant
CG1548	116	2	cathD
CG12262	116	4	CG12262
CG2210	115	2	Pibecemel metric L D0
CG/490	111	4	Kibosoinai protein LPU
CG4157	110	·)	Pnn17

CG5920	109	3	string of pearls
CG15442	106	5	Ribosomal protein L27A
CG1683	106	3	Adenine nucleotide translocase 2
CG5353	106	2	Threonyl-tRNA synthetase
CC6420	106	2	CG6420
CG6439	106	2	CG6439
CG/622	105	2	Ribosomal protein L36
CG5374	103	2	Tcp1-like
CG8355	102	3	slit
CG1341	100	3	Rpt1
CG2960	98	4	Ribosomal protein L40
CG2998	98	2	Ribosomal protein S28b
CG15792	07	3	zinner
CG10/52	97	5	Zippei
CG10652	9/	3	Ribosomal protein L30
CG15697	94	3	Ribosomal protein S30
CG1524	93	2	Ribosomal protein S14a
CG3024	92	3	torp4a
CG7726	91	2	Ribosomal protein L11
CG6181	91	2	Ge-1
CG8615	80	2	Bibosomel protein L 19
C08013	07	2	Ribosoniai protein £18
CG10305	89	1	Ribosomal protein S26
CG10944	88	2	Ribosomal protein S6
CG7961	87	2	Coat Protein (coatomer) α
CG31045	86	3	Myosin heavy chain-like
CG2098	84	2	ferrochelatase
CG6095	84	2	exo84
CG4581	83	1	Thiolase
CG11870	80	1	CG11870
0110/0	00	1	Small ribonucleonrotain nontiale materia
CG10753	80	1	Sman ribonucleoprotein particle protein
00000	=0		SmD1
CG6875	79	2	abnormal spindle
CG9327	79	3	Proteasome 29kD subunit
CC4290	79	2	Mitochondrial trifunctional protein a
CG4389	/ð	2	subunit
CG5474	76	2	Signal sequence receptor B
CG4651	76	4	Ribosomal protein L13
CG6253	75	2	Ribosomal protein I 14
CG18174	75	2	Ribbsoniai protein E14
CC1452	73	1	Khiili Khaloo
001455	74	1	KIPIOA
CG4454	/4	3	borealin-related
CG17528	74	3	CG17528
CG7434	73	3	Ribosomal protein L22
CG2078	73	2	Myd88
CG7945	73	2	CG7945
CG11734	72	1	HERC2
CG17949	72	2	His2B:CG17949
CG10360	70	1	refractory to sigma P
CC6450	70	1	CC6450
1 1 104 19	/0	1	0.06439
000107	=0		221002
CG1092	70	1	CG1092
CG1092 CG5934	70 70	1	CG1092 CG5934
CG1092 CG5934 CG3314	70 70 69	1 1 2	CG1092 CG5934 Ribosomal protein L7A
CG1092 CG5934 CG3314 CG9124	70 70 69 69	1 1 2 1	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit
CG1092 CG5934 CG3314 CG9124 CG11888	70 70 69 69 69	1 1 2 1 3	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764	70 70 69 69 69 69	$ \begin{array}{c} 1 \\ 2 \\ 1 \\ 3 \\ 2 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG13389	70 70 69 69 69 69 69 68	$ \begin{array}{c} 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13
CG1092 CG5934 CG5934 CG3314 CG9124 CG11888 CG31764 CG13389 CG11271	70 70 69 69 69 69 69 68 68	$ \begin{array}{c} 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Pibosomal protein S13
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG13389 CG11271	70 70 69 69 69 69 69 68 68 68	$ \begin{array}{c} 1\\ 1\\ 2\\ 1\\ 3\\ 2\\ 3\\ 2\\ 2\\ 2 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S12
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG13389 CG11271 CG18495 CG18495	70 70 69 69 69 69 68 68 68 68 67	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 1 1 3 2 3 3 3 3 4 4 4 4 4 $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S12 Proteasome a1 subunit
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG13389 CG11271 CG18495 CG7518	70 70 69 69 69 69 68 68 68 67 67	$ \begin{array}{r} 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S12 Proteasome al subunit CG7518
CG1092 CG5934 CG314 CG9124 CG11888 CG31764 CG1389 CG1271 CG18495 CG7518 CG9946	70 70 69 69 69 69 68 68 68 67 67 67	$ \begin{array}{c} 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Proteasome al subunit CG7518 eukaryotic translation Initiation Factor
CG1092 CG5934 CG3314 CG124 CG11888 CG31764 CG11888 CG31764 CG13899 CG11271 CG18495 CG7518 CG9946	70 70 69 69 69 68 68 68 67 67 67	$ \begin{array}{r} 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Proteasome α1 subunit CG7518 eukaryotic translation Initiation Factor 2α
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG11389 CG11271 CG18495 CG7518 CG9946 CG3157	70 70 69 69 69 68 68 67 67 67 67 67	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S12 Proteasome α1 subunit CG7518 eukaryotic translation Initiation Factor 2α γ-Tubulin at 23C
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG11888 CG31764 CG127 CG18495 CG7518 CG9946 CG3157 CG3195	70 70 69 69 69 69 68 68 67 67 67 67 67 66 66	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Proteasome α1 subunit CG7518 eukaryotic translation Initiation Factor 2α γ-Tubulin at 23C Ribosomal protein L12
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG13889 CG1271 CG18495 CG7518 CG9946 CG3157 CG3195 CG17291	70 70 69 69 69 68 68 68 67 67 67 67 66 66 66	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 1 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Proteasome α1 subunit CG7518 eukaryotic translation Initiation Factor 2α y-Tubulin at 23C Ribosomal protein L12 Protein phosphatase 2A at 29B
CG1092 CG5934 CG3314 CG9124 CG11888 CG31764 CG11888 CG31764 CG11271 CG18495 CG7518 CG9946 CG3157 CG3195 CG17291 CG11963	70 70 69 69 69 68 68 68 67 67 67 67 67 66 66 66 66	$ \begin{array}{r} 1 \\ 1 \\ 2 \\ 1 \\ 2 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 1 \\ 1 \end{array} $	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S12 Proteasome α1 subunit CG7518 eukaryotic translation Initiation Factor 2α γ-Tubulin at 23C Ribosomal protein L12 Protein phosphatase 2A at 29B skpA associated protein
CG1092 CG5934 CG5934 CG9124 CG11888 CG31764 CG1389 CG11271 CG18495 CG7518 CG9946 CG3157 CG3195 CG17291 CG11963 CG1964 CG1964	70 70 69 69 69 68 68 68 67 67 67 67 67 66 66 66 66 65 63	$ \begin{array}{c} 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 1 \\ 3 \\ 3 \\ 1 \\ 3 \\ 1 \\ 3 \\ 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1$	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Proteasome al subunit CG7518 eukaryotic translation Initiation Factor 2α γ-Tubulin at 23C Ribosomal protein L12 Protein phosphatase 2A at 29B skpA associated protein Ribosomal protein S16
CG1092 CG5934 CG314 CG9124 CG11888 CG31764 CG13889 CG11271 CG18495 CG7518 CG9946 CG3157 CG3195 CG17291 CG11963 CG1063 CG4046 CG5609	70 70 69 69 69 69 68 68 67 67 67 67 67 66 66 66 65 63 62	$ \begin{array}{c} 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 1 \\ 3 \\ 2 \\ 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2$	CG1092 CG5934 Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Proteasome α1 subunit CG7518 eukaryotic translation Initiation Factor 2α y-Tubulin at 23C Ribosomal protein L12 Protein phosphatase 2A at 29B skpA associated protein Ribosomal protein S16 Custaina protein S16
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CG1092 CG5934 CG3314 CG9124 CG12888 CG31764 CG11888 CG31764 CG13895 CG7518 CG9946 CG3157 CG3195 CG17291 CG11963 CG4046 CG6092 CG8282 CG4046 CG6094 CG6094 CG6094 CG6094 CG6094 CG6094 CG6094 CG15087 CG1188 CG6094 CG2028 CG7035 CG1084 CG2028 CG6094 CG7762 CG33162 CG14482 CG10948 CG10484 CG10948 CG1048 CG1048 CG10487 CG10488 CG1	$\begin{array}{c} 70\\ 70\\ 69\\ 69\\ 69\\ 68\\ 68\\ 68\\ 67\\ 67\\ 67\\ 67\\ 67\\ 67\\ 66\\ 66\\ 66\\ 66$	$\begin{array}{c} 1 \\ 1 \\ 2 \\ 1 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 1 \\ 1 \\ 1 \\ 2 \\ 2$	CG1092 $CG5934$ Ribosomal protein L7A Eukaryotic initiation factor 3 p40 subunit Rpn2 virus-induced RNA 1 Ribosomal protein S13 Ribosomal protein S13 Ribosomal protein S12 Proteasome al subunit $CG7518$ eukaryotic translation Initiation Factor 2a ··-Tubulin at 23C Ribosomal protein L12 Protein phosphatase 2A at 29B skpA associated protein Ribosomal protein S16 Cysteine protein S16 Cysteine protein S16 Ribosomal protein S16 Ribosomal protein S16 Cysteine protein S16 Cysteine protein S17 Ribosomal protein S16 Cysteine protein S16 Cysteine protein S16 Ribosomal protein S16 Cysteine protein S16 Cysteine protein S16 Cottaining protein S16 Cottaining protein S15Aa Vacuolar protein sorting 51 rough deal Receptor of activated protein Kinase C 1 CG6701 La related protein CG6226 CG8258 Coat Protein (coatomer) β' His1:CG31617 CG6940 CG5726 fizzy Rpn1 Signal recognition particle receptor β Ubiquinol-cytochrome c reductase 6.4 kDa subunit Proteasome a5 subunit BM-40-SPARC Regulatory particle non-ATPase 3 Om

Appendix A

CG4097	50	1	Proteasome 26kD subunit
001245	40		Glutamine:fructose-6-phosphate
CG1345	49	1	aminotransferase 2
CG13849	47	1	Nop56
CG9888	46	2	Fibrillarin
CG15224	45	1	Casein kinase II ß subunit
CG3008	45	1	CG3008
CG7185	45	1	CG7185
CG5266	45	1	Proteosome 25kD subunit
CG3595	43	1	spaghetti squash
CG14472	44	1	spagnetti squasn
CG1100	44	1	Punty of essence
CG4220	44	1	reptor
CG4320	44	1	Taploi Developmentiale and ATDeve 12
CG13349	44	2	Regulatory particle non-ATPase 13
CG/546	44	2	CG/546
CG33106	44	1	multiple ankyrin repeats single KH
			domain
CG8055	44	1	shrub
CG10315	43	1	eIF2B-ð
CG7595	41	3	crinkled
CG3210	41	1	Dynamin related protein 1
CG9938	41	1	Ndc80
CG8415	41	1	Ribosomal protein S23
CG32223	41	1	CG32223
CG33715	41	2	Muscle-specific protein 300
CG6684	40	1	Ribosomal protein S25
CG5004	40	1	CG5004
CG14469	39	2	dpr12
CG31009	39	2	Cad99C
CG5170	38	2	Dodeca-satellite-binding protein 1
CG8857	38	2	Ribosomal protein S11
CG9795	38	3	CG9795
CG9775	38	1	CG9775
CG11881	38	1	dim y-tubulin 6
CG2711	37	3	deformed wings
CG5319	37	1	lute
CG6223	36	1	Coat Protein (coatomer) ß
CG1403	36	1	Septin-1
CG6141	36	1	Ribosomal protein I 9
CG5316	36	1	CG5316
CG800/	35	1	evunerantia
CG12101	35	1	Heat shock protein 60
CC17281	25	1	neat shock protein ou
CC12740	25	1	Bibasamal metain L 28
002647	35	1	Kibosomai protein L28
CG364/	34	1	shuttle craft
CG1559	34	1	Upti
CG7637	34	1	CG7637
CG6090	34	1	Ribosomal protein L34a
CG7939	33	1	Ribosomal protein L32
CG17870	33	1	14-3-3ζ
CG1657	33	1	CG1657

CG11838	33	1	Oseg3
CG6509	33	1	Discs large 5
CG2213	33	1	mitotic spindle density 5
CG1483	32	1	Microtubule-associated protein 205
CG6510	32	2	Ribosomal protein L18A
CG12245	32	1	glial cells missing
CG1591	32	1	REG
CG10663	32	1	CG10663
CG17320	31	1	Sterol carrier protein X-related thiolase
CG10269	31	1	D19A
CG3126	31	1	C3G
CG7758	31	2	pumpless
CG14446	31	1	CG14446
CG18102	30	1	shibire
CG1101	30	1	Alv
CG10379	30	1	myoblast city
CG6428	30	1	CG6428
CG13126	30	1	CG13126
CG5450	29	1	Cytoplasmic dynein light chain 2
CG1528	29	1	Coat Protein (coatomer) y
CG6450	29	1	lava lamp
CG31426	29	1	ligatin
CG30477	29	1	CG30477
CG32191	29	1	CG32191
CG5825	28	1	Histone H3 3A
CG14816	28	1	Phosphoglycerate mutase 5
CG10370	28	1	Tat-binding protein-1
CG2253	28	1	Unf2
CG7041	28	1	HP1b
CG1691	28	1	IGF-II mRNA-binding protein
CG9091	28	1	Ribosomal protein L37a
CG3996	28	1	CG3996
CG99999	27	1	Ran GTPase activating protein
CG4297	27	1	CG4297
CG5604	27	1	CG5604
CG6116	27	1	UV-resistance associated gene
CG6042	27	1	Cyp12a4
CG10161	27	1	Eukaryotic initiation factor 3 p66 subunit
CG31792	27	1	CG31792
CG1666	26	1	Helicase
CG8571	26	1	smallminded
CG3751	26	1	Ribosomal protein S24
CG3051	25	1	SNF1A/AMP-activated protein kinase
CG6842	25	1	Vacuolar protein sorting 4
CG15255	25	1	CG15255
CG33131	25	1	SCAP
2000101	45	<u> </u>	50.11

A.11 pMT-Sas4-PrA +OA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG10061	24851	848	Sas-4
CG4264	10717	273	Heat shock protein cognate 4
CG9277	5948	176	β-Tubulin at 56D
CG1913	4682	123	α-Tubulin at 84B
CG15792	4332	95	zipper
CG4164	4043	90	CG4164
CG4183	3586	93	Heat shock protein 26
CG4463	3552	95	Heat shock protein 23
CG18743	1959	50	Heat-shock-protein-70Ab
CG5834	1901	48	Hsp70Bbb
CG5436	1767	42	Heat shock protein 68
CG3401	1704	38	β-Tubulin at 60D
CG4147	1558	39	Heat shock protein cognate 3
CG12233	1308	30	lethal (1) G0156
CG4869	1261	26	β-Tubulin at 97EF
CG10732	949	26	combover
CG10811	905	17	eukaryotic translation initiation factor 4G
CG8280	874	31	Elongation factor 1a48D
CG4027	871	27	Actin 5C
CG4466	732	23	Heat shock protein 27
CG11999	652	13	CG11999
CG9748	649	16	belle
CG10067	613	21	Actin 57B
CG2684	551	15	lodestar
CG6815	527	11	belphegor
CG3201	516	11	Myosin light chain cytoplasmic
CG17870	516	10	14-3-3ζ
CG17870	498	10	14-3-3ζ
CG7915	490	14	Ect4
CG31196	485	10	14-3-3ε
CG6450	460	11	lava lamp
CG3595	443	10	spaghetti squash
CG7439	410	13	Argonaute 2
CG14207	405	10	HspB8
CG7863	405	11	dream
CG8014	396	9	Receptor mediated endocytosis 8
CG31022	376	10	prolyl-4-hydroxylase-alpha EFB

CG4460	354	10	Heat shock protein 22
CG5353	354	9	Threonyl-tRNA synthetase
CG10578	353	13	DnaJ-like-1
CG1528	341	7	Coat Protein (coatomer) y
CG8571	337	5	smallminded
CG16858	329	7	viking
CG1242	323	7	Heat shock protein 83
CG8863	312	10	DnaJ-like-2
CG5092	308	7	Target of rapamycin
CG1569	302	6	rough deal
CG8478	297	8	CG8478
CG2216	295	7	Ferritin 1 heavy chain homologue
CG5028	294	7	CG5028
CG3024	293	9	torp4a
CG10230	290	6	Rpn9
CG16944	289	7	stress-sensitive B
CG8947	287	7	26-29kD-proteinase
CG4260	285	6	Adaptor Protein complex 2, α subunit
CG9325	283	7	hu li tai shao
CG12306	281	9	polo
CG11963	281	5	skpA associated protein
CG1548	271	5	cathD
CG6223	267	7	Coat Protein (coatomer) β
CG16916	259	4	Rpt3
CG5330	235	4	Nucleosome assembly protein 1
CG7865	234	6	PNGase-like
CG9281	232	8	CG9281
CG4389	224	4	Mitochondrial trifunctional protein a SUt
CG10077	224	7	CG10077
CG32164	224	6	CG32164
CG4145	222	5	Collagen type IV
CG1945	220	6	fat facets
CG3422	214	5	Proteasome 28kD subunit 1
CG3210	213	5	Dynamin related protein 1
CG9012	211	6	Clathrin heavy chain
CG1489	211	6	Pros45
CG1341	210	5	Rpt1
CG5174	210	5	CG5174
CG5289	208	4	Proteasome 26S subunit subunit 4

			ATPase
CG11198	206	3	Acetyl-CoA carboxylase
CG5119	205	5	polyA-binding protein
CG18495	202	6	Proteasome al subunit
CG11451	199	5	Spc105-related
CG4320	195	6	raptor
CG6439	193	4	CG6439
CG3612	189	3	bellwether
CG10596	188	2	Msr-110
CG7324	187	5	CG7324
CG10535	185	3	Elongator complex protein 1
CG8977	183	3	Ccty
CG1559	183	6	Upf1
CG7507	177	5	Dynein heavy chain 64C
CG5974	175	4	pelle
CG6692	174	4	Cysteine proteinase-1
CG10938	169	3	Proteasome α5 subunit
CG31012	169	5	CIN85 and CD2AP orthologue
CG1883	168	4	Ribosomal protein S/
CG18572	164	5	rudimentary
CG1657	164	3	CG1657
CG9900	162	4	mitotic 15
CG6760	158	4	peroxin 1
CG14792	157	4	stubarista
CG31618	155	2	His2A:CG31618
CG8309	154	3	Transport and Golgi organization 7
CG14472	153	4	purity of essence
CG17520	150	4	casein kinase IIa
CG7945	149	2	CG7945
CG5520	149	4	Glycoprotein 93
CG2028	148	6	Casein kinase la
CG22129	14/	2	CC22129
CG17409	147	2	med?
CG14648	145	5	growl
CG3981	145	3	Unc-76
000000			Cullin-associated and neddylation-
CG5366	144	4	dissociated 1
CG7546	144	2	CG7546
CG5650	141	2	Protein phosphatase 1 at 87B
CG9372	140	3	CG9372
CG5378	137	3	Rpn7
CG10360	135	4	refractory to sigma P
CG4157	134	2	Dodeca-satellite-binding protein 1 Rpn12
04157	132	2	Rpii12
(((+6509	1.37	/	Lises large 5
CG6509 CG33957	132	2	Discs large 5 cp309
CG6509 CG33957	132	2	cp309 Signal-transducer and activator of
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CG6509 CG33957 CG4257 CG18174 CG8295 CG7033	132 132 131 131 128 127	2 2 3 1 3	CG7033
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CG6509 CG33957 CG4257 CG18174 CG8295 CG7033 CG31739 CG17358 CG3074 CG1092 CG1092	132 132 131 128 127 127 126 126 125 124		Discs large 5 cp309 Signal-transducer and activator of transcription protein at 92E Rpn11 Myelodysplasia/myeloid leukemia factor CG7033 Aspartyl-tRNA synthetase, mitochondrial TBP-associated factor 12 Secreted Wg-interacting molecule CG1092 Vacuolar protein sorting 25
CG6509 CG33957 CG4257 CG18174 CG8295 CG7033 CG31739 CG17358 CG3074 CG1092 CG14750 CG14750	132 132 131 128 127 127 126 126 125 124 124		Discs large 5 cp309 Signal-transducer and activator of transcription protein at 92E Rpn11 Myelodysplasia'myeloid leukemia factor CG7033 Aspartyl-tRNA synthetase, mitochondrial TBP-associated factor 12 Secreted Wg-interacting molecule CG1092 Vacuolar protein sorting 25 Rn4
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CG18102	94	2	shibire
CG7146	93	1	Vacuolar protein sorting 39
CG9124	91	1	Eukaryotic initiation factor 3 p40 subunit
CG8282	91	2	Snx6
CG16/28	91	1	Git
CG3262	90	2	CG17/40
CG11888	89	4	Rpn2
CG5934	89	1	CG5934
CG2960	88	3	Ribosomal protein L40
CG11154	88	2	ATP synthase, β subunit
CG7581	88	4	Bub3
CG3265	88	1	Ebl Ninned A
033334	00	5	Ubiquinol-cytochrome c reductase 6.4
CG14482	87	2	kDa subunit
CG31764	87	3	virus-induced RNA 1
CG4978	86	2	Minichromosome maintenance 7
CG7769	86	1	DDB1
CG7762	86	3	Rpn1
CG7210	80	1	Palmitoyl-protein thioesterase 1 Mitoshondrial Transcription Factor P1
CG31045	85	2	Myosin heavy chain-like
CG4033	84	2	RNA polymerase I 135kD subunit
CG8368	84	3	CG8368
CG3180	83	4	RNA polymerase II 140kD subunit
CG5920	83	1	string of pearls
CG6617	82	1	CG6617
CG/0/4	82	1	missing oocyte
CG1851	81	1	Adv43A
CG14999	81	1	Replication factor C subunit 4
CG10379	79	2	myoblast city
CG7519	79	1	CG7519
CG8351	79	1	Тср-1η
CG3004	78	2	CG3004
CG13277	78	2	CG13277
CG10108	78	1	tumor suppressor protein 101
CG4003	78	2	pontin
001005	70	1	Succinyl coenzyme A synthetase
CG1/246	11	1	flavoprotein subunit
CG12262	77	2	CG12262
CG12265	77	1	Deterin
CG10701	76	2	Moesin
CG13387	70	1	secs1
CG8231	75	2	T-cnl
CG14695	75	1	CG14695
CG30497	75	1	CG30497
CG1059	75	3	Karyopherin ß 3
CG1453	74	1	Klp10A
CG15433	74	1	Elongator complex protein 3
CG10988	72	1	lethal (1) discs degenerate 4
CG3678	72	1	CG3678
CG4849	72	1	CG4849
CG30349	72	1	CG30349
CG4799	71	2	Pendulin
CG6556	71	1	connector enhancer of ksr
CG4858	71	1	CG4858
CG1100	70	2	Bran tumor Rpp5
CG1635	70	1	CG1635
CG2238	69	2	Elongation factor 2b
CG4087	69	1	Ribosomal protein LP1
CG6840	69	1	Rpb11
CG7791	69	1	CG7791
CG5266	69	2	Proteasome 25kD subunit
CG3011	67	1	CG3011
CG33484	67	1	zormin
CG11228	67	1	hippo
CG10484	66	3	Regulatory particle non-ATPase 3
CG7825	66	1	Rad17
CG3278	66	1	Tif-IA
CG7558	64	1	Actin-related protein 66B
CG5450	64	1	lingerer Cutoplasmic duppin light shain 2
CG3356	64	2	Cytopiasinic uynein right chain 2 CG3356
CG12244	64	2	licorne
CG12273	63	1	angel
CG3751	63	1	Ribosomal protein S24
CG4792	63	1	Dicer-1
CG9750	63	1	reptin
CG12532	62	3	Adaptor Protein complex $1/2$, β subunit
CG31452	62	3	CG/139
CG12163	62	2	CG12163
CG7831	61	1	non-claret disjunctional
CC7590	61	1	Ubiquinol-cytochrome c reductase
CG/380	01	1	ubiquinone-binding protein
CG11877	61	1	Autophagy-related 14
CG8322	60	1	ATP citrate lyase
CG2038	60	1	COP9 complex homolog subunit 7
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CG9446	60	1	COTO CC2205
CG3295 CG33162	59	2	Signal recognition particle recentor B
CG9940	59	2	CG9940
CG31048	59	2	sponge
CG1977	58	1	α Spectrin
CG11091	58	1	Septin-1 Proteasome 83 subunit
CG32045	57	1	furry
CG8426	57	1	lethal (2) NC136
CG9031	56	2	icarus
CG6850	55	1	UDP-glucose-glycoprotein
CG4201	55	1	immune response deficient 5
CG8777	55	1	CG8777
CG5625	55	1	Vacuolar protein sorting 35
CG6233	55	1	Ubiquitin fusion-degradation 1-like
CG3416	55	1	Nucleoporin 358 Moy34
CG8340	54	1	upstream of RpIII128
CG8578	54	1	CG8578
CG14211	54	1	MAPK Phosphatase 4
CG5094	54	2	small glutamine-rich tetratricopeptide
CG1104	54	1	CG1104
CG2656	54	1	CG2656
CG5723	53	1	Tenascin major
CG17158	53	1	capping protein beta
CG7008	53	1	Tudor-SN
CG18176	53	1	deflated
CG9888	52	2	Fibrillarin
CG2168	52	1	Ribosomal protein S3A
CG4993	52	2	PRL-1 Bub1 related kinsee
CG1486	52	1	CG1486
CG6444	52	1	Dpy-30-like 1
CG4662	52	1	CG4662
CG6831	52	1	rhea
CG2206	51	1	Grip163 lethal (1) G0193
CG9547	51	1	CG9547
CG31009	51	2	Cad99C
CG8448	50	2	mrj
CG1793	50	1	Mediator complex subunit 26
CG4904 CG8793	50	2	lethal (3) 76BDm
CG18740	49	1	moira
CG4897	49	1	Ribosomal protein L7
CC0084	49	1	TH1
0072222	40		
CG7238 CG6378	49 49	1	septin interacting protein 1
CG7238 CG6378 CG9769	49 49 49	1 3 1	septin interacting protein 1 BM-40-SPARC CG9769
CG7238 CG6378 CG9769 CG6369	49 49 49 49	1 3 1 1	septin interacting protein 1 BM-40-SPARC CG9769 Smg6
CG7238 CG6378 CG9769 CG6369 CG5692	49 49 49 49 49	1 3 1 1 1	septin interacting protein 1 BM-40-SPARC CG9769 Smg6 rapsynoid
CG7238 CG6378 CG9769 CG6369 CG5692 CG8472	49 49 49 49 49 49 48	$ \begin{array}{c} 1 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \end{array} $	septin interacting protein 1 BM-40-SPARC CG9769 Smg6 rapsynoid Calmodulin Pentagener 2010 charter
CG7238 CG6378 CG9769 CG6369 CG5692 CG8472 CG9327 CG8402	49 49 49 49 49 49 48 48 48 48	$ \begin{array}{c} 1 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \end{array} $	septin interacting protein 1 BM-40-SPARC CG9769 Smg6 rapsynoid Calmodulin Proteasome 29kD subunit Protein phosphatase D3
CG9984 CG7238 CG6378 CG9769 CG6369 CG5692 CG8472 CG9327 CG8402 CG9155	49 49 49 49 49 49 48 48 48 48 48	$ \begin{array}{c} 1 \\ 3 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 1 \\ 1 \end{array} $	septin interacting protein 1 BM-40-SPARC CG9769 Smg6 rapsynoid Calmodulin Proteasome 29kD subunit Protein phosphatase D3 Myosin 61F
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CG93984 CG7238 CG6378 CG9769 CG6369 CG5692 CG8472 CG9327 CG8402 CG9155 CG8439 CG11115 CG5902 CG3175 CG8903 CG12184	49 49 49 49 49 48 48 48 48 48 48 48 48 48 48 48 48 47 47	$ \begin{array}{c} 1\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	septin interacting protein 1 BM-40-SPARC CG9769 Smg6 rapsynoid Calmodulin Proteasome 29kD subunit Protein phosphatase D3 Myosin 61F T-complex Chaperonin 5 Ss11 CG5902 sprint extradenticle CG12184
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CG10305	41	1	Ribosomal protein S26
CG8344	41	1	RNA polymerase III 128kD subunit
CG4457	41	1	Signal recognition particle protein 19
CG12264	41	2	CG12264
CG8831	41	1	Nucleoporin 54
CG6303	41	1	Bruce
CG8142	40	1	CG8142
CG10540	40	1	capping protein alpha
CG12014	40	1	CG12014
CG7073	40	1	sarl
CG3696	40	1	kismet
CG5870	39	1	β Spectrin
CG15099	39	1	CG15099
CG9191	38	1	Kinesin-like protein at 61F
CG1594	38	1	hopscotch
CG3379	38	1	Histone H4 replacement
CG2146	38	2	dilute class unconventional myosin
CG9834	38	1	endophilin B
CG9946	38	1	eukaryotic translation Initiation Factor 2a
CG7619	37	1	Proteasome 54kD subunit
CG9086	37	1	CG9086
CG8609	37	1	Mediator complex subunit 4
CG3506	36	1	vasa
CG5163	36	1	Transcription-factor-IIA-S
CG3714	36	1	CG3714
CG8877	36	1	pre-mRNA processing factor 8
CG10315	36	1	eIF2B-δ
CG10663	36	2	CG10663
CG3329	35	1	Proteasome β2 subunit
CG5313	35	1	Replication factor C subunit 3
CG6846	35	1	Ribosomal protein L26
CG17484	35	1	Adherens junction protein p120
CG15224	34	1	Casein kinase II ß subunit
CG1591	34	1	REG
CG8184	34	1	CG8184
CG8605	34	1	RINT1 ortholog
CG10423	34	1	Ribosomal protein S27
CG7438	34	1	Myosin 31DF
CG2845	33	1	pole hole
CG4429	33	1	RNA-binding protein 2
CG16785	33	1	frizzled 3
CG7668	33	1	CG7668
CG9280	32	1	Glutactin
CG4097	32	1	Proteasome 26kD subunit
			Succinvl coenzyme A synthetase a
CG1065	32	1	subunit
CG5575	32	1	ken and barbie
CG4901	32	1	CG4901
CG10178	32	1	CG10178
CG5566	32	1	CG5566
CG4051	31	1	egalitarian
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CG3949	31	1	hoi-polloi
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A.12 pMT-Rcd4-PrA +MG132 purification from Drosophila cells

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CG7434973Ribosomal protein L22CG9282931Ribosomal protein L24CG12233902lethal (1) G0156CG7622891Ribosomal protein L36CG762189226-29kD-protein aseCG10824882Common Dpr-interacting proteinCG32315852discs lostCG1999853CG17999CG14066851La related proteinCG12008831karstCG1514281CG1768231CG1708231CG1708231CG1708231CG1708231CG170823CG14066851La related proteinCG9256CG17762CG940076CG115475CG115475CG115475CG9446471CG9748704belle	-	CG5504	98	1	lethal (2) tumorous imaginal discs	CG1242	31	1	Heat shock protein 83
CG9282 93 1 Ribosomal protein L24 CG12233 90 2 lethal (1) G0156 CG7622 89 1 Ribosomal protein L36 CG8947 89 2 2.6-29kD-proteinase CG122315 85 2 0.6-29kD-proteinase CG1824 88 2 Common Dpr-interacting protein CG32315 85 2 discs lost CG14066 85 1 La related protein CG12008 83 1 karst CG1511 80 1 REG CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	-	CG7434	97	3	Ribosomal protein L22	CG13609	9 31	2	CG13609
CG12233 90 2 lethal (1) G0156 CG7622 89 1 Ribosomal protein L36 CG8947 89 2 26-29kD-proteinase CG10824 88 2 Commo Dpr-interacting protein CG32315 85 2 discs lost CG1999 85 3 CG1999 CG12008 83 1 La related protein CG12008 83 1 karst CG8735 83 6 CG8735 CG119 77 1 CG4119 CG1974 76 2 CG9940 CG1154 75 1 ATP synthase, β subunit CG4944 70 4 belle	-	CG9282	93	1	Ribosomal protein L24	CG3595	30	1	spaghetti squash
CG7622 89 1 Ribosomal protein L36 CG8947 89 2 26-29kD-proteinase CG15134 28 1 tweek CG10824 88 2 Common Dpr-interacting protein CG15134 28 1 tweek CG10824 88 2 Common Dpr-interacting protein CG171768 25 1 Ribosomal protein S11 CG32315 85 2 discs lost CG17768 23 1 CG17768 CG12008 83 1 La related protein CG17768 23 1 CG10333 22 1 CG10333 CG1591 80 1 REG CG7977 21 1 Ribosomal protein L23A CG1591 80 1 REG CG9940 CG9940 CG1756 2 CG9940 CG17164 73 1 ATP synthase, § subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle belle S14 S14	-	CG12233	90	2	lethal (1) G0156	CG9660	30	1	toucan
CG8947 89 2 26-29kD-proteinase CG10824 88 2 Common Dpr-interacting protein CG32315 85 2 discs lost CG1999 85 3 CG11999 CG17768 CG12008 83 1 La related protein CG17768 23 1 CG17778 CG12008 83 1 karst CG10333 22 1 CG10333 CG12008 83 1 karst CG9256 22 1 Na+/H+ hydrogen exchanger 2 CG151 80 1 REG CG7977 21 1 Ribosomal protein L23A CG4119 77 1 CG4119 CG9940 76 2 CG9940 CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle belle 1 1	-	CG7622	89	1	Ribosomal protein L36	CG8857	30	1	Ribosomal protein S11
CG10824 88 2 Common Dpr-interacting protein CG13215 85 2 discs lost CG1999 85 3 CG11999 CG14066 85 1 La related protein CG12008 83 1 karst CG1199 77 1 CG4119 CG4119 77 1 CG4119 CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	-	CG8947	89	2	26-29kD-proteinase	CG15134	4 28	1	tweek
CG103215 85 2 Column D printertung protein CG11999 85 3 CG11999 CG14066 85 1 La related protein CG17768 23 1 CG17768 CG10333 22 1 CG10333 CG1008 83 1 karst CG8735 83 6 CG8735 CG191 80 1 REG CG4119 77 1 CG4119 CG9940 76 2 CG9940 CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	-	CG10824	88	2	Common Dpr-interacting protein	CG7283	25	1	Ribosomal protein L10Ab
CG12315 35 2 1 CG10333 22 1 CG10333 CG14066 85 1 La related protein CG10333 22 1 CG10333 CG10333 CG12008 83 1 La related protein CG0256 22 1 Na+/H+ hydrogen exchanger 2 CG12008 83 1 Karst CG0256 22 1 Na+/H+ hydrogen exchanger 2 CG1591 80 1 REG CG1031 CG7977 21 1 Ribosomal protein L23A CG191 77 1 CG4119 CG4119 CG9200 CG7977 21 1 Ribosomal protein L23A CG1151 75 1 ATP synthase, § subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle belle 1 1 1	-	CG32315	85	2	diece loet	CG1776	3 23	1	CG17768
CG11006 85 1 La related protein CG12008 83 1 karst CG12008 83 1 karst CG12008 83 1 karst CG1201 80 1 REG CG1191 80 1 REG CG4119 77 1 CG4119 CG9940 76 2 CG9940 CG1154 75 1 ATP synthase, β subunit CG9748 70 4 belle	-	CG11000	85	3	CG11000	CG1033	3 22	1	CG10333
CG14000 83 1 La related protein CG12008 83 1 karst CG8735 83 6 CG8735 CG1591 80 1 REG CG9401 77 1 CG419 CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	-	CG14066	85	1	L a related protein	CG9256	22	1	Na+/H+ hydrogen exchanger 2
CG12006 83 6 CG8735 CG1591 80 1 REG CG4119 77 1 CG4119 CG9400 76 2 CG9940 CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein \$19a CG9748 70 4 belle	-	CC12008	0.0	1	La related protein	CG7977	21	1	Ribosomal protein I 23A
CG151 80 1 REG CG4119 77 1 CG4119 CG9940 76 2 CG9940 CG11154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	ŀ	CG12008	03 92	6	Kaisi	com	21		Ribbsoniai protein E25A
CG1271 ov 1 REO CG4119 77 1 CG4119 CG9940 76 2 CG9940 CG1154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	ŀ	CG1501	0.0	0	DEC				
CG4119 // 1 CG4119 CG9940 76 2 CG9940 CG11154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	ŀ	001391	80	1	KEG OCAULO				
CG9940 /b 2 CG9940 CG11154 75 1 ATP synthase, β subunit CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	ŀ	CG4119	77	1	CG4119				
CG1154/51A1P synthase, β subunitCG4464712Ribosomal protein S19aCG9748704belle	ŀ	CG9940	76	2	CG9940				
CG4464 71 2 Ribosomal protein S19a CG9748 70 4 belle	Ļ	CG11154	1/5	1	ATP synthase, β subunit				
CG9748 70 4 belle	Ļ	CG4464	71	2	Ribosomal protein S19a				
	L	CG9748	70	4	belle				

A.13 pMT-Rcd4-PrA +OA +MG132 purification from Drosophila ce	lls

CG #	Score	#pep	Full name	
CG15792	6816	222	zipper	
CG4027	2393	83	Actin 5C	
CG12051	2366	82	Actin 42A	
CG10067	1631	61	Actin 57B	
CG4264	1390	50	Heat shock protein cognate 4	
CG9277	1238	36	β-Tubulin at 56D	
CG1913	827	21	α-Tubulin at 84B	
CG3201	762	21	Myosin light chain cytoplasmic	
CG4898	701	23	Tropomyosin 1	
CG3401	660	21	β-Tubulin at 60D	
CG2146	509	18	dilute class unconventional myosin	
CG17295	438	17	Reduction in Cnn dots 4	
CG3595	369	11	spaghetti squash	
CG8578	369	10	CG8578	
CG10540	333	7	capping protein alpha	
CG8280	284	9	Elongation factor 1a48D	
CG9155	267	10	Myosin 61F	
CG4183	259	6	Heat shock protein 26	
CG5695	250	8	jaguar	
CG5436	219	6	Heat shock protein 68	

CG1484	210	8	flightless I
CG13162	207	8	anastral spindle 3
CG4147	205	9	Heat shock protein cognate 3
CG8472	189	7	Calmodulin
CG17158	177	6	capping protein beta
CG4466	173	5	Heat shock protein 27
CG12008	171	4	karst
CG7581	169	4	Bub3
CG7438	151	5	Myosin 31DF
CG1106	141	4	Gelsolin
CG10641	132	4	CG10641
CG8947	119	2	26-29kD-proteinase
CG4463	109	2	Heat shock protein 23
CG1977	108	4	a Spectrin
CG3379	102	4	Histone H4 replacement
CG8863	89	2	DnaJ-like-2
CG12101	87	2	Heat shock protein 60
CG32315	83	2	discs lost
CG4119	81	1	CG4119
CG5499	70	2	Histone H2A variant
CG11999	70	1	CG11999
CG5825	64	3	Histone H3.3A
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CG1591	60	1	REG
CG8396	56	1	Single stranded-binding protein c31A
CG10663	56	3	CG10663
CG8735	53	4	CG8735
CG14648	52	1	growl
CG9940	51	1	CG9940
CG9888	49	1	Fibrillarin
CG10811	49	1	eukaryotic translation initiation factor 4G
CG14419	48	1	CG14419
CG17949	48	2	His2B:CG17949

CG1539	46	2	tropomodulin
CG10546	41	1	Cellular retinaldehyde binding protein
CG2207	36	2	Decondensation factor 31
CG13387	35	1	embargoed
CG2168	33	1	Ribosomal protein S3A
CG17209	30	1	CG17209
CG10539	26	1	RPS6-p70-protein kinase
CG5047	26	1	mTerf3
CG5467	23	1	scribbled
CG6355	21	1	fab1
CG7595	0	1	crinkled

A.14 pMT-PrA-Cep97 +OA +MG132 purification from Drosophila cells

CG #	Score	#pep	Full name
CG15792	7020	205	zipper
CG4027	2860	93	Actin 5C
CG12051	2854	93	Actin 42A
CG12008	2681	83	karst
CG10067	2132	72	Actin 57B
CG1977	1557	54	a Spectrin
CG3980	1465	50	Cep97
CG2146	978	33	dilute class unconventional myosin
CG7438	940	30	Myosin 31DF
CG3201	919	23	Myosin light chain cytoplasmic
CG9155	902	28	Myosin 61F
CG5695	666	26	jaguar
CG3595	536	17	spaghetti squash
CG1106	512	16	Gelsolin
CG10641	481	14	CG10641
CG9277	470	19	β-Tubulin at 56D
CG1913	445	17	α-Tubulin at 84B
CG4898	367	10	Tropomyosin 1
CG10540	361	9	capping protein alpha
CG4264	358	13	Heat shock protein cognate 4
CG3379	357	9	Histone H4 replacement
CG17158	326	11	capping protein beta
CG8280	298	8	Elongation factor 1a48D
CG8472	282	8	Calmodulin
CG4147	239	9	Heat shock protein cognate 3
CG1242	197	8	Heat shock protein 83
CG6998	197	5	cut up
CG14617	178	5	Cp110
CG7558	160	6	Actin-related protein 66B
CG3401	132	7	β-Tubulin at 60D
CG9446	115	3	coro
CG1258	105	2	pavarotti
CG5972	98	2	Arc-p20
CG8578	97	2	CG8578
CG8055	97	3	Vps32
CG17949	96	4	His2B:CG17949
CG3937	89	2	cheerio

CG10954	88	3	Arc-p34
CG4145	87	2	Collagen type IV
CG16858	84	2	viking
CG8978	80	2	Suppressor of profilin 2
CG32315	80	2	discs lost
CG14648	78	3	growl
CG2238	77	2	Elongation factor 2b
CG1524	66	1	Ribosomal protein S14a
CG11901	64	2	Eflγ
CG17870	59	2	14-3-3ζ
CG10701	58	1	Moesin
CG1484	52	1	flightless I
CG5499	52	2	Histone H2A variant
CG4183	52	2	Heat shock protein 26
CG9881	50	1	p16-ARC
CG5825	47	1	Histone H3.3A
CG33957	44	1	cp309
CG8983	43	1	ERp60
CG2179	41	1	Xe7
CC10546	41	1	Cellular retinaldehyde binding
C010540	41	1	protein
CG7581	40	1	Bub3
CG14897	35	1	CG14897
CG2207	31	1	Decondensation factor 31
CG13389	30	1	Ribosomal protein S13
CG4042	30	2	CG4042
CG10385	29	1	male-specific lethal 1
CG5920	28	1	string of pearls
CG1702	28	1	Glutathione S transferase T3
CG5047	26	1	mTerf3
CG6355	23	1	fab1
CG6375	21	1	pitchoune
CG5467	20	1	scribbled
CG10859	19	1	CG10859

A.15 pMT-Cep97-PrA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG3980	7109	208	Cep97
CG9277	2480	48	β-Tubulin at 56D
CG4264	2277	45	Heat shock protein cognate 4
CG15792	1747	44	zipper
CG3401	1544	33	β-Tubulin at 60D
CG1913	1398	29	α-Tubulin at 84B
CG31012	982	23	CIN85 and CD2AP orthologue
CG12051	846	25	Actin 42A
CG4147	751	18	Heat shock protein cognate 3
CG10067	629	20	Actin 57B
CG3201	422	7	Myosin light chain cytoplasmic
CG9940	402	12	CG9940
CG5119	376	12	polyA-binding protein
CG5502	374	9	Ribosomal protein L4
CG8280	363	10	Elongation factor 1a48D
CG14207	359	7	HspB8
CG5436	350	7	Heat shock protein 68
CG5779	321	9	Black cells
CG1483	297	7	Microtubule-associated protein 205
CG5174	260	7	CG5174
CG12101	256	4	Heat shock protein 60
CG7808	252	4	Ribosomal protein S8
CG12233	235	6	lethal (1) G0156
CG8262	235	3	anastral spindle 2
CG4087	191	5	Ribosomal protein LP1
CG7915	176	9	Ect4
CG4463	171	4	Heat shock protein 23
CG1883	170	5	Ribosomal protein S7
CG6253	162	2	Ribosomal protein L14
CG5920	159	4	string of pearls
CG3203	156	2	Ribosomal protein L17
CG31618	151	2	His2A:CG31618
CG3751	133	2	Ribosomal protein S24

$\begin{array}{c ccccc} CG7971 & 132 & 2 & CG7971 \\ CG8571 & 124 & 1 & small minded \\ CG7490 & 122 & 5 & Ribosomal protein LP0 \\ CG6181 & 116 & 2 & Ge-1 \\ CG10377 & 113 & 3 & Heterogeneous nuclear \\ ribonucleoprotein at 27C \\ CG9282 & 110 & 1 & Ribosomal protein L24 \\ CG10944 & 108 & 3 & Ribosomal protein S6 \\ CG679 & 106 & 3 & Ribosomal protein S3 \\ CG17498 & 101 & 2 & mad2 \\ CG7581 & 98 & 5 & Ribosomal protein L3A \\ CG2960 & 95 & 2 & Ribosomal protein L40 \\ CG10851 & 92 & 5 & Ribosomal protein L40 \\ CG10851 & 92 & 5 & Ribosomal protein L40 \\ CG459 & 90 & 1 & CG6459 \\ CG6459 & 90 & 1 & CG6459 \\ CG6459 & 90 & 1 & CG6459 \\ CG10851 & 92 & 5 & Ribosomal protein L13 \\ CG6459 & 90 & 1 & CG6459 \\ CG10689 & 89 & 3 & lethal (2) 37Cb \\ CG3051 & 89 & 2 & Ribosomal protein L18 \\ CG14648 & 89 & 3 & growl \\ CG3395 & 87 & 4 & Spaghetti squash \\ CG3395 & 87 & 4 & Ribosomal protein S9 \\ CG3612 & 87 & 2 & bellwether \\ CG11522 & 87 & 4 & Ribosomal protein S9 \\ CG3612 & 87 & 2 & bellwether \\ CG11522 & 87 & 4 & Ribosomal protein S9 \\ CG3612 & 87 & 2 & bellwether \\ CG1152 & 87 & 4 & Ribosomal protein S9 \\ CG3612 & 87 & 2 & bellwether \\ CG1152 & 87 & 4 & Ribosomal protein L03 \\ CG1476 & 81 & 2 & Ribosomal protein S9 \\ CG3612 & 87 & 2 & bellwether \\ CG11527 & 74 & 3 & CG8478 \\ CG6988 & 74 & 2 & Protein disulfide isomerase \\ CG8478 & 74 & 3 & CG8478 \\ CG69901 & 73 & 1 & Ribosomal protein L17a \\ CG86363 & 73 & 1 & Dna1-like-2 \\ CG7726 & 70 & 2 & Ribosomal protein L11 \\ \end{array}$	CG4897	132	4	Ribosomal protein L7
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG7971	132	2	CG7971
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	CG8571	124	1	smallminded
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	CG7490	122	5	Ribosomal protein LP0
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG6181	116	2	Ge-1
CG10377 113 3 ribonucleoprotein at 27C CG9282 110 1 Ribosomal protein S6 CG10944 108 3 Ribosomal protein S6 CG6779 106 3 Ribosomal protein S3 CG17498 101 2 mad2 CG7581 98 5 Bub3 CG777 98 5 Ribosomal protein L23A CG2960 95 2 Ribosomal protein L40 CG1841 94 3 Rpt1 CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG4659 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG4651 89 2 Ribosomal protein L18 CG10689 89 3 growl CG3595 87 4 Ribosomal protein S6 CG3545 87 2 bellwether CG1520 74 Ribosomal protein S6	CC10277	112	2	Heterogeneous nuclear
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG10577	115	3	ribonucleoprotein at 27C
CG10944 108 3 Ribosomal protein S6 CG6779 106 3 Ribosomal protein S3 CG17498 101 2 mad2 CG7581 98 5 Bub3 CG7977 98 5 Ribosomal protein L23A CG2960 95 2 Ribosomal protein L40 CG1341 94 3 Rpt1 CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG6459 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG14648 89 3 grow1 CG3595 87 4 spaghetti squash CG3612 87 2 bellwether CG1528 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG1529 82 2 Histone H2A variant <	CG9282	110	1	Ribosomal protein L24
$\begin{array}{c cccc} CG6779 & 106 & 3 & Ribosomal protein S3 \\ CG17498 & 101 & 2 & mad2 \\ CG7581 & 98 & 5 & Ribosomal protein L23A \\ CG2960 & 95 & 2 & Ribosomal protein L40 \\ CG1341 & 94 & 3 & Rpt1 \\ CG10851 & 92 & 5 & B52 \\ CG4651 & 90 & 5 & Ribosomal protein L13 \\ CG6459 & 90 & 1 & CG6459 \\ CG10689 & 89 & 3 & lethal (2) 37Cb \\ CG8615 & 89 & 2 & Ribosomal protein L18 \\ CG14648 & 89 & 3 & growl \\ CG3955 & 87 & 4 & spaghetti squash \\ CG3955 & 87 & 4 & Ribosomal protein S9 \\ CG3051 & 87 & 2 & bellwether \\ CG11522 & 87 & 4 & Ribosomal protein S9 \\ CG3152 & 87 & 4 & Ribosomal protein S9 \\ CG1528 & 84 & 4 & A kinase anchor protein 200 \\ CG5499 & 82 & 2 & Histone H2A variant \\ CG1276 & 81 & 2 & Ribosomal protein S4 \\ CG6988 & 74 & 2 & Protein disulfide isomerase \\ CG8478 & 74 & 3 & CG8478 \\ CG12750 & 74 & 3 & nucampholin \\ CG9901 & 73 & 1 & Ribosomal protein L37a \\ CG8638 & 73 & 1 & Dna1-like-2 \\ CG7726 & 70 & 2 & Ribosomal protein L11 \\ \end{array}$	CG10944	108	3	Ribosomal protein S6
CG17498 101 2 mad2 CG7581 98 5 Bub3 CG7977 98 5 Ribosomal protein L23A CG2960 95 2 Ribosomal protein L23A CG1341 94 3 Rpt1 CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG6459 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spagheti squash CG3595 87 4 Ribosomal protein L18 CG3162 87 2 bellwether CG1522 87 4 Ribosomal protein L6 CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal prot	CG6779	106	3	Ribosomal protein S3
CG7581 98 5 Bub3 CG7977 98 5 Ribosomal protein L23A CG2960 95 2 Ribosomal protein L40 CG1341 94 3 Rpt1 CG10851 92 5 B52 CG4559 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG16689 89 3 grow1 CG3595 87 4 spagheti squash CG3505 87 4 Ribosomal protein S9 CG3512 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG1338 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3	CG17498	101	2	mad2
CG7977 98 5 Ribosomal protein L23A CG2960 95 2 Ribosomal protein L40 CG1341 94 3 Rpt1 CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG6459 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3512 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG1520 87 4 Ribosomal protein L6 CG1328 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 CG2478	CG7581	98	5	Bub3
CG2960 95 2 Ribosomal protein L40 CG1341 94 3 Rpt1 CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG4659 90 1 CG6459 CG10851 89 3 lethal (2) 37Cb CG4651 89 2 Ribosomal protein L18 CG10689 89 3 growl CG3505 87 4 spaghetti squash CG3595 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG13288 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 CG28478 CG28478 CG12750 CG12750 74 <td< td=""><td>CG7977</td><td>98</td><td>5</td><td>Ribosomal protein L23A</td></td<>	CG7977	98	5	Ribosomal protein L23A
CG1341 94 3 Rpt1 CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG4659 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG16651 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3612 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 <td< td=""><td>CG2960</td><td>95</td><td>2</td><td>Ribosomal protein L40</td></td<>	CG2960	95	2	Ribosomal protein L40
CG10851 92 5 B52 CG4651 90 5 Ribosomal protein L13 CG6459 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3595 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG1288 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 <td>CG1341</td> <td>94</td> <td>3</td> <td>Rpt1</td>	CG1341	94	3	Rpt1
CG4651 90 5 Ribosomal protein L13 CG4659 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3595 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG1522 87 4 Ribosomal protein L6 CG13288 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG1276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 <t< td=""><td>CG10851</td><td>92</td><td>5</td><td>B52</td></t<>	CG10851	92	5	B52
CG6459 90 1 CG6459 CG10689 89 3 lethal (2) 37Cb CG8615 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spagheti squash CG3595 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG1522 87 4 Ribosomal protein L6 CG1528 87 2 bellwether CG1529 87 4 Ribosomal protein L6 CG1549 82 2 Histone H2A variant CG5499 82 2 Histone H2A variant CG1276 81 2 Ribosomal protein S4 CG68478 74 3 mucampholin CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 2 R	CG4651	90	5	Ribosomal protein L13
CG10689 89 3 lethal (2) 37Cb CG8015 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3395 87 4 Ribosomal protein S9 CG3102 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 Dmal-like-2 CG7726 70 2 Ribosomal protein L11	CG6459	90	1	CG6459
CG8615 89 2 Ribosomal protein L18 CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3395 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG1522 87 4 Ribosomal protein L6 CG1388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CC68478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 2 Ribosomal protein L11	CG10689	89	3	lethal (2) 37Cb
CG14648 89 3 growl CG3595 87 4 spaghetti squash CG3595 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG1388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CC68478 CG12750 74 3 nucampholin CG8638 73 1 DnaJ-like-2 CG726 70 2 Ribosomal protein L11	CG8615	89	2	Ribosomal protein L18
CG3595 87 4 spaghetti squash CG3395 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG1522 87 4 Ribosomal protein L6 CG1388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG86363 73 1 Dnal-like-2 CG7726 70 2 Ribosomal protein L11	CG14648	89	3	growl
CG3395 87 4 Ribosomal protein S9 CG3612 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 Dnal-like-2 CG7726 70 2 Ribosomal protein L11	CG3595	87	4	spaghetti squash
CG3612 87 2 bellwether CG11522 87 4 Ribosomal protein L6 CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CC68478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 2 Ribosomal protein L11	CG3395	87	4	Ribosomal protein S9
CG11522 87 4 Ribosomal protein L6 CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG62478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 Dnal-like-2 CG7726 70 2 Ribosomal protein L11	CG3612	87	2	bellwether
CG13388 84 4 A kinase anchor protein 200 CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 Dnal-like-2 CG7726 70 2 Ribosomal protein L11	CG11522	87	4	Ribosomal protein L6
CG5499 82 2 Histone H2A variant CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 Dnal-like-2 CG7726 70 2 Ribosomal protein L11	CG13388	84	4	A kinase anchor protein 200
CG11276 81 2 Ribosomal protein S4 CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 2 Ribosomal protein L11	CG5499	82	2	Histone H2A variant
CG6988 74 2 Protein disulfide isomerase CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 2 Ribosomal protein L11	CG11276	81	2	Ribosomal protein S4
CG8478 74 3 CG8478 CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 Dnal-like-2 CG7726 70 2 Ribosomal protein L11	CG6988	74	2	Protein disulfide isomerase
CG12750 74 3 nucampholin CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaI-like-2 CG7726 70 2 Ribosomal protein L11	CG8478	74	3	CG8478
CG9091 73 1 Ribosomal protein L37a CG8863 73 1 DnaJ-like-2 CG7726 70 2 Ribosomal protein L11	CG12750	74	3	nucampholin
CG8863 73 1 DnaJ-like-2 CG7726 70 2 Ribosomal protein L11	CG9091	73	1	Ribosomal protein L37a
CG7726 70 2 Ribosomal protein L11	CG8863	73	1	DnaJ-like-2
	CG7726	70	2	Ribosomal protein L11

CG8947	70	2	26-29kD-proteinase
CG1516	69	2	Pyruvate carboxylase
CG2216	68	1	Ferritin 1 heavy chain homologue
CG3922	66	1	Ribosomal protein S17
CG5934	65	1	CG5934
CG2671	64	2	lethal (2) giant larvae
002071	04	2	small alutamina rich tatratricopantida
CG5094	64	1	containing protein
CG2746	62	3	Ribosomal protein L19
CG10360	62	1	refractory to sigma P
CG3126	61	4	C3G
CG7028	59	1	CG7028
CG6617	59	1	CG6617
CG4182	59	2	Heat shock protein 26
CC5450	50	2	Cutanlaamia dunain light shoin 2
CG3430	50	2	
CG6686	58	3	CG0080
CG1821	57	1	Ribosomal protein L31
CG3981	57	1	Unc-76
CG31764	57	1	virus-induced RNA 1
CG15442	56	4	Ribosomal protein L27A
CG6692	55	2	Cysteine proteinase-1
CG1263	55	3	Ribosomal protein L8
CG7507	55	3	Dynein heavy chain 64C
CG13389	53	2	Ribosomal protein S13
CG14637	53	2	abetrakt
CG1548	52	1	aostraki
CG1348	55	1	calliD
CG31022	55	2	prolyi-4-nydroxylase-alpha EFB
CG/185	52	1	CG/185
CG7439	52	2	Argonaute 2
CG8922	49	1	Ribosomal protein S5a
CG17158	49	2	capping protein beta
CG9684	49	2	CG9684
CG5520	49	2	Glycoprotein 93
CG8472	47	2	Calmodulin
CG3379	47	2	Histone H4 replacement
CG5654	46	2	vpsilon schachtel
CG11963	46	1	sknA associated protein
CG8857	40	2	Bibosomal protein \$11
CG6000	45	2	Diharanal protein 511
CG0090	45	2	Ribosomai protein L54a
CG2152	45	1	Protein-L-isoaspartate (D-aspartate)
000.00		L	O-methyltransferase
CG7622	44	1	Ribosomal protein L36
CG5422	44	1	Rox8
CG7939	43	1	Ribosomal protein L32
CG12264	43	2	CG12264
CG8542	42	2	Heat shock protein cognate 5
CG10305	42	1	Ribosomal protein S26
CG7434	42	1	Ribosomal protein L22
CG10540	42	2	capping protein alpha
CG1242	41	2	Heat shock protein 83
CC12202	41		neals
002214	41	1	poio
CG3314	41	1	Ribosomai protein L/A
CG15770	41	1	CG15770
CG10546	41	1	Cellular retinaldehyde binding protein
CG17520	40	2	casein kinase IIa
CG4898	39	1	Tropomyosin 1
CG8415	30	2	Ribosomal protein \$23
CG4046	20	2	Dibosomal protein \$15
CG4040	37	2	Ribosoniai protein 516

CG1677	37	1	CG1677
CG3542	36	1	CG3542
CG6684	36	2	Ribosomal protein S25
CG10149	34	1	Proteasome p44.5 subunit
CG10824	34	1	Common Dpr-interacting protein
CG1633	34	1	thioredoxin peroxidase 1
CG2168	33	1	Ribosomal protein S3A
CG12775	22	1	Ribosomal protein I 21
CG11856	22	1	Nucleoperin 258
CG16044	22	1	stross consitive P
CC1524	22	1	Bibasamal protain \$14a
CG1324	32	1	Ribosoniai protein S14a
CG14235	32	1	Cytochrome c oxidase subunit 6B
CG10665	32	2	CG10663
CG3836	31	1	stonewall
CG11949	30	1	coracle
CG17949	30	2	His2B:CG1/949
CG6428	29	1	CG6428
CG5916	29	1	CG5916
CG1977	29	1	a Spectrin
CG6510	28	1	Ribosomal protein L18A
CG1489	27	1	Pros45
CG32680	27	2	sprint
CG2692	26	1	gooseberry-neuro
CG3661	26	1	Ribosomal protein L23
CG34130	26	2	CG34130
CG7111	25	1	Receptor of activated protein kinase C 1
CG7961	25	1	Coat Protein (coatomer) a
CG17521	24	1	Qm
CG8476	24	1	CG8476
CG1683	23	1	Adenine nucleotide translocase 2
CG4164	23	1	CG4164
CG7219	23	1	Serpin 28D
CG18522	23	1	Aldehyde oxidase 1
CG7595	22	1	crinkled
CG4918	22	1	Ribosomal protein LP2
CG4215	22	1	spellchecker1
CG6773	22	1	sec13
CG33715	22	1	Muscle-specific protein 300
CG10071	21	1	Ribosomal protein L29
CG4863	21	1	Ribosomal protein L3
CG11143	21	1	Inos
CG3711	21	1	CG3711
CG4863	20	2	Ribosomal protein L3
CG17209	20	1	CG17209
CG12070	19	1	Saposin-related
CG8715	19	1	lingerer
CG6699	19	1	Coat Protein (coatomer) B'
CG4678	19	1	CG4678
CG11274	10	1	SRm160
CG6169	19	1	Decapping protein 2
CG32689	19	1	Hyperkinetic
CG0889	10	2	Eibrillorin
CU9000	10	2	FIDEIIIATIII

A.16 pMT-Cep97-PrA +OA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG3980	16796	437	Cep97
CG15792	2652	65	zipper
CG4264	1993	41	Heat shock protein cognate 4
CG9277	1433	33	β-Tubulin at 56D
CG4027	1180	30	Actin 5C
CG1913	921	25	α-Tubulin at 84B
CG3401	902	21	β-Tubulin at 60D
CG10067	851	26	Actin 57B
CG3201	753	12	Myosin light chain cytoplasmic
CG4147	722	21	Heat shock protein cognate 3
CG31618	616	9	His2A:CG31618
CG5834	448	9	Hsp70Bbb
CG5436	446	8	Heat shock protein 68
CG8280	344	9	Elongation factor 1a48D
CG14617	330	11	Cp110
CG8472	281	9	Calmodulin
CG12101	246	5	Heat shock protein 60
CG5499	241	6	Histone H2A variant
CG12233	179	4	lethal (1) G0156
CG10641	179	6	Swiprosin-1
CG10377	156	2	Heterogeneous nuclear
CG9940	1/18	5	CG9940
CG10540	139	3	capping protein alpha
CG14637	131	4	abstrakt
CG5450	131	4	Cytoplasmic dynein light chain 2
CG3595	120	4	spaghetti squash
CG9155	118	3	Myosin 61F
CG14207	118	2	HspB8
CG6453	117	3	Glucosidase 2 ß subunit

- 1	CG2216	106	1	Ferritin 1 heavy chain homologue
	CG3379	105	2	Histone H4 replacement
	CG9282	93	1	Ribosomal protein L24
	CG5779	91	4	Black cells
	CG33332	89	1	CG33332
	CG11963	85	3	skpA associated protein
	CG1242	84	2	Heat shock protein 83
	CG16901	74	1	squid
	CG17498	73	1	mad2
	CG3612	70	2	bellwether
	CG18572	69	2	rudimentary
	CG15770	67	2	CG15770
	CG10689	59	2	lethal (2) 37Cb
	CG1341	58	1	Rpt1
	CG8947	57	1	26-29kD-proteinase
	CG8578	57	1	CG8578
	CG8542	56	3	Heat shock protein cognate 5
	CG3203	56	1	Ribosomal protein L17
	CG10851	55	3	B52
	CG6509	55	2	Discs large 5
	CG12750	54	1	nucampholin
	CG8863	54	2	DnaJ-like-2
	CG7507	53	1	Dynein heavy chain 64C
	CG17158	52	1	capping protein beta
	CG6692	52	1	Cysteine proteinase-1
	CG5422	49	2	Rox8
	CG5119	49	2	polyA-binding protein
	CG5520	47	2	Glycoprotein 93
	CG9888	46	3	Fibrillarin
	CG31764	46	1	virus-induced RNA 1
	CG1483	44	1	Microtubule-associated protein 205

CG10546	41	1	Cellular retinaldehyde binding
CG14648	40	1	growl
CG17040	40	2	His2B:CG17040
CG4463	37	1	Heat shock protein 23
CG9075	37	1	Fukervotic initiation factor 4a
CG5174	37	1	CG5174
CG9684	36	1	CG9684
CG31012	35	2	CIN85 and CD2AP orthologue
CG31022	35	1	prolyl-4-bydroxylase-alpha FFB
CG3662	34	1	CG3662
CG10596	33	2	Mer-110
CG7762	33	1	Ppn1
CG6617	33	1	CG6617
CG0749	22	1	balla
CG2060	32	1	Bibosomel protein L 40
CG2900	22	1	Kibosofilai proteini L40
CG3823	22	1	Eat4
CG/915	32	1	Ect4
CG4145	31	1	Collagen type IV
CG2175	31	1	defective chorion 1
CG12306	31	1	polo
CG6341	31	1	Elongation factor 1 p
CG1548	31	1	cathD
CG6428	31	1	CG6428
CG17209	31	1	CG17209
CG2152	30	1	Protein-L-isoaspartate (D-aspartate)
			O-methyltransferase
CG2168	30	1	Ribosomal protein S3A
CG10663	30	2	CG10663
CG7611	30	1	CG7611
CG10360	29	1	refractory to sigma P
CG3836	29	1	stonewall
CG3661	29	1	Ribosomal protein L23
CG4651	29	2	Ribosomal protein L13
CG15784	29	1	CG15784
CG4064	29	1	CG4064
CG4164	29	1	CG4164
CG32196	29	1	CG32196
CG7581	28	1	Bub3
CG17768	28	1	CG17768
CG3382	27	1	Organic anion transporting

		I	polypeptide 58Db
CG4087	26	1	Ribosomal protein LP1
CG7144	26	1	lysine ketoglutarate reductase
CG8677	26	1	CG8677
CG1883	26	1	Ribosomal protein S7
CG11123	25	1	CG11123
CG14996	25	1	Chd64
CG33715	25	1	Muscle-specific protein 300
CG1524	24	1	Ribosomal protein S14a
CG10385	24	1	male-specific lethal 1
CG1683	24	1	Adenine nucleotide translocase 2
CG3711	24	1	CG3711
CG34130	24	2	CG34130
CG5330	23	1	Nucleosome assembly protein 1
CG7219	23	1	Serpin 28D
CG1869	23	1	Cht7
CG4289	23	1	Peroxin 14
CG7595	22	1	crinkled
CG31196	22	1	14-3-3ε
CG4678	22	1	CG4678
CG7971	22	1	CG7971
CG13833	22	1	CG13833
CG32680	22	1	sprint
CG3561	22	1	KH1
CG2146	22	1	dilute class unconventional myosin
CG2692	21	2	gooseberry-neuro
CG12775	20	1	Ribosomal protein L21
CG4849	20	1	CG4849
CG32688	19	2	Hyperkinetic
CG5502	19	1	Ribosomal protein L4
CG18255	19	1	Stretchin-Mlck
CG33715	19	1	Muscle-specific protein 300
CG10986	18	1	garnet
CG4183	18	1	Heat shock protein 26
CG9934	18	1	CG9934
CG5432	18	1	CG5432
CG33464	18	1	slit

A.17 pMT-PrA-CP110 +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG4027	85941	1322	Actin 5C
CG12051	85843	1313	Actin 42A
CG15792	47870	840	zipper
CG18290	17848	580	Actin 87E
CG3595	8513	158	spaghetti squash
CG1977	4876	98	a Spectrin
CG3201	4751	95	Myosin light chain cytoplasmic
CG9155	4575	99	Myosin 61F
CG4264	3673	76	Heat shock protein cognate 4
CG6831	3631	77	rhea
CG7438	2988	84	Myosin 31DF
CG9277	2841	74	β-Tubulin at 56D
CG8472	2757	46	Calmodulin
CG10540	2698	89	capping protein alpha
CG1913	2261	43	α-Tubulin at 84B
CG17158	2155	46	capping protein beta
CG1539	2111	40	tropomodulin
CG8280	2093	45	Elongation factor 1a48D
CG14617	2046	46	Cp110
CG2146	2015	46	dilute class unconventional myosin
CG12008	1938	67	karst
CG1484	1854	41	flightless I
CG3401	1676	45	β-Tubulin at 60D
CG9325	1673	33	hu li tai shao
CG10641	1622	46	CG10641
CG3937	1394	31	cheerio
CG5870	1346	32	β Spectrin
CG31618	1294	18	His2A:CG31618
CG7558	1224	25	Actin-related protein 66B
CG5695	1080	26	jaguar
CG1106	1066	30	Gelsolin
CG8578	976	28	CG8578
CG4147	914	15	Heat shock protein cognate 3
CG31196	862	16	14-3-3ε
CG1883	850	16	Ribosomal protein S7
CG7490	733	12	Ribosomal protein LP0
CG4087	586	9	Ribosomal protein LP1
CG1242	556	14	Heat shock protein 83
CG18572	541	13	rudimentary
CG4463	535	10	Heat shock protein 23
CG5499	528	8	Histone H2A variant
CG5502	453	15	Ribosomal protein L4
CG14792	416	6	stubarista
CG3299	412	7	Vinculin
CG9901	409	12	Actin-related protein 14D
CG10922	396	6	La autoantigen-like
CG31794	386	6	Paxillin

CG17291	379	7	Protein phosphatase 2A at 29B
CG2238	376	13	Elongation factor 2b
CG7507	373	7	Dynein heavy chain 64C
CG4145	333	8	Collagen type IV
CG10954	332	6	Arc-p34
CG3203	327	6	Ribosomal protein L17
CG4897	315	7	Ribosomal protein L7
CG8978	312	8	Suppressor of profilin 2
CG9881	311	6	p16-ARC
CG9748	305	8	belle
CG9012	303	11	Clathrin heavy chain
CG8055	303	3	shrub
CG8977	299	4	Ccty
CG15784	295	9	CG15784
CG8309	278	7	Transport and Golgi organization 7
CG1258	276	7	pavarotti
CG7033	276	4	CG7033
CG7283	275	9	Ribosomal protein L10Ab
CG7595	268	7	crinkled
CG9282	266	4	Ribosomal protein L24
CG18076	248	6	short stop
CG4560	241	6	Arpc3A
CG5119	235	8	polyA-binding protein
CG11522	233	6	Ribosomal protein L6
CG1059	233	4	Karyopherin ß 3
CG8900	229	6	Ribosomal protein S18
CG33484	229	4	zormin
CG7380	227	4	barrier to autointegration factor
CG5825	225	5	Histone H3.3A
CG31764	220	4	virus-induced RNA 1
CG4376	214	8	α actinin
CG31613	212	5	His3:CG31613
CG17272	208	4	CG17272
CG5020	207	4	Cytoplasmic linker protein 190
CG3379	204	5	Histone H4 replacement
CG17949	202	8	His2B:CG17949
CG30349	199	3	CG30349
CG8332	198	5	Ribosomal protein S15
CG2331	193	2	TER94
CG1782	192	5	Ubiquitin activating enzyme 1
CG10811	189	3	eukaryotic translation initiation factor 4G
CG18076	188	3	short stop
CG8439	179	4	T-complex Chaperonin 5
CG4183	173	4	Heat shock protein 26
CG3751	168	5	Ribosomal protein S24
CG12030	167	5	UDP-galactose 4'-epimerase
CG7439	167	3	Argonaute 2
CG1263	165	3	Ribosomal protein L8

CC 9092	162	4	Ribosomal protein L14
CG8985	162	4	ERp60
CG1822	161	6	bifocal
CG40045	160	2	CG40045
CG3314	159	7	Ribosomal protein L7A
CG4466	158	4	Heat shock protein 27
CG11271	158	3	Ribosomal protein S12
CG1524	157	4	Ribosomal protein S14a
CG1483	149	5	Microtubule-associated protein 205
CG17489	148	4	Ribosomal protein L5
CG33957	148	5	cp309
CG11276	147	3	Ribosomal protein S4
CG12740	146	2	Ribosomal protein L28
CG16916	145	2	Rnt3
CG4898	144	5	Tropomyosin 1
CG16858	143	4	viking
CG5525	143	2	CG5525
CG3455	141	2	Rpt4
CG12363	140	2	Dynein light chain 90F
CG32164	138	2	CG32164
CG14207	134	4	HspB8
CG6522	134	4	Testin ortholog
CG31352	133	5	CG31352
CG9075	131	3	Eukarvotic initiation factor 4a
CG6148	130	2	Putative Achaete Scute Target 1
CG5520	127	2	Glycoprotein 93
CG7581	126	2	Bub3
CG11888	126	2	Rnn2
CG5972	126	3	Arc-n20
CG3949	124	3	hoi-polloi
CG3821	127	2	Aspartyl-tRNA synthetase
CG10596	122	5	Msr-110
CG6779	110	2	Ribosomal protein \$3
CG3077	110	3	Ribosomal protein \$17
CG5274	117	3	Ten1-like
CG17454	117	5	Epoloso
CG7261	113	1	tubulin folding cofector D
CG4012	114	1	aFF18
CC2168	102	1	Dihasamal matain \$2.4
CC6088	108	4	Ribosofilai protein SSA
CG0988	104	0	CC15717
CG13/17	99	2	0-
CG17321	98	2	QIII
CG12840	98	3	moleskin Nar56
007765	98	1	Nop56
CG/765	97	2	Kinesin neavy chain
CG4799	97	3	Pendulin
CG9281	96	2	CG9281
CG31852	95	1	CINES and CD2AD arthologue
CG31012	94	3	CIN85 and CD2AP orthologue
CG3195	94	3	Ribosomai protein L12
CG2/46	92	2	Ribosomai protein L19
CG10652	92	1	Ribosomal protein L30
CG5920	91	2	string of pearls
CG8351	91	2	1cp-1η
CG13389	90	2	Ribosomai protein S13
CG/96/	90	1	CG/96/
CG9769	88	2	CG9769
CG6684	8/	3	Ribosomai protein S25
((15.584	8/	2	Ubiquitin specific protease 14
002222	0.4	0	NIICIEOJAL DIOTEIN AL OUB
CG3333	84	2	
CG3333 CG10230	84 82	2	Rpn9
CG3333 CG10230 CG32075	84 82 82	2 2 1	Rpn9 CG32075
CG3333 CG10230 CG32075 CG9888	84 82 82 81	2 2 1 3	Rpn9 CG32075 Fibrillarin
CG3333 CG10230 CG32075 CG9888 CG4665	84 82 82 81 81		Rpn9 CG32075 Fibrillarin Dihydropteridine reductase
CG3333 CG10230 CG32075 CG9888 CG4665 CG3172	84 82 82 81 81 81 81		Rpn9 CG32075 Fibrillarin Dihydropteridine reductase twinfilin
CG3333 CG10230 CG32075 CG9888 CG4665 CG3172 CG3523 CG10000	84 82 81 81 81 80 80	2 2 1 3 1 2 2	Rpn9 CG32075 Fibrillarin Dihydropteridine reductase twinfilin Fatty acid synthase 1 Pronzemund call death 4 catholy
CG3333 CG10230 CG32075 CG9888 CG4665 CG3172 CG3523 CG10990 CG3011	84 82 81 81 81 80 80 78		Rpn9 CG32075 Fibrillarin Dihydropteridine reductase twinfilin Fatty acid synthase 1 Programmed cell death 4 ortholog CG3011
CG33333 CG10230 CG32075 CG9888 CG4665 CG3172 CG3523 CG10990 CG10990 CG3011	84 82 81 81 81 80 80 78 78	2 2 1 3 1 2 2 1 1 1	Rpn9 CG32075 Fibrillarin Dihydropteridine reductase twinfilin Fatty acid synthase 1 Programmed cell death 4 ortholog CG3011 L a redutad ceretain
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CG4265	63	1	Ubiquitin carboxy-terminal hydrolase
CG12262	63	1	CG12262
CG4800	63	1	Translationally controlled tumor protein
CG11527	62	2	Tiggrin
CG3081	62	1	Unc-76
005981	02	1	Une-70
CG6842	61	3	vacuolar protein sorting 4
CG32306	61	2	CG32306
CG13391	60	1	Alanyl-tRNA synthetase
CG4046	60	2	Ribosomal protein S16
CG6846	60	1	Ribosomal protein L26
CG4420	50	1	PNA binding protoin 2
004429	39	1	KINA-bilding protein 2
CG18408	59	1	CAP
CG4759	59	2	Ribosomal protein L27
CG10701	58	1	Moesin
CG21262	59	1	Iunitor
001505	58	1	Jupitei
CG6598	57	1	Formaldehyde dehydrogenase
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CG10944	57	2	Ribosomal protein S6
CG12306	56	1	polo
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0010385		3	male-specific lethal 1
CG7977	56	1	Ribosomal protein L23A
CG3262	55	1	CG3262
CG18174	54	1	Rpn11
CG15100	52	1	CC15100
CC10710	53	2	0013700
CG12/13	55	3	CG12/15
CG10522	52	1	sticky
CG8882	52	1	Trip1
CG6223	51	2	Coat Protein (coatomer) B
CC0422	51	1	Ranligation Destain A 70
09033	51	1	Replication Flotein A 70
CG5433	51	1	Kinesin light chain
CG5688	51	1	Grip163
CG1837	51	2	pretaporter
CG2767	51	1	CG2767
CC1542	50	1	001540
CG1542	50	1	CG1542
CG30084	50	1	Z band alternatively spliced PDZ-motif
C030004	50	1	protein 52
CG6944	49	2	Lamin
CG3752	/0	1	Aldebyde debydrogenase
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CG/808	49	Z	Ribosomai protein 58
CG7762	48	2	Rpn1
CG31022	48	1	prolyl-4-hydroxylase-alpha EFB
CG7915	48	1	Ect4
CG31617	47	2	His1:CG31617
002416	45	1	Ma-24
CG3416	45	1	M0V34
CG5353	45	2	Threonyl-tRNA synthetase
CG6751	45	2	no child left behind
CC14006	45	1	Chd64
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CG14996 CG74913 CG11949 CG4651 CG7434 CG4236 CG7326 CG13226 CG10527 CG14535 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG1737 CG4551 CG1737 CG4551 CG1737 CG4551 CG1737 CG4551 CG1737 CG4551 CG1737 CG4551 CG1737 CG4551 CG1737 CG4551 CG10527 CG1057	43 44 43 44 40 40 40 40 40 40 40 40 40 40 40 38 38 38 37 37 37 37 37 37 36 36 36 36 37 38	1 1 2 1 2 1 1 2 1 2 2 1 <t< td=""><td>PP2A-B' coracle Ribosomal protein L13 Ribosomal protein L22 Chromatin assembly factor 1 subunit CG3226 Helicase Ribosomal protein S15Aa CG6961 Ribosomal protein S15Aa CG6961 Ribosomal protein S15Aa Cysteinyl-tRNA synthetase Ribosomal protein S9 lin-19-like Pyruvate carboxylase licorne microtubule star Diphthamide methyltransferase PTEN-induced putative kinase 1 eIF3-S8 novel GTPase indispensable for equal segregation of chromosomes Roughened Tryptophanyl-tRNA synthetase CG17528 hippo BM-40-SPARC peroxisomal Multifunctional enzyme type 2 CG17337 Small ribonucleoprotein particle protein SmD3 CG9436 tumbleweed Succinyl coenzyme A synthetase α subunit CG10527 Proteome of centrioles 1 Phosphoglycerate kinase Vacuolar H+-ATPase 26kD E subunit RPS6-p70-protein kinase CG13955 Serpin 47C Ribosomal protein L18 CG8936</td></t<>	PP2A-B' coracle Ribosomal protein L13 Ribosomal protein L22 Chromatin assembly factor 1 subunit CG3226 Helicase Ribosomal protein S15Aa CG6961 Ribosomal protein S15Aa CG6961 Ribosomal protein S15Aa Cysteinyl-tRNA synthetase Ribosomal protein S9 lin-19-like Pyruvate carboxylase licorne microtubule star Diphthamide methyltransferase PTEN-induced putative kinase 1 eIF3-S8 novel GTPase indispensable for equal segregation of chromosomes Roughened Tryptophanyl-tRNA synthetase CG17528 hippo BM-40-SPARC peroxisomal Multifunctional enzyme type 2 CG17337 Small ribonucleoprotein particle protein SmD3 CG9436 tumbleweed Succinyl coenzyme A synthetase α subunit CG10527 Proteome of centrioles 1 Phosphoglycerate kinase Vacuolar H+-ATPase 26kD E subunit RPS6-p70-protein kinase CG13955 Serpin 47C Ribosomal protein L18 CG8936
CG14996 CG79913 CG14994 CG4651 CG7434 CG4236 CG3226 CG1666 CG2033 CG6961 CG9354 CG3257 CG8431 CG3955 CG1877 CG12244 CG7109 CG4253 CG4954 CG7109 CG4553 CG4954 CG7891 CG1956 CG9735 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG17528 CG1055 CG10577 CG1088 CG10557 CG1058 CG10559 CG1055	43 44 43 43 44 41 40 40 40 40 40 38 38 38 38 38 37 37 37 37 36 36 36 36 36 36 37 38 33	1 1 2 1 1 2 1 1 2 1 <t< td=""><td>PP2A-B' coracle Ribosomal protein L13 Ribosomal protein L22 Chromatin assembly factor 1 subunit CG3226 Helicase Ribosomal protein S15Aa CG6961 Ribosomal protein L34b pch2 Cysteinyl-tRNA synthetase Ribosomal protein S9 lin-19-like Pyruvate carboxylase licorne microtubule star Diphthamide methyltransferase PTEN-induced putative kinase 1 eIF3-S8 novel GTPase indispensable for equal segregation of chromosomes Roughened Tryptophanyl-tRNA synthetase CG17528 hippo BM-40-SPARC peroxisomal Multifunctional enzyme type 2 CG17337 Small ribonucleoprotein particle protein SmD3 CG9436 tumbleweed Succinyl coenzyme A synthetase α subunit CG10527 Proteome of centrioles 1 Phosphoglycerate kinase Vacuolar H+-ATPase 26kD E subunit RPS6-p70-protein kinase CG8036</td></t<>	PP2A-B' coracle Ribosomal protein L13 Ribosomal protein L22 Chromatin assembly factor 1 subunit CG3226 Helicase Ribosomal protein S15Aa CG6961 Ribosomal protein L34b pch2 Cysteinyl-tRNA synthetase Ribosomal protein S9 lin-19-like Pyruvate carboxylase licorne microtubule star Diphthamide methyltransferase PTEN-induced putative kinase 1 eIF3-S8 novel GTPase indispensable for equal segregation of chromosomes Roughened Tryptophanyl-tRNA synthetase CG17528 hippo BM-40-SPARC peroxisomal Multifunctional enzyme type 2 CG17337 Small ribonucleoprotein particle protein SmD3 CG9436 tumbleweed Succinyl coenzyme A synthetase α subunit CG10527 Proteome of centrioles 1 Phosphoglycerate kinase Vacuolar H+-ATPase 26kD E subunit RPS6-p70-protein kinase CG8036
CG14996 CG79913 CG11949 CG4651 CG7434 CG4236 CG7326 CG7326 CG6961 CG9354 CG33453 CG8431 CG3395 CG12244 CG31453 CG8431 CG12244 CG7109 CG31289 CG4523 CG4523 CG4523 CG4524 CG77891 CG17337 CG17528 CG17228 CG6378 CG17337 CG8427 CG9735 CG17328 CG17337 CG8427 CG9436 CG13345 CG10527 CG10527 CG10521 CG10527 CG10527 CG10527 CG10529 CG10527 CG10529 CG10529 CG10527 CG10529 CG10527 CG10529 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10527 CG10529 CG	$\begin{array}{r} 43\\ 44\\ 43\\ 43\\ 43\\ 43\\ 43\\ 43\\ 43\\ 41\\ 40\\ 40\\ 40\\ 40\\ 40\\ 40\\ 40\\ 39\\ 38\\ 38\\ 38\\ 38\\ 38\\ 38\\ 38\\ 38\\ 37\\ 37\\ 37\\ 37\\ 37\\ 37\\ 37\\ 37\\ 37\\ 37$	$\begin{array}{c} 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1 \\$	PP2A-B' coracle Ribosomal protein L13 Ribosomal protein L22 Chromatin assembly factor 1 subunit CG3226 Helicase Ribosomal protein S15Aa CG6961 Ribosomal protein S15Aa CG6961 Ribosomal protein S14b pch2 Cysteinyl-tRNA synthetase Ribosomal protein S9 lin-19-like Pyruvate carboxylase licorne microtubule star Diphthamide methyltransferase PTEN-induced putative kinase 1 eIF3-S8 novel GTPase indispensable for equal segregation of chromosomes Roughened Tryptophanyl-tRNA synthetase CG17528 hippo BM-40-SPARC peroxisomal Multifunctional enzyme type 2 CG17337 Small ribonucleoprotein particle protein SmD3 CG9436 tumbleweed Succinyl coenzyme A synthetase a subunit CG10527 Proteome of centrioles 1 Phosphoglycerate kinase Vacuolar H+-ATPase 26kD E subunit RPS6-p70-protein kinase CG13955 Serpin 47C Ribosomal protein L18 CG8036 CG4164
CG14996 CG74913 CG14949 CG4651 CG7434 CG4236 CG7434 CG4236 CG3226 CG1666 CG2033 CG6961 CG9354 CG3453 CG8431 CG3395 CG1877 CG1516 CG12244 CG7109 CG1526 CG1224 CG7891 CG1526 CG9735 CG17528 CG1055 CG1055 CG1055 CG1055 CG1055 CG1055 CG1055 CG1055 CG1055 CG1055 CG1055 CG17528 CG1055 C	$\begin{array}{c} 43\\ 44\\ 43\\ 43\\ 43\\ 43\\ 43\\ 43\\ 43\\ 43\\$	$\begin{array}{c} 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1 \\$	PP2A-B' coracle Ribosomal protein L13 Ribosomal protein L22 Chromatin assembly factor 1 subunit CG3226 Helicase Ribosomal protein S15Aa CG6961 Ribosomal protein L34b pch2 Cysteinyl-tRNA synthetase Ribosomal protein S9 lin-19-like Pyruvate carboxylase licorne microtubule star Diphthamide methyltransferase PTEN-induced putative kinase 1 elF3-S8 novel GTPase indispensable for equal segregation of chromosomes Roughened Tryptophanyl-tRNA synthetase CG17528 hippo BM-40-SPARC peroxisomal Multifunctional enzyme type 2 CG17337 Small ribonucleoprotein particle protein SmD3 CG9436 tumbleweed Succinyl coenzyme A synthetase a subunit CG10527 Proteome of centrioles 1 Phosphoglycerate kinase Vacuolar H+-ATPase 26kD E subunit RPS6-p70-protein kinase CG13955 Serpin 47C Ribosomal protein L18 CG8036 CG31918

CG18490	31	1	CG18490
CG14648	31	1	growl
CG15697	31	1	Ribosomal protein S30
CG4464	30	1	Ribosomal protein S19a
CG10206	30	1	nop5
CG17286	30	1	spindle defective 2
CG4535	30	1	FK506-binding protein FKBP59
CG12202	30	1	Nat1
CG17599	30	1	CG17599
CG12775	30	1	Ribosomal protein L21
CG6050	29	1	Elongation factor Tu mitochondrial
CG1387	29	1	CG1387
CG11154	28	1	ATP synthase, β subunit
CG6948	28	1	Clathrin light chain
CG5394	27	1	Glutamyl-prolyl-tRNA synthetase
CG6084	27	1	CG6084
CG2099	27	1	Ribosomal protein L35A
CG6904	27	1	Glycogen synthase
CG5857	27	1	Ndc1 ortholog
CG31549	27	1	CG31549
CG5915	26	1	Rab-protein 7
CC0082	25	1	Heterogeneous nuclear
CG9983	23	1	ribonucleoprotein at 98DE
CG7111	25	1	Receptor of activated protein kinase C 1
CG5726	25	1	CG5726
CG6822	25	1	ergic53
CG5366	24	1	Cullin-associated and neddylation- dissociated 1
CG1810	24	1	mRNA-capping-enzyme

CG10859	24	2	CG10859
CG8187	24	1	CG8187
CG7003	24	1	Msh6
CG5432	23	1	CG5432
CG17520	22	1	casein kinase Πα
CG7939	22	1	Ribosomal protein L32
CG8014	22	1	Receptor mediated endocytosis 8
CG3097	22	1	CG3097
CG10778	22	2	CG10778
CG4428	22	1	Autophagy-specific gene 4
CG6510	21	1	Ribosomal protein L18A
CG7269	21	1	Helicase at 25E
CG6382	21	1	Eflα-like factor
CG4199	21	1	CG4199
CG14442	21	1	CG14442
CG4774	21	1	Cardiolipin synthase
CG1721	20	1	Phosphoglyceromutase
CG7144	20	1	lysine ketoglutarate reductase
CG8231	20	1	T-cp1ζ
CG4218	19	1	CG4218
CG3382	19	1	Organic anion transporting polypeptide
000002	.,		58Db
CG1475	19	1	Ribosomal protein L13A
CG10845	19	1	CG10845
CG8443	18	1	clueless
CG14457	18	3	CG14457
CG13213	17	1	fbl6

A.18 pMT-PrA-Cp110 +OA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG4027	73719	1157	Actin 5C
CG12051	72277	1105	Actin 42A
CG15792	48614	826	zipper
CG18290	16058	477	Actin 87E
CG10067	16052	478	Actin 57B
CG3595	6610	131	spaghetti squash
CG3201	3457	57	Myosin light chain cytoplasmic
CG7438	3089	80	Myosin 31DF
CG10540	2707	99	capping protein alpha
CG9155	2486	57	Myosin 61F
CG4264	2440	54	Heat shock protein cognate 4
CG7558	1961	35	Actin-related protein 66B
CG1484	1806	42	flightless I
CG9277	1673	38	ß-Tubulin at 56D
CG1913	1659	39	a-Tubulin at 84B
CG17158	1637	37	capping protein beta
CG31618	1511	20	His2A:CG31618
CG14617	1506	20	Cp110
CG2146	1/06	40	dilute class unconventional myosin
CG10641	1470	27	CG10641
CG10041	1330	24	Elongation faster 1=49D
CG8280	1252	20	Elongation factor 1048D
CG3695	1202	35	Jaguar
CG1106	1201	30	Geisolin
CG19//	1164	24	a Spectrin
CG1539	1133	21	tropomodulin
CG31196	1122	18	14-3-38
CG8472	1065	17	Calmodulin
CG8578	1046	31	CG8578
CG3401	1018	23	β-Tubulin at 60D
CG12008	996	31	karst
CG6831	860	14	rhea
CG9325	702	12	hu li tai shao
CG5499	685	11	Histone H2A variant
CG1242	550	21	Heat shock protein 83
CG9901	502	11	Actin-related protein 14D
CG3937	489	12	cheerio
CG8978	468	12	Suppressor of profilin 2
CG9748	435	8	belle
CG4147	396	6	Heat shock protein cognate 3
CG17291	389	6	Protein phosphatase 2A at 29B
CG4560	353	9	Arpc3A
CG4087	340	6	Ribosomal protein LP1
CG5870	337	7	β Spectrin
CG10954	333	8	Arc-p34
CG15784	315	8	CG15784
CG17870	314	6	14-3-3ζ
CG2331	310	5	TER94
CG4376	298	8	a actinin
CG4463	287	4	Heat shock protein 23
CG9012	281	6	Clathrin heavy chain
CG1258	275	4	pavarotti
CG6148	268	5	Putative Achaete Scute Target 1
CG10811	251	3	eukaryotic translation initiation factor
CG1883	250	6	Ribosomal protein \$7
CG1782	230	6	Ubiquitin activating enzyme 1
CG18572	245	6	rudimentary
CG7032	230	4	CG7033
CG8082	230	7	EP::60
CG0903	217	1	n16-APC
1005001	214	4	DI0-AKC

CG8309	213	6	Transport and Golgi organization 7
CG4898	212	5	Tropomyosin 1
CG5502	210	5	Ribosomal protein L4
CG4145	203	4	Collagen type IV
CG5119	194	8	polyA-binding protein
CG12030	191	4	UDP-galactose 4'-epimerase
CG4183	189	6	Heat shock protein 26
CG5825	183	4	Histone H3.3A
CG31613	177	5	His3:CG31613
CG14996	175	2	Chd64
CG3379	174	4	Histone H4 replacement
CG11522	170	4	Ribosomal protein L6
CG5972	167	4	Arc-p20
CG14792	165	2	stubarista
CG7507	165	2	Dynein heavy chain 64C
CG7490	160	4	Ribosomal protein I PO
CG1262	152	2	Ribosomal protein L 8
CC21617	132	5	Lie 1.CC21617
CC4265	140	2	Ubiquitin conhexy terminal hydrologe
CG4265	144	3	Dily and a set of a s
CG3/51	145	4	Ribosomai protein S24
CG1/654	139	5	Enolase
CG4466	136	3	Heat shock protein 27
CG/0/3	134	2	sari
CG3523	124	2	Fatty acid synthase 1
CG17272	124	4	CG17272
CG5020	123	2	Cytoplasmic linker protein 190
CG14207	122	3	HspB8
CG3011	121	2	CG3011
CG6699	120	2	Coat Protein (coatomer) β'
CG2238	118	4	Elongation factor 2b
CG7762	118	3	Rpn1
CG8055	111	1	shrub
CG7967	110	2	CG7967
CG1528	108	2	Coat Protein (coatomer) y
CG8977	101	2	Ccty
CG16858	101	2	viking
CG9423	99	2	karyopherin α3
CG3455	99	1	Rpt4
CG32164	98	2	CG32164
CG17521	97	2	Om
CG9281	96	3	CG9281
CG10922	94	2	La autoantigen-like
CG15717	93	1	CG15717
CG9282	92	1	Ribosomal protein I 24
CG10652	92	1	Ribosomal protein L30
CG8900	90	2	Ribosomal protein S18
CG40045	80	1	CG40045
CG5274	87	2	Ten1 like
CU3374	0/	2	Multidrug register as motoin 4
CG14709	86	1	ortholog
CG4897	85	2	Ribosomal protein L7
CG3314	85	4	Ribosomal protein L7A
CG10230	85	2	Rpn9
CG17949	82	4	His2B:CG17949
CG9579	80	1	Annexin X
CG3299	79	1	Vinculin
CG1059	77	6	Karvopherin ß 3
CG8922	76	3	Ribosomal protein S5a
CG3949	75	2	hoi-polloi
CG30349	75	1	CG30349
CG15000	73	1	CG15099
CO15099	15	1	CU1J077

CG9311	73	1	myopic
CG6944	72	2	Lamin
CG6598	72	1	Formaldehyde dehydrogenase
CG9888	71	2	Fibrillarin
CG10377	71	2	Heterogeneous nuclear ribonucleoprotein at 27C
CG7961	71	3	Coat Protein (coatomer) a
CG10527	71	2	CG10527
CG3821	70	1	Aspartyl-tRNA synthetase
CG8439	69	1	T-complex Chaperonin 5
CG13345	69	3	RacGAP50C
CG7831	67	1	non-claret disjunctional
CG7595	66	2	crinkled
CG2022	65	2	Pibesomal protein \$17
CG12289	65	2	A kinese anghor protein 200
CG10000	65	1	Programmed call death 4 ortholog
CC(522	65	2	Testin ortholog
CG0322	65	2	Testili ortholog
CG8551	65	1	
CG6988	63	3	Protein disulfide isomerase
CG/935	63	1	moleskin
CG4157	63	1	Kpn12
CG13849	63	1	Nop56
CG9429	61	1	Calreticulin
CG11276	61	2	Ribosomal protein S4
CG3416	59	2	Mov34
CG10385	59	5	male-specific lethal 1
CG15693	59	2	Ribosomal protein S20
CG12262	59	1	CG12262
CG4878	58	1	eIF3-S9
CG4759	58	2	Ribosomal protein L27
CG17489	58	2	Ribosomal protein L5
CG14206	58	2	Ribosomal protein S10b
CG1524	56	1	Ribosomal protein \$14a
CG4799	56	2	Pendulin
CG10506	56	2	Mer-110
CG12201	56	1	AlanyLtDNA conthetese
CG4012	54	1	Analys-trank synthetase
0012005	30	1	eef10
0021764	56	1	NIMS19
000075	56	1	virus-induced RNA I
CG9075	55	2	Eukaryotic initiation factor 4a
CG/439	54	1	Argonaute 2
CG2092	54	1	scraps
CG10522	53	1	sticky
CG10863	52	1	CG10863
CG5170	50	1	Dodeca-satellite-binding protein 1
CG8235	49	1	aaRS-interacting multifunctional
200255	-77	1	protein 1
CG31453	48	1	pch2
CG6223	47	1	Coat Protein (coatomer) B
CG10944	47	2	Ribosomal protein S6
CG1837	46	1	pretaporter
CG9436	46	1	CG9436
CG6090	46	1	Ribosomal protein L34a
CG13389	45	1	Ribosomal protein S13
CG11527	45	1	Tiggrin
CG16916	45	2	Rpt3
CG4046	44	1	Ribosomal protein S16
CG1877	43	1	lin-19-like
CG14066	42	1	La related protein
CG8231	41	1	T-cn17
CG11271	41	1	Ribosomal protein \$12
CG12240	40	1	Regulatory partials non_ATDess_12
CG3105	40	1	Ribosomal protoin I 12
CC14649	40	2	Kibosoniai piotein L12
0002772	40	5	growi
CG2/6/	40	1	CG2/6/
CG4429	39	1	RNA-binding protein 2
CG8332	38	1	Ribosomal protein S15
	38	4	Glutamine:fructose-6-phosphate aminotransferase 2
CG1345			Ribosomal protein \$25
CG1345 CG6684	37	1	Ribbsoniai brotein 525
CG1345 CG6684 CG17599	37 37	1	CG17599
CG1345 CG6684 CG17599 CG15100	37 37 37	1 1 1	CG17599 Methionyl-tRNA synthetase
CG1345 CG6684 CG17599 CG15100 CG1387	37 37 37 36	1 1 1	CG1387
CG1345 CG6684 CG17599 CG15100 CG1387 CG4225	37 37 37 36 36	1 1 1 1	CG17599 Methionyl-tRNA synthetase CG1387 Heavy metal tolerance factor 1
CG1345 CG6684 CG17599 CG15100 CG1387 CG4225 CG1542	37 37 37 36 36 36	1 1 1 1 1	CG17599 Methionyl-tRNA synthetase CG1387 Heavy metal tolerance factor 1 CG1542

1	l i	1	subunit
CG3226	35	1	CG3226
CG7722	35	4	Serpin 47C
CG7182	34	1	CG7182
CG2216	33	1	Ferritin 1 heavy chain homologue
CG4863	33	1	Ribosomal protein L3
CC10101	22	1	Distance of contribution 1
CG10191	22	1	Proteonie of centrioles 1
CG11984	33	1	CG11984
CG5450	32	1	Cytoplasmic dynein light chain 2
CG4535	32	1	FK506-binding protein FKBP59
CG6846	32	1	Ribosomal protein L26
CG8036	31	2	CG8036
CG15697	31	1	Ribosomal protein S30
CG5394	29	1	Glutamyl-prolyl-tRNA synthetase
CG6092	29	1	Dak1
CG11888	28	1	Rpn2
CG15102	28	1	Juvenile hormone epoxide hydrolase 2
CG8615	28	1	Ribosomal protein L18
CG3333	28	1	Nucleolar protein at 60B
CG4651	27	1	Ribosomal protein L13
CG3203	27	2	Ribosomal protein L17
CG9819	26	1	Calcineurin A at 14F
CG3186	26	1	eIF-5A
CG8588	26	1	nastrel
CG2168	20	1	Pibosomel protein \$2.4
CC5720	25	1	CC5720
CC03720	25	1	Dealisation matrix A2
CG9273	25	1	Replication protein A2
CG7891	25	1	novel GTPase indispensable for equal
		_	segregation of chromosomes
CG8863	25	1	DnaJ-like-2
CG9553	24	1	chickadee
CG1065	24	1	Succinyl coenzyme A synthetase a
		-	subunit
CG1721	24	1	Phosphoglyceromutase
CG1444	24	1	CG1444
CG1810	24	1	mRNA-capping-enzyme
CG10638	24	1	CG10638
CG7003	24	1	Msh6
CG14457	24	1	CG14457
CG9738	23	1	MAP kinase kinase 4
CG7999	23	1	Mediator complex subunit 24
CG3996	23	1	CG3996
CG5432	23	1	CG5432
CG3981	23	1	Unc-76
005701	20		Guanine nucleotide exchange factor in
CG30115	23	2	mesoderm
CG2050	22	1	modulo
CG5353	22	1	Threonyl-tRNA synthetase
CG1601	22	1	IGE-II mRNA-binding protein
CG21222	22	1	unc 115
CG15904	22	1	Duncin hoose shoir at 62D
0015804	21	1	Small ribonuclearnetsin norticl
CG5352	21	1	Small ribonucleoprotein particle
000000	20	<u> </u>	protein SmB
CG2830	20		Heat shock protein 60 related
CG1822	20		bitocal
CG5726	20	1	CG5726
CG3382	20	1	Organic anion transporting
			polypeptide 58Db
CG4832	19	1	centrosomin
CG7207	19	1	ceramide transfer protein
CG10778	19	1	CG10778
CG32458	19	1	neuromusculin
CG3661	18	1	Ribosomal protein L23
CG12522	19	1	Adaptor Protein complex 1/2, β
0012552	18	1	subunit
CG18076	18	1	short stop
CG4236	18	1	Chromatin assembly factor 1 subunit
CG2774	18	1	Sorting nexin 1
CG17028	17	1	CG17028

A.19 pMT-CP110-PrA +OA +MG132 purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG1913	8208	282	α-Tubulin at 84B
CG15792	7953	167	zipper
CG4183	7393	128	Heat shock protein 26
CG4264	7345	181	Heat shock protein cognate 4
CG9277	6607	224	β-Tubulin at 56D
CG4027	4349	110	Actin 5C
CG14617	2607	72	Cp110
CG4463	2549	53	Heat shock protein 23
CG18572	2293	56	rudimentary
CG3401	2154	41	β-Tubulin at 60D
CG10067	1811	58	Actin 57B
CG5834	1472	34	Hsp70Bbb
CG18743	1396	32	Heat-shock-protein-70Ab

CG4869	1225	26	β-Tubulin at 97EF
CG12101	1225	24	Heat shock protein 60
CG5436	1185	26	Heat shock protein 68
CG4147	1109	26	Heat shock protein cognate 3
CG6453	1068	31	CG6453
CG8280	983	23	Elongation factor 1a48D
CG17291	851	16	Protein phosphatase 2A at 29B
CG3595	818	19	spaghetti squash
CG12233	797	19	lethal (1) G0156
CG6815	693	14	belphegor
CG3201	661	12	Myosin light chain cytoplasmic
CG31618	660	9	His2A:CG31618
CG1569	640	14	rough deal
CG1528	624	14	Coat Protein (coatomer) y

CG10811	617	10	eukaryotic translation initiation factor
CG5366	616	16	CG5366
CG14476	615	16	CG14476
CG7507	603	15	Dynein heavy chain 64C
CG11963	581	10	skpA associated protein
CG17870	567	9	14-3-3ζ
CG9155	534	15	Myosin 61F
CG31196	525	9	14-3-3s
CG7961	509	21	Coat Protein (coatomer) a
CG7769	509	8	piccolo
CG1242	501	15	Heat shock protein 83
CG7935	498	12	moleskin
CG7439	490	20	Argonaute 2
CG32164	488	9	CG32164
CG6223	481	13	Coat Protein (coatomer) β
CG9748	479	12	belle
CG4466	444	14	Heat shock protein 27
CG1884	441	7	Not1
CG5520	426	10	Glycoprotein 93
CG31022	423	13	prolyl-4-hydroxylase-alpha EFB
CG9012	421	11	Clathrin heavy chain
CG5252	420	8	Ranop9
CG1059	403	7	Karvonhorin 6.3
CG8047	200	7	26 20kD proteinese
CG9674	388	10	CG9674
CG10535	380	6	Elongator complex protein 1
CG8571	375	5	smallminded
CG16916	370	8	Rpt3
CG1977	352	10	α Spectrin
CG9888	344	12	Fibrillarin
CG14472	339	9	purity of essence
CG17870	328	8	14-3-3ζ
CG2238	319	16	Elongation factor 2b
CG8309	262	6	Transport and Golgi organization 7
CG10938	250	3	Proteasome a5 subunit
CG10360	248	6	refractory to sigma P
CG3210	247	6	Dynamin related protein 1
CG14792	241	4	stubarista
CG103/0	241	8	Tat-binding protein-1
CG11154	240	5	ATR conthese & cubunit
CG2331	230	7	TER04
CG7438	233	8	Myosin 31DF
CG5330	222	4	Nucleosome assembly protein 1
CG10596	220	4	Msr-110
CG1516	217	5	CG1516
CG4389	217	9	CG4389
CG8863	215	6	DnaJ-like-2
CG8472	214	6	Calmodulin
CG11943	213	5	CG11943
CG14637	205	4	abstrakt
CG11198	201	2	Acetyl-CoA carboxylase
CG14648	201	6	growl
CG6476	200	5	Suppressor of variegation 3-9
CG10540	200	0	DNA polymoroso S
CG16944	190	4	stress-sensitive B
CG10080	190	6	mahiong
CG5934	190	2	CG5934
CG2146	189	6	dilute class unconventional myosin
CG12008	188	5	karst
CG1341	186	7	Rpt1
CG18174	185	4	Rpn11
CG1591	185	4	REG
CG9282	184	2	Ribosomal protein L24
CG10289	183	2	CG10289
CG1883	179	4	Ribosomal protein S7
CG2422	1/8	2	Conagen type IV
CG32626	177	2	AMP deaminana
CU32020	1//	2	eukaryotic translation Initiation Factor
CG9946	173	5	
CG11888	173	5	Rpn2
CG4164	172	3	CG4164
CG4581	171	8	Thiolase
CG10230	171	3	Rpn9
CG9819	169	7	Calcineurin A at 14F
CG7762	167	8	Rpn1
CG9842	166	5	Protein phosphatase 2B at 14D
CG13849	160	5	Nop56
CG14996	157	4	Chd64
CG1851	153	2	Ady43A
CG6439	153	5	CG6439
CG5110	152	5	nistone H2A variant
CG0520	151	4	poryA-binding protein Sec61 a subusit
CG6303	149	3	Bruce
CG2960	147	4	Ribosomal protein I 40
CG11700	146	5	CR11700
CG8963	142	2	CG8963
CG6050	140	3	Elongation factor Tu mitochondrial
CG10641	138	4	CG10641
CG1683	137	6	Adenine nucleotide translocase 2

CG1489	136	4	Pros45
CG3612	133	4	bellwether
CG8331 CG9325	133	4	hu li tai shao
CG5064	128	2	Srp68
CG11793	127	2	Superoxide dismutase
CG3455	127	2	Rpt4
CG2216 CG3379	126	2	Ferritin 1 heavy chain homologue
CG6459	125	1	CG6459
CG11228	125	2	hippo
CG8996	124	1	walrus
CG32210	124	2	Listerin E3 ubiquitin protein ligase 1
CG8231	123	4	Τ-cp1ζ
CG7033	123	3	mitotic 15
CG3523	122	3	Fatty acid synthase 1
CG3961	120	2	CG3961
CG6988	119	3	Protein disulfide isomerase
CG5504	117	3	lethal (2) tumorous imaginal discs
CG8798	117	2	L on protease
CG9327	117	3	Proteasome 29kD subunit
CG8287	116	2	Rab-protein 8
CG17158	115	4	capping protein beta
CG31764	115	3	virus-induced RNA 1
CG3937	114	2	cheerio
CG8/15 CG14207	114	1	lingerer HopP8
CG7070	112	3	Pyruvate kinase
CG7808	112	2	Ribosomal protein S8
CG5374	111	3	Tcp1-like
CG33162	111	3	Signal recognition particle receptor β
CG4260	111	3	Adaptor Protein complex 2, α subunit
CG33180	110	2	Kanbp16
CG10753	109	2	protein SmD1
CG10630	106	2	blanks
CG15433	105	1	Elongator complex protein 3
CG4087	104	2	Ribosomal protein LP1
CG12306	104	5	polo
CG12005	104	3	Mms19
CG12005	104	3	Helicase
CG8882	102	3	Trip1
CG31794	101	3	Paxillin
CG7831	99	2	non-claret disjunctional
CG3725	98	2	Calcium ATPase at 60A
CG3200	98	3	Cety
CG3949	98	2	hoi-polloi
CG14813	98	4	Coat Protein (coatomer) δ
CG10198	98	1	Nucleoporin 98
CG3265	97	1	Eb1
CG5180 CG6692	96	4	Cysteine proteinase-1
CG1092	95	2	CG1092
CG11999	95	3	CG11999
CG12202	93	1	Nat1
CG10484	93	2	Regulatory particle non-ATPase 3
CG4878	92	3	Int6 homologue
CG11984	91	1	CG11984
CG3981	91	1	Unc-76
CG10701	90	2	Moesin
CG6617	90	1	CG6617
CG5028	89	4	CG5028
CG1/484 CG2637	88 87	2	Eemale sterile (2) Ketel
0001	07	-	Eukaryotic initiation factor 3 p40
CG9124	87	2	subunit
CG7144	86	3	lysine ketoglutarate reductase
CG6521	86	1	Signal transducing adaptor molecule
CG2080	86	2	CG15784
CG4033	83	2	RNA polymerase I 135kD subunit
CG11276	83	1	Ribosomal protein S4
CG10805	83	4	lethal (2) k09022
CG5684	83	4	Pop2
CG3585	82	2	Rabconnectin-3A
CG7610	81 81	2	Ribosomal protein L/
CG16858	81	3	viking
CG33554	81	2	Nipped-A
CG13349	79	1	Regulatory particle non-ATPase 13
CG5651	79	2	pixie
CG5170	78	2	Dodeca-satellite-binding protein 1
CG18405	77	1	Aldehyde dehydrogenase Proteasome al subunit
CG9484	75	2	hyperplastic discs
CG7074	75	1	missing oocyte
CG6756	75	1	Translocase of outer membrane 70
CG2118	75	1	CG2118
CG30084	75	2	Z band alternatively spliced PDZ-motif
	1	l	protein 52
CG4254	74	1	twinstar

CG13387	74	1	embargoed
6615567			Aspartyl-tRNA synthetase.
CG31739	74	2	mitochondrial
CG7490	73	3	Ribosomal protein LP0
CG3661	73	2	Ribosomal protein L23
CG8900	73	2	Ribosomal protein S18
CG2206	73	3	lethal (1) G0193
CG4659	72	1	Signal recognition particle protein 54k
CG31137	72	1	twin
CG8578	72	2	CG8578
CG5650	71	1	Protein phosphatase 1 at 87B
CG6948	71	2	Clathrin light chain
CG7558	70	1	Actin-related protein 66B
CG6998	70	3	cut up
CG5604	70	2	CG5604
CG12264	70	5	CG12264
CG11856	70	1	Nucleoporin 358
CG10149	69	2	Proteasome p44.5 subunit
CG17746	69	1	CG17746
CG4738	69	1	Nucleoporin 160
CG5974	68	2	pelle
CG9769	68	1	CG9769
CG12163	68	2	CG12163
CG1600	67	2	Death resistor Adh domain containing
661000	07	2	target
CG10527	67	4	CG10527
CG5394	65	1	GlutamyI-prolyl-tRNA synthetase
CG12792	65	1	lethal (2) 09851
CG1987	65	1	Rbp1-like
CG3751	65	1	Ribosomal protein S24
CG5495	65	3	I hioredoxin-like
CG4003	65	2	pontin
CG5363	64	1	cdc2
CG1524	64	1	Kibosomal protein S14a
CG4257	64	1	Signal-transducer and activator of
CC0009	64	2	little imaginal diago
CG9088	04 64	2 1	roptin
CG7726	62	1	Pibecomel protein L 11
CG4821	63	2	Tequila
CG7375	63	1	Ubiquitin conjugating anzyme E2M
CG12532	62	2	Adaptor Protein complex 1/2 ß subunit
CG14750	62	2	Vacuolar protein sorting 25
CG6095	62	1	exo84
CG5920	61	2	string of pearls
CG6235	61	1	twins
CG17498	61	1	mad2
66.000			Translationally controlled tumor
CG4800	60	1	protein
			protein
CG12019	59	1	Cdc37
CG12019 CG5838	59 59	1	Cdc37 DNA replication-related element factor
CG12019 CG5838 CG12737	59 59 59	1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to
CG12019 CG5838 CG12737	59 59 59	1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein
CG12019 CG5838 CG12737 CG15618	59 59 59 59	1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618
CG12019 CG5838 CG12737 CG15618 CG5608	59 59 59 59 59 59	1 1 1 2	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG5608
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272	59 59 59 59 59 59 59 59	1 1 1 2 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG520	59 59 59 59 59 59 59 59 59 58 58	1 1 1 2 1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin Ule AB190
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG0986	59 59 59 59 59 59 59 59 58 58 58	1 1 1 2 1 1 1 1 2	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubrt bioinitio linena
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945	59 59 59 59 59 59 59 59 58 58 58 58	1 1 1 2 1 1 1 1 2 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945 CG18596	59 59 59 59 59 59 59 58 58 58 58 58 58	$\begin{array}{c} 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1$	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945 CG18596 CG18596 CG18596	59 59 59 59 59 59 59 58 58 58 58 58 58 58 58	1 1 1 2 1 1 1 1 2 1 1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945 CG18596 CG7837 CG9840	59 59 59 59 59 59 59 59 58 58 58 58 58 58 58 57 57	1 1 1 2 1 1 2 1 1 2 1 1 1 2	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940
CG12019 CG5838 CG12737 CG15618 CG5608 CG7945 CG7945 CG7945 CG7945 CG7947 CG9940 CG6840	59 59 59 59 59 59 59 59 58 58 58 58 58 58 57 57	1 1 1 2 1 1 1 2 1 1 1 2 1 1 2 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945 CG18596 CG5837 CG9940 CG6840 CG1657	59 59 59 59 59 59 59 59 58 58 58 58 58 58 58 58 57 57 57 57	1 1 2 1 1 1 2 1 1 1 2 1 1 2 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11 CG1657
CG12019 CG5838 CG12737 CG15618 CG5608 CG7272 CG6944 CG2520 CG9086 CG7945 CG18596 CG5837 CG9940 CG6840 CG6840 CG1657 CG8266	59 59 59 59 59 59 59 59 59 59 59 59 59 59 59 59 58 58 58 58 58 58 57 57 56 56	$ \begin{array}{c} 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 2\\ 1\\ 2 \end{array} $	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11 CG1657 sec31
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CG12019 CG5838 CG12737 CG15618 CG5608 CG7945 CG7945 CG7945 CG7945 CG8837 CG9940 CG6840 CG6840 CG6840 CG6964 CG6904 CG6904	59 59 59 59 59 59 58 58 58 58 58 58 57 57 57 56 56 55	$ \begin{array}{c} 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 2\\ 2\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\$	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11 CG1657 sec31 Glycogen synthase Stromalin
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CG12019 CG5838 CG12737 CG15618 CG5608 CG5608 CG7945 CG18596 CG7945 CG18596 CG7945 CG18596 CG6840 CG6985 CG6985 CG6985 CG6985 CG6985 CG6985 CG6985 CG7855 CG6985 CG7855 CG6856 CG7855 CG6985 CG7855 CG6985 CG7855 CG7855 CG6856 CG7855 CG7	59 59 59 59 59 59 58 58 58 58 58 58 58 58 58 58 58 58 58 58 58 58 57 57 56 55 55	1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG15618 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11 CG1657 sec31 Glycogen synthase Stromalin falafel CTP:phosphocholine cytidylyltransferase 1
CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945 CG18596 CG5837 CG9940 CG6840 CG6840 CG6840 CG6957 CG8266 CG6904 CG6904 CG6904 CG423 CG9351 CG1049 CG17654	59 59 59 59 59 59 58 58 58 58 57 56 56 55 55 55 54	1 1 1 1 2 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11 CG1657 sec31 Glycogen synthase Stromalin falafel CTP:phosphocholine cytidyllytransferase 1 Enolase
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CG12019 CG5838 CG12737 CG15618 CG5608 CG17272 CG6944 CG2520 CG9086 CG7945 CG18596 CG7945 CG18596 CG5837 CG9940 CG6840 CG1657 CG8266 CG6904 CG1657 CG8266 CG6904 CG1657 CG9251 CG1049 CG17654 CG13388 CG13388 CG13388 CG13388	59 59 59 59 59 59 58 58 58 58 58 57 56 56 55 55 54 54 53 53	1 1 1 1 2 1 1 1 1 1 1 1 1 2 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1	Cdc37 DNA replication-related element factor Calmodulin-binding protein related to a Rab3 GDP/GTP exchange protein CG15618 CG5608 CG17272 Lamin like-AP180 Ubr1 ubiquitin ligase CG7945 CG18596 HEM-protein CG9940 Rpb11 CG1657 sec31 Glycogen synthase Stromalin falafel CTP:phosphocholine cytidylyltransferase 1 Enolase flightless 1 CG10663 A kinase anchor protein 200 Ribosomal protein L35A
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CG13900	47	2	CG13900
CG7324	47	2	CG7324
CG4931	47	2	specifically Rac1-associated protein 1
CG10652	46	1	Ribosomal protein L30
CG2200	40	1	Dpy-30-like 1
CG7870	40	1	wollknaeuel
CG6148	45	1	Putative Achaete Scute Target 1
CG7398	45	2	Transportin
CG7915	45	2	Ect4
CG2097	45	2	Symplekin
CG8542	44	1	Heat shock protein cognate 5
CG6647	44	1	porin
CG9901	44	1	Actin-related protein 14D
CG4199	44	1	CG4199
CG4808	44	1	Kpn/ Tronomyosin 1
CG11981	43	1	Proteasome 63 subunit
CG8478	43	1	CG8478
CG9423	42	1	karyopherin α3
CG8368	42	1	CG8368
CG18102	41	1	shibire
CG4046	41	1	Ribosomal protein S16
CG8588	41	2	pastrel
CG3061	41	1	CG3061
CG31332	41	1	unc-115
CG7017	40	1	Nucleoplasmin
CG6768	40	1	DNA polymerase s 255kD subunit
CG9581	40	1	CG9581
CG17949	40	2	His2B:CG17949
CG17520	39	2	casein kinase IIa
CG10385	39	2	male-specific lethal 1
CG5422	39	1	Rox8
CG7581	39	2	Bub3
CG40478	39	1	Dyrk3
CG3756	39	1	CG3/56
CG//91	39	1	21E2 S8
CG1651	39	2	Ankwrin
CG9543	38	1	Coat Protein (coatomer) a
CG8415	38	1	Ribosomal protein S23
CG16908	38	1	CG16908
CG2684	37	1	lodestar
CG4978	37	1	Minichromosome maintenance 7
CG4261	37	1	Helicase 89B
CG1782	37	1	Ubiquitin activating enzyme 1
CG1945	37	1	CG8/40 fat facets
CG3957	36	1	wing morphogenesis defect
CG8036	36	1	CG8036
CG7434	35	1	Ribosomal protein L22
CG5092	35	2	Target of rapamycin
CG5972	35	1	Arc-p20
CG13389	34	1	Ribosomal protein S13
CG6378	34	1	BM-40-SPARC
CG4153	34	1	Eukarvotic initiation factor 28
CG4429	33	1	RNA-binding protein 2
CG5695	33	3	jaguar
CG2028	33	1	Casein kinase Ia
CG11092	33	1	Nucleoporin 93kD-1
CG10212	33	1	SMC2
CG9031	33	1	icarus
CG1387	33	4	CG1387
CG10226	35 22	1	rhea Lominin A
CG9209	32	1	vacuolar neduncle
CG1810	32	2	mRNA-capping-enzyme
CG5688	31	1	Grip163
CG2064	31	1	CG2064
CG10315	31	1	eIF2B-δ
CG2692	30	2	gooseberry-neuro
CG16973	30	2	misshapen
CG7041	30	1	HP15
CG3004	30	1	CG3004
CG3714	30	1	CG3714
CG6509	30	1	Discs large 5
CG13277	30	1	CG13277
CG1512	30	1	Cullin-2
CG8632	30	1	Zinc transporter 49B
CG15099	30	1	CG15099
CG0000	29	1	CTINKIEG Ran GTPasa activating protein
CG15603	29	1	Ribosomal protein \$20
CG1100	29	2	Rpn5
CG12225	29	1	Spt6
CG2941	29	1	CG2941
CG6428	29	1	CG6428
CG7865	29	1	PNGase-like
CG8983	29	1	ERp60
CG3996	20	2	/ / / / / / / / / / / / / / / / / / / /
CG12070	29	2	CG3996 Sanosin-related
CG12070 CG16721	29 28 28	2 1 1	CG3996 Saposin-related CG16721

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	CG4097	21	1	Proteasome 26kD subunit

CG3431	21	1	Ubiquitin C-terminal hydrolase
CG2168	21	1	Ribosomal protein S3A
CG5796	21	1	Protoporphyrinogen oxidase
CG9291	21	1	Elongin C
CG15667	21	1	Smad anchor for receptor activation
			Mitochondrial phosphate carrier
CG4994	21	1	protein
CG4218	21	1	CG4218
CG10778	21	1	CG10778
			Required for cell differentiation 1
CG14213	21	1	ortholog
CG17593	21	1	CG17593
CG11887	21	2	Elongator complex protein 2
CG18176	21	1	deflated
CG3711	21	1	CG3711
CG33715	21	1	Muscle-specific protein 300
CG6551	20	1	fused
CG1112	20	1	α-Esterase-7
CG9212	20	1	Nipsnap
CG13096	20	1	CG13096
CG8709	20	1	Lipin
CG8332	20	1	Ribosomal protein S15
			Organic anion transporting polypeptide
CG3382	20	1	58Db
CG6432	20	1	CG6432
CG4849	20	1	CG4849
CG12750	20	1	nucampholin
CG11471	19	1	Isoleucyl-tRNA synthetase
CG5729	19	1	Dgp-1
00(710	10		calcium-independent phospholipase A2
CG6/18	19	1	VIA
CG10585	19	1	CG10585
CG6042	19	1	Cyp12a4
CG10712	19	1	Chromator
CG15105	18	1	another B-box affiliate
CG6811	18	1	RhoGAP68F
	-		
CG3359	18	1	midline fasciclin
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CG3359 CG8014 CG13325	18 17 17	1 1 1	Receptor mediated endocytosis 8 CG13325

Appendix B: Autoradiograms of *in vitro* studies.

A-H showing autoradiographic signals from binding assays of ³⁵S-Methionine-labelled centriole duplication proteins with (A) GST-Ana2, (B) AsI-GST, (C) GST-Cep97, (D) GST-CP110 1/3, (E) GST-CP110 3/3, (F) MBP-Plk4, (G) GST-Rcd4, and (H) GST-Sas4 immobilised on resin; the according negative control (GST- or MBP-alone immobilised on resin; and 1% input of the ³⁵S-Methionine-labelled centriole duplication protein used in each binding assay. Autoradiographic signals were applied to categorise the analysed direct protein-protein interactions into weak, good, strong and no interaction in Table 3-3.





A) In vitro interaction with GST-Ana2



B) In vitro Interaction with AsI-GST



C) In vitro interaction with GST-Cep97

E) In vitro interaction with GST-CP110 2/3



D) In vitro Interaction with GST-CP110 1/3



F) In vitro Interaction with MBP-PIk4









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Appendix C: Mass spectrometry results from purifications of centriole duplication proteins from cultured *Drosophila* cells and syncytial *Drosophila* embryos.

Tables show the full list of hits identified from the stated purification; indicating CG numbers, Mascot scores, Number of peptides (#pep), and the Full name of the protein if available. Tables are supplementary to Table 5-1 and Table 5-2.

C.1 pMT-PrA-Sas6 +MG132 purification from Drosophila cells

CG #	Score	#pep	Full name
CG15524	4576	281	spindle assembly abnormal 6
CG4264	1587	111	Heat shock protein cognate 4
CG9277	1404	51	β-Tubulin at 56D
CG1913	919	47	α-Tubulin at 84B
CG3401	329	19	β-Tubulin at 60D
CG5834	299	23	Hsp70Bbb
CG1524	223	6	Ribosomal protein S14a
CG4463	198	9	Heat shock protein 23
CG7434	175	6	Ribosomal protein L22
CG2960	139	4	Ribosomal protein L40
CG12051	114	5	Actin 42A
CG4466	94	3	Heat shock protein 27
CG11522	87	3	Ribosomal protein L6
CG8274	84	2	Megator
CG15697	84	3	Ribosomal protein S30
CG4183	83	3	Heat shock protein 26
CG3201	81	3	Myosin light chain cytoplasmic
CG6684	76	2	Ribosomal protein S25
CG10944	76	4	Ribosomal protein S6
CG12775	73	1	Ribosomal protein L21
CG33052	69	5	CG33052
CG7808	64	3	Ribosomal protein S8
CG6253	62	3	Ribosomal protein L14
CG9282	61	3	Ribosomal protein L24
CG13389	60	2	Ribosomal protein S13
CG11276	59	1	Ribosomal protein S4
CG1354	59	3	CG1354
CG9795	57	1	CG9795
CG4087	56	2	Ribosomal protein LP1
CG2746	56	1	Ribosomal protein L19
CG3395	54	3	Ribosomal protein S9
CG10824	54	1	Common Dpr-interacting protein
CG8900	52	1	Ribosomal protein S18
CG10465	50	2	CG10465

CG1873	49	1	Elongation factor 1a100E
CG15442	49	1	Ribosomal protein L27A
CG7622	48	1	Ribosomal protein L36
CG12109	47	2	Caf1-180
CG2168	46	2	Ribosomal protein S3A
CG11734	46	1	HERC2
CG5119	44	1	polyA-binding protein
CG4651	44	1	Ribosomal protein L13
CG1821	44	1	Ribosomal protein L31
CG3203	44	1	Ribosomal protein L17
CG8615	44	2	Ribosomal protein L18
CG2050	42	2	modulo
CG4863	42	1	Ribosomal protein L3
CG9680	41	1	Dead box protein 73D
CG2998	41	1	Ribosomal protein S28b
CG17521	40	1	Qm
CG4897	38	2	Ribosomal protein L7
CG14025	37	1	Blastoderm-specific gene 25D
CG5920	35	1	string of pearls
CG3253	35	1	CG3253
CG7490	34	1	Ribosomal protein LP0
CG4631	34	2	CG4631
CG8735	34	1	CG8735
CG17034	34	1	CG17034
CG7946	31	1	CG7946
CG6846	30	1	Ribosomal protein L26
CG8415	29	1	Ribosomal protein S23
CG8947	28	1	26-29kD-proteinase
CG1506	27	1	Ac3
CG31551	27	2	CG31551
CG7283	25	1	Ribosomal protein L10Ab
CG6773	0	1	sec13

C.2 pMT-PrA-Sas6 +OA +MG132 purification from Drosophila cells

CG #	Score	#pep	Full name
CG15524	4606	280	spindle assembly abnormal 6
CG15792	1530	86	zipper
CG4264	1499	83	Heat shock protein cognate 4
CG4027	974	45	Actin 5C
CG1913	710	36	α-Tubulin at 84B
CG10067	558	23	Actin 57B
CG9277	296	16	β-Tubulin at 56D
CG2960	263	8	Ribosomal protein L40
CG3201	261	14	Myosin light chain cytoplasmic
CG3595	122	6	spaghetti squash
CG4183	102	5	Heat shock protein 26
CG8274	81	3	Megator
CG2050	64	4	modulo
CG8578	61	1	CG8578
CG4145	58	1	Collagen type IV
CG4463	55	1	Heat shock protein 23
CG33052	55	2	CG33052
CG8472	54	2	Calmodulin

CG7438	42	2	Myosin 31DF
CG17158	41	1	capping protein beta
CG4466	39	1	Heat shock protein 27
CG8280	38	1	Elongation factor 1a48D
CG5588	38	1	Mig-2-like
CG8735	37	2	CG8735
CG13708	36	1	CG13708
CG17034	34	1	CG17034
CG13624	32	1	Repressed by TOR
CG32025	32	1	desert
CG33958	31	1	CG33958
CG4898	30	1	Tropomyosin 1
CG7595	29	1	crinkled
CG11384	29	1	CG11384
CG3253	29	1	CG3253
CG31551	26	2	CG31551
CG4444	25	1	plexus
CG6428	0	1	CG6428

C.3 pUb-Sas6-GFP purification from syncytial Drosophila embryos

CG #	Score	#pep	Full name
CG15524	13751	272	spindle assembly abnormal 6
CG33052	6514	105	CG33052
CG4264	1134	25	Heat shock protein cognate 4
CG11129	1022	14	Yolk protein 3

CG2985	719	13	Yolk protein 1
CG9277	619	10	β-Tubulin at 56D
CG9277	549	8	β-Tubulin at 56D
CG9277	549	8	β-Tubulin at 56D
CG1913	482	10	α-Tubulin at 84B

CG8280	473	10	Elongation factor 1a48D
CG2979	462	8	Yolk protein 2
CG9359	441	6	β-Tubulin at 85D
CG4634	407	6	Nucleosome remodeling factor - 38kD
CG5261	354	8	CG5261
CG5261	337	7	CG5261
CG9476	306	7	α-Tubulin at 85E
CG7660	283	4	pxt
CG8937	243	6	Heat shock protein cognate 1
CG5436	229	5	Heat shock protein 68
CG8251	221	2	Phosphoglucose isomerase
CG8262	219	4	anastral spindle 2
CG4147	207	5	Heat shock 70-kDa protein cognate 3
CG8937	181	3	Heat shock protein cognate 1
CG8937	181	3	Heat shock protein cognate 1
CG7756	178	4	Heat shock protein cognate 2
CG1873	169	4	Elongation factor 1g100E
CG1873	169	4	Elongation factor 1/100E
CG1873	169	4	Elongation factor 1g100E
CG1873	160	4	Elongation factor 1g100E
CG4869	164	2	B-Tubulin at 97FF
CG8963	146	2	CG8963
CG8/39	140	2	T-complex Chaperonin 5
CG0457	150	2	Cullin-associated and neddylation-
CG5366	134	2	dissociated 1
CG11793	121	1	Superovide dismutase
CG1633	110	3	thioredoxin peroxidase 1
CG1782	117	2	Libiquitin activating enzyme 1
CG5252	105	1	Ranhn0
CG4898	103	2	Tropomyosin 1
CG1489	104	1	Regulatory particle triple A ATPase 6
CG11876	101	2	CG11876
CG12233	00	2	lethal (1) G0156
CG17246	07	3	Succinate debudrogenase A
CG17240	71	5	Ubiquinol-cytochrome c reductase core
CG4169	96	1	protein 2
CG4254	95	1	twinstar
CG3024	95	1	Torsin
CG8947	90	1	26-29kD-proteinase
CG6439	88	2	CG6439
CG4898	87	1	Tropomyosin 1
CG4898	87	1	Tropomyosin 1
CG4898	87	1	Tropomyosin 1
CG4898	87	1	Tropomyosin 1
CG7010	85	1	lothal (1) G0224
CG3751	85	1	Ribosomal protein \$24
CG4581	78	1	Thiolase
CG8351	78	1	Tep-1n
CG5374	75	2	Tep-III
CG3612	75		hellwether
003012	15	1	Eukaruotia initiation factor 2 = 40
CG9124	74	1	subunit
CG14792	73	1	stubarista
1 0017/74	1.5		5100/01/510

CG3455	72	1	Regulatory particle triple-A ATPase 4
CG17754	72	3	CG17754
CG2960	71	2	Ribosomal protein L40
CG6186	71	1	Transferrin 1
CG2982	66	1	CG2982
CG11276	65	1	Ribosomal protein S4
CG32855	64	7	CG32855
CG10811	63	1	eukaryotic translation initiation factor 4G
CG14648	62	1	growl
CG8893	61	1	Glyceraldehyde 3 phosphate dehydrogenase 2
CG3203	61	1	Ribosomal protein L17
CG2048	59	1	discs overgrown
CG4916	59	1	maternal expression at 31B
CG8231	56	1	T-cp1ζ
CG1242	55	1	Heat shock protein 83
CG10489	55	1	Pole2
CG7583	52	1	C-terminal Binding Protein
CG17333	51	1	CG17333
CG12708	51	2	CG12708
CG7490	49	2	Ribosomal protein LP0
CG8308	49	1	α-Tubulin at 67C
CG5330	48	1	Nucleosome assembly protein 1
CG6598	47	1	Formaldehyde dehydrogenase
CG2151	47	1	Thioredoxin reductase-1
CG5119	47	1	polyA-binding protein
CG3201	44	1	Myosin light chain cytoplasmic
CG7425	42	1	effete
CG10045	41	1	Glutathione S transferase D1
CG11512	41	1	Glutathione S transferase D4
CG8542	36	1	Heat shock protein cognate 5
CG8740	35	1	CG8740
CG8905	34	1	Superoxide dismutase 2 (Mn)
CG5371	34	1	Ribonucleoside diphosphate reductase large subunit
CG4200	33	1	small wing
CG2168	33	1	Ribosomal protein S3A
CG9913	33	1	Kinesin family member 19A ortholog
CG11522	33	1	Ribosomal protein L6
CG13387	32	1	embargoed
CG12836	32	1	CG12836
CG17870	31	1	14-3-3ζ
CG32683	31	1	CG32683
CG2925	30	1	noisette
CG14206	30	1	Ribosomal protein S10b
CG5098	30	1	CG5098

C.4 pUb-Sas6-GFP purification from syncytial *Drosophila* embryos with 440mM NaCl concentration (high salt)

CG #	Score	#pep	Full name
CG15524	5900	123	spindle assembly abnormal 6
CG33052	1641	27	CG33052
CG4264	933	21	Heat shock protein cognate 4
CG1913	458	7	α-Tubulin at 84B
CG2979	455	8	Yolk protein 2
CG8280	440	11	Elongation factor 1a48D
CG4634	436	8	Nucleosome remodeling factor - 38kD
CG9277	433	10	β-Tubulin at 56D
CG4634	407	7	Nucleosome remodeling factor - 38kD
CG7808	361	6	Ribosomal protein S8
CG9277	326	9	β-Tubulin at 56D
CG9476	323	5	α-Tubulin at 85E
CG4916	311	7	maternal expression at 31B
CG11129	309	4	Yolk protein 3
CG1782	309	6	Ubiquitin activating enzyme 1
CG1873	280	7	Elongation factor 1a100E
CG1873	280	7	Elongation factor 1a100E
CG1873	280	7	Elongation factor 1a100E
CG1873	280	7	Elongation factor 1a100E
CG17246	276	5	Succinyl coenzyme A synthetase flavoprotein subunit
CG9277	273	8	β-Tubulin at 56D
CG9277	273	8	β-Tubulin at 56D
CG7660	268	3	pxt
CG4147	258	4	Heat shock protein cognate 3
CG8937	226	4	Heat shock protein cognate 1
CG8251	216	3	Phosphoglucose isomerase
CG2985	216	4	Yolk protein 1
CG16944	212	4	stress-sensitive B
CG2168	207	5	Ribosomal protein S3A
CG8308	201	2	α-Tubulin at 67C
CG8937	191	3	Heat shock protein cognate 1
CG8937	191	3	Heat shock protein cognate 1

	CG5252	191	2	Ranbp9
ſ	CG4169	186	2	CG4169
ſ	CG9359	179	6	β-Tubulin at 85D
ſ	CG5920	173	3	Ribosomal protein S2
ľ	CG7033	173	2	CG7033
ſ	CG10489	168	2	Pole2
ſ	CG5436	166	2	Heat shock protein 68
ſ	CG3922	166	4	Ribosomal protein S17
	CG8947	166	2	26-29kD-proteinase
ſ	CG8262	164	2	anastral spindle 2
ſ	CG7014	155	2	Ribosomal protein S5b
[CG6439	153	4	CG6439
	CG2168	148	3	Ribosomal protein S3A
ſ	CG6235	145	2	twins
ſ	CG1349	144	3	dj-1β
[CG4863	139	3	Ribosomal protein L3
ſ	CG10686	136	2	trailer hitch
ſ	CG8900	134	3	Ribosomal protein S18
ſ	CG17521	133	1	Ribosomal protein L10
ſ	CG9748	124	1	belle
[CG8231	115	2	T-cp1ζ
ſ	CG4254	114	1	twinstar
	CG5371	113	3	Ribonucleoside diphosphate reductase large subunit
ſ	CG6779	112	2	Ribosomal protein S3
I	CG5366	112	1	Cullin-associated and neddylation- dissociated 1
ſ	CG2238	111	2	Elongation factor 2b
ſ	CG3195	111	2	Ribosomal protein L12
	CG6253	110	2	Ribosomal protein L14
ſ	CG1633	110	2	thioredoxin peroxidase 1
ſ	CG8439	106	2	T-complex Chaperonin 5
[CG7490	105	2	Ribosomal protein LP0
Г	CG10535	101	1	Elongator complex protein 1

CG11276	99	2	Ribosomal protein S4
CG8857	94	2	Ribosomal protein S11
CG13281	93	1	CAS/CSE1 segregation protein
CG11943	93	2	Nucleoporin 205
CG3612	92	1	bellwether
CG10652	92	1	Ribosomal protein L30
CG3752	91	1	Aldehyde dehydrogenase
CG1837	91	1	pretaporter
GG 0000			Glyceraldehyde 3 phosphate
CG8893	90	1	dehydrogenase 2
CG33180	88	1	Ranbp16
CG2960	87	2	Ribosomal protein L40
CG8415	87	1	Ribosomal protein S23
CG11522	87	1	Ribosomal protein L6
CG7340	87	1	granny smith
CG3661	84	2	Ribosomal protein L23
CG6543	84	1	CG6543
CG3751	84	1	Ribosomal protein S24
CG11793	83	1	Superoxide dismutase
CG1129	83	1	CG1129
CG12101	82	1	Heat shock protein 60
CG6186	82	1	Transferrin 1
CG1372	81	1	yolkless
CG2151	81	1	Thioredoxin reductase-1
CG2046	80	1	CG2046
CG9075	79	1	Eukaryotic initiation factor 4a
CG3203	79	1	Ribosomal protein L17
CG8922	77	1	Ribosomal protein S5a
CG17286	76	1	spindle defective 2
CG17291	75	1	Protein phosphatase 2A at 29B
CG3401	74	1	β-Tubulin at 60D
CG4869	74	1	β-Tubulin at 97EF
CG4869	74	1	β-Tubulin at 97EF
CG11154	74	1	ATP synthase, β subunit
CG6180	74	1	CG6180
CG8963	74	1	CG8963
CG1218	73	1	CG1218
CG6513	73	1	endosulfine
CG9677	70	1	Int6 homologue
CG12202	68	1	Nat1
CG12233	67	2	lethal (1) G0156
CG4898	65	2	Tropomyosin 1
CG1945	65	1	fat facets
CG15442	65	1	Ribosomal protein L27A
CG4087	64	1	Ribosomal protein LP1
CG6141	61	1	Ribosomal protein L9
CG4581	61	1	Thiolase
CG9769	61	1	CG9769
CG11001	60	1	FK506-binding protein 2
CG7111	60	1	Receptor of activated protein kinase C
CG17333	60	1	CG17333
CG9282	60	1	Ribosomal protein L24
CG3379	59	1	Histone H4 replacement
CG3455	58	1	Regulatory particle triple-A ATPase 4
CG17566	55	1	γ-Tubulin at 37C
CG6852	54	1	CG6852
CG10198	54	1	Nucleoporin 98-96
CG8740	53	4	CG8740
CG1683	52	1	Adenine nucleotide translocase 2

Correst 1 Ribosomal protein S30 CG15697 52 1 Ribosomal protein S30 CG1524 49 1 Ribosomal protein S30 CG2982 49 1 CG2982 CG6004 48 1 Glycogen synthase CG4046 47 1 Ribosomal protein S16 CG8925 47 1 Ribosomal protein S29 CG11064 45 1 Retinoid- and fatty acid-binding glycoprotein CG9012 44 1 Clathrin heavy chain CG18572 44 1 Ribosomal protein S9 CG13822 44 1 Ribosomal protein S9 CG1754 42 1 CG4408 CG31618 41 1 mis2A:CG31618 CG1764 1 1 Ribosomal protein L38 CG1604 1 Ribosomal protein S0 CG1708 39 1 CG12708 CG17040 38 1 14-3-3ζ CG7400 38 1 <th>CG1683</th> <th>52</th> <th>1</th> <th>Adenine nucleotide translocase 2</th>	CG1683	52	1	Adenine nucleotide translocase 2
CG1523 42 1 Ribosomal protein S14a CG2982 49 1 CG2982 CG4046 47 1 Ribosomal protein S16 CG4046 47 1 Ribosomal protein S16 CG4046 47 1 Retinoid- and fatty acid-binding glycoprotein CG9012 44 1 Clathrin heavy chain CG18572 44 1 Retinoid- and fatty acid-binding glycoprotein CG3395 44 1 Ribosomal protein S9 CG13822 44 1 Ribosomal protein S9 CG13822 44 1 CG4408 CG1382 41 1 rough deal CG1382 41 1 Ribosomal protein S16 CG1382 41 1 Ribosomal protein S16 CG1380 42 1 CG4408 CG16169 41 1 Ribosomal protein S3 CG1208 39 1 CG1208 CG1204 39 1 CG1208 CG	CG15697	52	1	Ribosomal protein \$30
CG122 49 1 CG2982 CG2904 48 1 Glycogen synthase CG4046 47 1 Ribosomal protein S16 CG8495 47 1 Ribosomal protein S29 CG11064 45 1 Retinoid- and fatty acid-binding glycoprotein CG3395 44 1 Clathrin heavy chain CG13822 44 1 Ribosomal protein S9 CG13822 44 1 Clathrin heavy chain CG13822 44 1 Clathrin heavy chain CG1382 44 1 Clathrin heavy chain CG1401 40 1 Ribosomal protein L38 CG1708 9 1 CG12708	CG1524	49	1	Ribosomal protein S14a
CG6904 48 1 Clocogen synthase CG4046 47 1 Ribosomal protein S16 CG4046 47 1 Ribosomal protein S29 CG11064 45 1 Retinoid- and fatty acid-binding glycoprotein CG102 44 1 Clathrin heavy chain CG18572 44 1 Ribosomal protein S9 CG13822 44 1 Ribosomal protein S9 CG13822 44 1 Gamma-interferon-inducible lysosomal thiol reductase 3 CG17754 42 1 CG4408 CG16754 42 1 CG4408 CG1764 42 1 Ribosomal protein L38 CG16769 41 1 His2A:CG31618 CG18001 40 1 Ribosomal protein L38 CG1270 39 1 CG12708 CG1770 38 1 14-3-3ζ CG10045 37 1 Glutathione S transferase D1 CG1045 37 1 Glutathione S transferas	CG2982	49	1	CG2982
CG4046 47 1 Ribosomal protein S16 CG4046 47 1 Ribosomal protein S29 CG11064 45 1 Retinoid- and fatty acid-binding glycoprotein CG9012 44 1 Clathrin heavy chain CG18572 44 1 Rotinoid- and fatty acid-binding glycoprotein CG3395 44 1 Rotinoid- and fatty acid-binding glycoprotein CG13822 44 1 Rotinoid- and fatty acid-binding glycoprotein CG1784 2 1 CG17754 CG4048 42 1 CG17754 CG1786 41 1 rough deal CG1859 41 1 Robosomal protein L38 CG10944 40 1 Ribosomal protein S3 CG12708 39 1 CG12708 CG1780 38 1 14-3-3ζ CG7400 38 1 Fatty acid (long chain) transport protein CG1770 37 2 IdICp-related protein CG173 37	CG6904	48	1	Glycogen synthase
CG8495 47 1 Ribosomal protein S29 CG11064 45 1 Retinoid- and fatty acid-binding glycoprotein CG9012 44 1 Clattrin heavy chain CG13822 44 1 Ribosomal protein S9 CG13822 44 1 Ribosomal protein S9 CG13822 44 1 Gamma-interferon-inducible lysosomal thiol reductase 3 CG1754 42 1 CG4408 CG1656 41 1 rough deal CG1801 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG1708 39 1 CG12708 CG1040 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 Argonaute 2 CG7400 38 1 Fatty acid (long chain) transport protein CG1045 37 1 Glutathione S transferase D1 CG2048	CG4046	47	1	Ribosomal protein \$16
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CGI 1064 45 1 Refinition and vy factoring glycoprotein CG9012 44 1 Clathrin heavy chain CG18572 44 1 Ribosomal protein S9 CG3395 44 1 Ribosomal protein S9 CG13822 44 1 Ribosomal protein S9 CG1754 42 1 CG4764 CG408 42 1 CG4764 CG1754 42 1 CG4764 CG1754 CG400 41 1 CG1754 CG17754 CG400 1 CG1764 42 1 CG4708 CG1800 40 1 Ribosomal protein 128 CG19208 39 1 Heat shock protein 83 CG1270 38 1 14-3-3\zeta CG7400 38 1 Fatty acid (long chain) transport protein CG102045 37 1 discs overgrown CG6177 37 2 IdICp-related protein CG7439 37	000475		•	Retinoid, and fatty acid-binding
CG9012 44 1 Clathrin heavy chain CG18572 44 1 rudimentary CG3395 44 1 Ribosomal protein S9 CG13822 44 1 Gamma-interferon-inducible lysosomal thiol reductase 3 CG1754 42 1 CG1754 CG4008 42 1 CG1754 CG1754 42 1 CG1754 CG1754 42 1 CG1408 CG1569 41 1 rough deal CG18001 40 1 Ribosomal protein L38 CG1242 39 1 Heat shock protein 83 CG12708 39 1 CG12708 CG7400 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 Argonaute 2 CG8036 36 1 CG8036 CG177 37 2 IdICp-related protein CG1639 <td< td=""><td>CG11064</td><td>45</td><td>1</td><td>glycoprotein</td></td<>	CG11064	45	1	glycoprotein
CG18572 44 1 rudimentary CG3395 44 1 Ribosomal protein S9 CG13822 44 1 Gamma-interferon-inducible lysosomal thiol reductase 3 CG1754 42 1 CG17754 CG408 42 1 CG17754 CG408 42 1 CG17754 CG1569 41 1 rough deal CG31618 41 1 Ribosomal protein L38 CG1202 39 1 Ribosomal protein S6 CG12108 39 1 CG12708 CG1707 38 1 14.3-3ζ CG7400 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG1503 35 1 Ribosomal protein S20 CG4398 34 1 Tropomyosin 1 CG4898 34 1 Tropomyosin 1 CG4898	CG9012	44	1	Clathrin heavy chain
CG3395 44 1 Ribosomal protein S9 CG13822 44 1 Gamma-interferon-inducible lysosomal thiol reductase 3 CG17754 42 1 CG17754 CG4408 42 1 CG17754 CG4108 42 1 CG17754 CG31618 41 1 rough deal CG31618 41 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG17870 38 1 14-3-3ζ CG17870 38 1 Fatty acid (long chain) transport protein CG17040 38 1 Glutathione S transferase D1 CG1048 37 1 Glutathione S transferase D1 CG400 36 1 Puromycin sensitive aminopeptidase CG1773 7 2 IdICp-related protein CG6177 37 2 IdICp-related protein CG45693 35 1 Ruboso	CG18572	44	1	rudimentary
CG13822 44 1 Gamma-interferon-inducible lysosomal thiol reductase 3 CG17754 42 1 CG1754 CG4408 42 1 CG47754 CG1754 42 1 CG4408 CG1569 41 1 rough deal CG31618 41 1 His2A:CG31618 CG10944 40 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein L38 CG1270 39 1 Heat shock protein 83 CG1770 38 1 14-3-3 ζ CG7400 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 Argonaute 2 CG6036 36 1 Puromycin sensitive aminopeptidase CG1437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 <td>CG3395</td> <td>44</td> <td>1</td> <td>Ribosomal protein S9</td>	CG3395	44	1	Ribosomal protein S9
CG1322 44 1 thiol reductase 3 CG1754 42 1 CG17754 CG4408 42 1 CG4408 CG1569 41 1 rough deal CG31618 41 1 Ribosomal protein L38 CG1904 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG1708 39 1 CG12708 CG7400 38 1 14.3-3ζ CG7400 38 1 Fatty acid (long chain) transport protein CG1045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG1737 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 Tropomyosin 1 CG4898 34 1 Tropomyosin 1 CG4898 34	0012822	4.4	1	Gamma-interferon-inducible lysosomal
CG17754 42 1 CG17754 CG4408 42 1 CG4408 CG1569 41 1 rough deal CG31618 41 1 His2A:CG31618 CG1901 40 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein S3 CG1242 39 1 Heat shock protein 83 CG1708 39 1 CG12708 CG1770 38 1 14-3-3; CG7400 38 1 Gltathione S transferase D1 CG0045 37 1 Gltathione S transferase D1 CG1049 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 Tropomyosin 1 CG4898 34 1 Tropomyosin 1 CG4898 34	CG13822	44	1	thiol reductase 3
CG4408 42 1 CG4408 CG1569 41 1 rough deal CG31618 41 1 His2A:CG31618 CG18001 40 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG1708 39 1 CG12708 CG1770 38 1 14-3-3ζ CG7400 38 1 Fatty acid (long chain) transport protein CG1045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG6177 37 2 IdICp-related protein CG7439 37 1 Argonaute 2 CG8036 6 1 CG8036 CG1009 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34	CG17754	42	1	CG17754
CG1569 41 1 rough deal CG31618 41 1 His2A:CG31618 CG18001 40 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG12708 39 1 CG12708 CG17870 38 1 14.3-3ζ CG7400 38 1 Fatty acid (long chain) transport protein CG10870 37 1 Glutathione S transferase D1 CG2048 37 1 Argonaute 2 CG6177 37 2 IdlCp-related protein CG7439 37 1 Argonaute 2 CG8036 36 1 CG8036 CG1009 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898<	CG4408	42	1	CG4408
CG31618 41 1 His2A:CG31618 CG18001 40 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein S6 CG12708 39 1 Heat shock protein 83 CG12708 39 1 $CG12708$ CG7470 38 1 $14-3.3\zeta$ CG7400 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG170 37 2 Idl/Cp-related protein CG7430 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1	CG1569	41	1	rough deal
CG18001 40 1 Ribosomal protein L38 CG10944 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG12708 39 1 CG12708 CG17870 38 1 14:3-3ζ CG1708 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG6177 37 2 IdICp-related protein CG7439 37 1 Argonaute 2 CG8036 6 1 CG8036 CG1009 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 <td< td=""><td>CG31618</td><td>41</td><td>1</td><td>His2A:CG31618</td></td<>	CG31618	41	1	His2A:CG31618
CG10944 40 1 Ribosomal protein S6 CG1242 39 1 Heat shock protein 83 CG12708 39 1 CG12708 CG17700 38 1 14-3-3 ζ CG7400 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 Argonaute 2 CG6045 37 1 Argonaute 2 CG6036 6 1 CG8036 CG1009 36 1 Puromycin sensitive aminopeptidase CG1437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 <	CG18001	40	1	Ribosomal protein L38
CG1242 39 1 Heat shock protein 83 CG12708 39 1 CG12708 CG17870 38 1 Fatty acid (long chain) transport protein CG10870 38 1 Fatty acid (long chain) transport protein CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG6177 37 2 IdICp-related protein CG7439 37 1 Argonaute 2 CG8036 36 1 CG8036 G1009 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1	CG10944	40	1	Ribosomal protein S6
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG1242	39	1	Heat shock protein 83
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG12708	39	1	CG12708
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG17870	38	1	14-3-3ζ
CG10045 37 1 Glutathione S transferase D1 CG2048 37 1 discs overgrown CG6177 37 2 ldlCp-related protein CG7439 37 1 Argonaute 2 CG8036 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 Cf017904 CG17904 <	CG7400	38	1	Fatty acid (long chain) transport protein
CG2048 37 1 discs overgrown CG6177 37 2 IdICp-related protein CG7439 37 1 Argonaute 2 CG8036 36 1 CG8036 CG1009 36 1 Puromycin sensitive aminopeptidase CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG17904 CG17904 34 1 CG17904	CG10045	37	1	Glutathione S transferase D1
CG6177 37 2 IdlCp-related protein CG7439 37 1 Argonaute 2 CG8036 36 1 CG8036 CG1009 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG17904 CG17904 34 1 CG17	CG2048	37	1	discs overgrown
CG7439 37 1 Argonaute 2 CG8036 36 1 CG8036 CG1009 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG17904 CG17904 2 CG122 2 CG32015 33 1 CG32015 <td>CG6177</td> <td>37</td> <td>2</td> <td>ldlCp-related protein</td>	CG6177	37	2	ldlCp-related protein
CG8036 36 1 CG8036 CG1009 36 1 Puromycin sensitive aminopeptidase CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 Cf07904 CG4898 34 1 CG17904 CG10704 34 1 CG17904 CG5122 33 1 CG3140 CG34015 33 1 CG3120 <tr< td=""><td>CG7439</td><td>37</td><td>1</td><td>Argonaute 2</td></tr<>	CG7439	37	1	Argonaute 2
CG1009 36 1 Puromycin sensitive aminopeptidase CG1373 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 <td< td=""><td>CG8036</td><td>36</td><td>1</td><td>CG8036</td></td<>	CG8036	36	1	CG8036
CG7437 36 1 mushroom-body expressed CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG17904 CG1904 34 1 CG17904 CG121 33 1 CG3245	CG1009	36	1	Puromycin sensitive aminopeptidase
CG15693 35 1 Ribosomal protein S20 CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG0000000 CG17904 34 1 CG17904 CG1201 34 1 CG122 CG32015 33 1 CG31015 CG123015 32 1 CG12836 CG1236	CG7437	36	1	mushroom-body expressed
CG4898 34 1 Tropomyosin 1 CG4898 34 1 Cforpomyosin 1 CG1704 34 1 Cfl7904 CG5122 33 1 CG5122 <t< td=""><td>CG15693</td><td>35</td><td>1</td><td>Ribosomal protein S20</td></t<>	CG15693	35	1	Ribosomal protein S20
CG4898 34 1 Tropomyosin 1 CG4994 34 1 CG17904 CG1904 34 1 CG17904 CG10338 34 1 CG17904 CG121 33 1 CG5122 CG31015 33 1 CG3205 CG12336	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG4898 34 1 Copmyosin 1 CG4898 34 1 Cropomyosin 1 CG4898 34 1 Copmyosin 1 CG1704 34 1 CG17904 CG171 34 1 CdGAPr CG32171 34 1 CG3205 CG12306 32 1 CG12836 CG12306 32 1 CG120306 CG12306 <	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG007904 CG17904 34 1 CG17904 CG1038 34 1 CG17904 CG10318 34 1 CG17904 CG10318 34 1 CG17904 CG32015 33 1 CG122 CG34015 33 1 CG1236 CG1236 32 1 CG10306 CG1236 32 1 CG10306 CG1239 31 1 Ulp1 CG32855 31 1 <td>CG4898</td> <td>34</td> <td>1</td> <td>Tropomyosin 1</td>	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG4898 34 1 Cf17904 CG10538 34 1 CG17904 CG10538 34 1 CG17904 CG10538 34 1 CG17904 CG10512 33 1 CG6APr CG2171 34 1 Trise phosphate isomerase CG5122 33 1 CG324015 CG1236 32 1 CG12336 CG10306 32 1 CG12336 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG4898 34 1 CG17904 CG17904 34 1 CG17904 CG1710 34 1 CG17904 CG5122 33 1 CG5122 CG34015 33 1 CG34015 CG12836 32 1 CG10306 CG10306 32 1 CG10306 CG10306 32 1 CG10306 CG6084 32 1 CG10306 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 </td <td>CG4898</td> <td>34</td> <td>1</td> <td>Tropomyosin 1</td>	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG17904 34 1 CG17904 CG1701 34 1 CdGAPr CG5122 33 1 CG5122 CG34015 33 1 CG32015 CG12036 32 1 CG10306 CG10306 32 1 CG10306 CG12359 31 1 Ulp1 CG32855 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG3283	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG4898 34 1 Tropomyosin 1 CG17904 34 1 Tropomyosin 1 CG17904 34 1 CG17904 CG10538 34 1 CG17904 CG10538 34 1 CGAPr CG2171 34 1 Trise phosphate isomerase CG5122 33 1 CG312 CG34015 33 1 CG34015 CG12836 32 1 CG12836 CG10306 32 1 CG10306 CG10306 32 1 CG10306 CG12837 31 1 Ulp1 CG32855 31 1 Ulp1 CG32055 30 1 Discs large 5 CG32683 30 1 CG3283	CG4898	34	1	Tropomyosin 1
CG4898 34 1 Tropomyosin 1 CG17904 34 1 CG17904 CG10538 34 1 CG17904 CG10538 34 1 CGAPr CG2171 34 1 Trisse phosphate isomerase CG5122 33 1 CG5122 CG34015 33 1 CG34015 CG1236 32 1 CG12336 CG10306 32 1 CG12336 CG10306 32 1 CG10306 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6309 30 1 Discs large 5 CG32683 30 1 CG3283	CG4898	34	1	Tropomyosin 1
CG17904 34 1 CG17904 CG10538 34 1 CdGAPr CG2171 34 1 Triose phosphate isomerase CG5122 33 1 CG5122 CG34015 33 1 CG34015 CG12836 32 1 CG12836 CG10306 32 1 CG10306 CG6084 32 1 CG6084 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG3283	CG4898	34	1	Tropomyosin 1
CG10538 34 1 CdGAPr CG2171 34 1 Triose phosphate isomerase CG5122 33 1 CG5122 CG34015 33 1 CG34015 CG12836 32 1 CG12836 CG10306 32 1 CG10306 CG6084 32 1 CG10306 CG12835 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6309 30 1 Discs large 5 CG32683 30 1 CG3283	CG17904	34	1	CG17904
CG2171 34 1 Triose phosphate isomerase CG5122 33 1 CG5122 CG34015 33 1 CG34015 CG1285 32 1 CG12836 CG10306 32 1 CG12836 CG10306 32 1 CG10306 CG12359 31 1 Up1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG62663 30 1 Discs large 5 CG32683 30 1 CG3283	CG10538	34	1	CdGAPr
CG5122 33 1 CG5122 CG34015 33 1 CG34015 CG12836 32 1 CG12836 CG10306 32 1 CG10306 CG6084 32 1 CG6084 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG2171	34	1	Triose phosphate isomerase
CG34015 33 1 CG34015 CG12836 32 1 CG12836 CG10306 32 1 CG10306 CG6084 32 1 CG10306 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG3283	CG5122	33	1	CG5122
CG12836 32 1 CG12836 CG10306 32 1 CG10306 CG6084 32 1 CG0306 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG34015	33	1	CG34015
CG10306 32 1 CG10306 CG6084 32 1 CG6084 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG12836	32	1	CG12836
CG6084 32 1 CG6084 CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG10306	32	1	CG10306
CG12359 31 1 Ulp1 CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG6084	32	1	CG6084
CG32855 31 1 CG32855 CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG12359	31	1	Ulp1
CG31062 30 1 sidestep CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG32855	31	1	CG32855
CG6509 30 1 Discs large 5 CG32683 30 1 CG32683	CG31062	30	1	sidestep
CG32683 30 1 CG32683	CG6509	30	1	Discs large 5
	CG32683	30	1	CG32683

C.5 pUb-Sas6-GFP +OA purification from syncytial *Drosophila* embryos with 440mM NaCl concentration (high salt)

CG #	Score	#pep	Full name
CG15524	4677	131	spindle assembly abnormal 6
CG33052	1380	27	CG33052
CG4264	586	12	Heat shock protein cognate 4
CG8280	292	7	Elongation factor 1a48D
CG4634	253	4	Nucleosome remodeling factor - 38kD
CG1913	210	4	α-Tubulin at 84B
CG1873	173	4	Elongation factor 1a100E
CG1873	173	4	Elongation factor 1a100E
CG1873	173	4	Elongation factor 1a100E
CG1873	173	4	Elongation factor 1a100E
CG8937	170	3	Heat shock protein cognate 1
CG9277	145	3	β-Tubulin at 56D
CG8937	138	2	Heat shock protein cognate 1
CG8937	138	2	Heat shock protein cognate 1
CG17246	135	3	Succinate dehydrogenase A
CG17521	123	2	Ribosomal protein L10
CG6235	114	1	twins
CG4147	112	1	Heat shock protein cognate 3
CG4147	112	1	Heat shock protein cognate 3
CG4147	112	1	Heat shock protein cognate 3
CG4147	112	1	Heat shock protein cognate 3
CG5436	112	1	Heat shock protein 68
CG2979	104	3	Yolk protein 2
CG3751	98	2	Ribosomal protein S24
CG6779	90	2	Ribosomal protein S3
CG4916	90	2	maternal expression at 31B

CG9359	85	2	β-Tubulin at 85D
CG5920	85	1	Ribosomal protein S2
CG8251	82	1	Phosphoglucose isomerase
CG10652	82	1	Ribosomal protein L30
CG3203	79	1	Ribosomal protein L17
CG2960	78	2	Ribosomal protein L40
CG10045	76	1	Glutathione S transferase D1
CG11512	76	1	Glutathione S transferase D4
CG5371	75	1	Ribonucleoside diphosphate reductase
005571	15	1	large subunit
CG8900	74	1	Ribosomal protein S18
CG6253	72	1	Ribosomal protein L14
CG9476	69	2	α-Tubulin at 85E
CG7660	68	1	Peroxinectin-like
CG3661	67	1	Ribosomal protein L23
CG4863	63	2	Ribosomal protein L3
CG8857	62	1	Ribosomal protein S11
CG10944	58	2	Ribosomal protein S6
CG1633	58	1	thioredoxin peroxidase 1
CG11276	56	1	Ribosomal protein S4
CG2168	54	1	Ribosomal protein S3A
CG11129	50	1	Yolk protein 3
0010011	40	1	eukaryotic translation initiation factor
CG10811	49	1	4G
CG7340	48	1	granny smith
CG8495	47	1	Ribosomal protein S29
CG10489	43	1	Pole2

CG4466	41	1	Heat shock protein 27
CG4898	39	1	Tropomyosin 1
CG12708	39	1	CG12708
CG10538	38	1	CdGAPr
CG8963	38	1	CG8963
CG2668	37	1	Protein ejaculatory bulb
CG3922	37	1	Ribosomal protein S17
CG17870	36	1	14-3-3ζ

CG4863	35	1	Ribosomal protein L3
CG4863	35	1	Ribosomal protein L3
CG8740	35	1	CG8740
CG4046	34	1	Ribosomal protein S16
CG32082	34	1	CG32082
CG6509	33	1	Discs large 5
CG12836	33	1	CG12836
CG6177	32	1	ldlCp-related protein

C.6 pUb-GFP-Dragon purification from Drosophila cells

CG #	Score	#pep	Full name
CG33052	18036	290	CG33052
CG4264	4556	65	Heat shock protein cognate 4
CG9277	4140	56	β-Tubulin at 56D
CG9277	3875	52	B-Tubulin at 56D
CG1012	2021	19	a Tubulin at 84P
001913	3031	40	d-Tubulili at 84B
CG8280	2423	38	Elongation factor 1a48D
CG17949	2364	37	His2B:CG17949
CG4147	2315	35	Heat shock 70-kDa protein cognate 3
CG3401	2055	34	β-Tubulin at 60D
CG9/76	1947	32	a-Tubulin at 85E
CC1528	1747	32	Cent Protein (centerner)
CG1528	1792	29	Coat Protein (coatomer) y
CG12051	1712	26	Actin 42A
CG4027	1575	25	Actin 5C
CG31613	1557	42	His3:CG31613
0010015	1510	42	0010065
CG12065	1513	30	CG12065
CG3379	1458	29	Histone H4 replacement
CG2238	1426	22	Elongation factor 2
CG9359	1367	29	β-Tubulin at 85D
CC8027	1224	14	Heat shock protein cognete 1
003937	1334	14	
CG33869	1314	25	His4:CG33869
CG5825	1290	42	Histone H3.3A
CG6223	1263	19	Coat Protein (coatomer) B
CG12065	1259	28	CG12065
0012003	1237	20	CG12003
CG10067	1255	17	Actin 57B
CG31618	1200	20	His2A:CG31618
CG7478	1157	15	Actin 79B
CG5520	1146	20	Glycoprotein 93
CC5179	1110	20	
CG5178	1112	16	Actin 88F
CG7961	1106	26	Coat Protein (coatomer) a
CG9748	1062	17	belle
CG8937	1038	9	Heat shock protein cognate 1
CC1972	1022	10	Elangetian faster 1a100E
C018/5	1052	19	Elongation factor 10100E
CG6718	1016	21	calcium-independent phospholipase
000/10	1010	21	A2 VIA
CG3752	903	11	Aldehvde dehvdrogenase
CG7/30	800	14	Argonaute 2
CC2216	077	14	Frankin 1 house she in house house
CG2210	880	10	Ferritin T neavy chain nonologue
CG10279	874	11	Rm62
CG4869	861	17	β-Tubulin at 97EF
CG2216	829	15	Ferritin 1 heavy chain homologue
CG9888	773	16	Fibrillarin
009888	773	10	Fibrinarin
CG9012	763	14	Clathrin heavy chain
CG5825	754	37	Histone H3.3A
CG2331	740	13	TER94
CG2216	711	14	Ferritin 1 heavy chain homologue
CC19742	706	0	Heat sheels protein 70 Ab
018/45	700	0	Heat-shock-protein-70A0
CG68/1	694	10	Catalase
CG32626	671	16	AMP deaminase
CG7583	655	11	C-terminal Binding Protein
CG4897	622	10	Ribosomal protein I 7
CG7754	620	.0	Hast shoals protein assesses 2
CG7/50	020	9	rieat shock protein cognate 2
CG5261	619	- 11	midline uncoordinated
CG12030	598	14	UDP-galactose 4'-epimerase
CG5119	587	9	polyA-binding protein
CG2151	586	8	Thioredoxin reductase-1
CC1250	200	7	
001250	582	/	sec25
CG10701	562	13	Moesin
CG12389	541	7	Farnesyl pyrophosphate synthase
CG5502	537	10	Ribosomal protein L4
CG1340	536	7	di 18
CC10701	530	12	uj-1p
CG10/01	527	12	Nioesin
CG16944	526	14	stress-sensitive B
CG18212	510	8	aluminum tubes
CG11522	494	10	Ribosomal protein L6
CG1242	487	10	Heat shock protein 83
CC0075	100	.0	Eukomotia initiatia - f 4
009075	480	7	Eukaryouc initiation factor 4a
CG8983	484	10	ERp60
CG4581	483	11	Thiolase
CG4347	478	7	UGP
CG10204	172	, 0	
010206	4/3	6	порэ
CG1973	456	6	yata
000770		6	Threonyl-tRNA synthetase
CG5353	428		
CG5353	428		Ribonucleoside dinhosphate reductase
CG5353 CG5371	428 425	7	Ribonucleoside diphosphate reductase
CG5353 CG5371	428 425	7	Ribonucleoside diphosphate reductase large subunit
CG5353 CG5371 CG4863	428 425 425	7	Ribonucleoside diphosphate reductase large subunit Ribosomal protein L3
CG5353 CG5371 CG4863 CG7380	428 425 425 424	7 5 8	Ribonucleoside diphosphate reductase large subunit Ribosomal protein L3 barrier to autointegration factor
CG5353 CG5371 CG4863 CG7380 CG2331	428 425 425 424 419	7 5 8 6	Ribonucleoside diphosphate reductase large subunit Ribosomal protein L3 barrier to autointegration factor TER94
CG5353 CG5353 CG5371 CG4863 CG7380 CG2331 CG5261	428 425 425 424 419 402	7 5 8 6 7	Ribonucleoside diphosphate reductase large subunit Ribosomal protein L3 barrier to autointegration factor TER94 midline uncoordinated
CG5353 CG5371 CG4863 CG7380 CG2331 CG5261 CG520	428 425 425 424 419 402 395	7 5 8 6 7 5	Ribonucleoside diphosphate reductase large subunit Ribosomal protein L3 barrier to autointegration factor TER94 midline uncoordinated Ribosomal versain \$2
CG5353 CG5353 CG5371 CG4863 CG7380 CG2331 CG5261 CG5920 CG5920	428 425 425 424 419 402 395 202	7 5 8 6 7 5	Ribonucleoside diphosphate reductase large subunit Ribosomal protein L3 barrier to autointegration factor TER94 midline uncoordinated Ribosomal protein S2

CG4863	387	4	Ribosomal protein L3
CG11276	384	7	Ribosomal protein S4
CG1489	384	7	Regulatory particle triple-A ATPase 6
CG6988	382	7	Protein disulfide isomerase
CG1472	382	6	Sec24AB ortholog (H. sapiens)
CG6779	362	8	Ribosomal protein S3
CG6543	362	7	CG6543
CG4389	361	9	Mitochondrial trifunctional protein α
CC2612	255	5	subunit
CG14648	355	5	beilwetner
CG14048	252	6	Dibosomel protein L 7 A
CG5499	351	8	Histone H2A variant
CG4916	345	5	maternal expression at 31B
CG1404	340	6	Ran
CG9577	328	5	CG9577
CG10944	323	6	Ribosomal protein S6
CG6699	322	8	Coat Protein (coatomer) B'
CG1475	320	7	Ribosomal protein L13A
CG2918	318	4	CG2918
CG2098	317	7	Ferrochelatase
CG7762	313	5	Regulatory particle non-ATPase 1
CG10990	310	5	Programmed cell death 4 ortholog
CG10882	309	6	stenosis
CG7111	308	8	Receptor of activated protein kinase C
CG8615	308	6	Ribosomal protein L18
CG8036	307	5	CG8036
CG2168	305	7	Ribosomal protein S3A
CG4199	301	5	CG4199
CG31363	301	4	Jupiter
CG9244	296	4	Aconitase
CG17291	296	5	Protein phosphatase 2A at 29B
CG6513	295	3	endosulfine
CG1422	294	5	p115
CG7808	291	5	Ribosomal protein S8
CG1633	291	5	thioredoxin peroxidase 1
CG9805	288	5	eIF3-S10
CG5366	285	4	Cullin-associated and neddylation-
004070	070	-	dissociated 1
CG4878	278	1	elF3-S9
CG52349	276	3	Top1 like
CG1516	276	4	Puruvate carboxylase
CG3661	270	5	Ribosomal protein I 23
CG2098	271	6	Ferrochelatase
002070	2/1	0	Regulatory particle triple-A ATPase
CG2241	270	5	6-related
CG2098	270	5	Ferrochelatase
CG3751	267	5	Ribosomal protein S24
CG8036	266	4	CG8036
CG12775	260	5	Ribosomal protein L21
CG8900	258	6	Ribosomal protein S18
CG17420	257	4	Ribosomal protein L15
CG3922	255	4	Ribosomal protein S17
CG1883	254	3	Ribosomal protein S7
CG6253	253	3	Ribosomal protein L14
CG9124	253	4	Eukaryotic initiation factor 3 p40
CG1262	240	2	SUDUINII Ribosomal protoin I 9
CG1203	249	5	
CG6235	240	3	twine
CG8877	235	4	pre-mRNA processing factor 8
CG6831	233	4	rhea
CG2522	233	4	GTP-binding protein
0017046	222		Succinyl coenzyme A synthetase
CG17246	233	3	flavoprotein subunit
CG42668	232	6	CG42668
CG31196	231	6	14-3-3ε
CG5289	218	4	Regulatory particle triple-A ATPase 2
CG11198	212	3	Acetyl-CoA carboxylase
CG2922	210	4	krasavietz
CG1483	209	4	Microtubule-associated protein 205
CG7935	209	4	moleskin
CG2621	207	4	shaggy
CG8893	206	2	Giyceraidenyde 3 phosphate dehydrogenase 2
CG15784	205	4	CG15784
CG9282	205	3	Ribosomal protein L24
CG9705	203	4	CG9705
CG8857	199	4	Ribosomal protein S11
CG14792	198	3	stubarista

Appendix C

000002	198	1	Ribosomal protein S15
CG42668	198	4	CG42668
CG8542 CG2168	196	4	Heat shock protein cognate 5
CG6084	196	3	CG6084
CG6510	195	5	Ribosomal protein L18A
CG4747	194	5	CG4747
CG32549	194	3	CG32549
CG4651	193	4	Ribosomal protein L13
CG10652	193	2	Ribosomal protein L30
CG13343	193	18	Ubiquitin activating enzyme 3
CG14207	191	1	CG14207
CG/89/	190	4	Gp210 ortholog (H. sapiens)
CG5024	189	4	CG5024
CG10691	189	2	lethal (2) 37Cc
CG3107	188	5	CG3107
CG31764	188	5	virus-induced RNA 1
CG6143	187	3	Protein on ecdysone puffs
CG1403	187	4	Septin 1
CG9677	184	4	Int6 homologue
CG1548	184	2	cathD
CG2050	182	3	modulo
CG8322	181	5	ATP citrate lyase
CG8857	180	3	Ribosomal protein S11
CG4994	179	2	Mitochondrial phosphate carrier
004774	177	2	protein
CG1345	179	4	Glutamine:fructose-6-phosphate
0015			aminotransferase 2
CG1524	178	4	Ribosomal protein S14a
CG17727	1//	3	Kibosomai protein S23
CG3196	176	2	۵IE-5۸
001100	170	2	ADP-ribosylation factor GTPase
CG6838	176	3	activating protein 3
CG2637	172	4	Female sterile (2) Ketel
CG1782	170	3	Ubiquitin activating enzyme 1
CG9273	169	1	Replication protein A2
CG6439	169	4	CG6439
CG10504	168	3	Integrin linked kinase
CG7507	167	5	Dynein heavy chain 64C
CG6988	167	2	Protein disulfide isomerase
CG8705	166	4	peanut
CG15717	164	4	CG15717
CG10377	163	2	Heterogeneous nuclear
0015100			ribonucleoprotein at 27C
CG15433	163	3	Elongator complex protein 3
CG3520	162	3	Rabi
C010225	150	2	Signal recognition partials protain 54k
CC4650			
CG4659 CG11963	159	3	skpA associated protein
CG4659 CG11963	159	3	skpA associated protein Spindle assembly abnormal 6 ortholog
CG4659 CG11963 CG15524	159 159	3	skpA associated protein Spindle assembly abnormal 6 ortholog (C. elegans)
CG4659 CG11963 CG15524 CG34407	159 159 159	3 3 4 2	skpA associated protein 34k skpA associated protein Spindle assembly abnormal 6 ortholog (C. elegans) Not1
CG4659 CG11963 CG15524 CG34407 CG1092	139 159 159 159 154	3 4 2 2	signal recognition particle protein 34k skpA associated protein Spindle assembly abnormal 6 ortholog (C. elegans) Notl CG1092
CG4659 CG11963 CG15524 CG34407 CG1092 CG3395	139 159 159 159 154 153	3 4 2 2 4	signal recognition particle protein 34k skpA associated protein Spindle assembly abnormal 6 ortholog (C. elegans) Not1 CG1092 Ribosomal protein S9
CG4659 CG11963 CG15524 CG34407 CG1092 CG3395 CG9160	139 159 159 159 154 153 153	$\begin{array}{c} 3\\ 3\\ 4\\ \hline 2\\ 2\\ \hline 4\\ 3 \end{array}$	signal recognition particle protein 34k skpA associated protein Spindle assembly abnormal 6 ortholog (C. elegans) Not1 CG1092 Ribosomal protein S9 mitochondrial acyl carrier protein 1
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	128	2	CG3800
CG21617	120	4	High:CC21617
0031017	128	4	HIST:COSTOT/
CG42668	128	4	CG42668
CG1691	128	4	IGF-II mRNA-binding protein
CG7843	127	4	Ars2
CG6084	127	2	CG6084
CG8552	125	3	Phoenhatidic Acid Phoenholinase A1
000002	125	5	Versela II. ATD a 60 lD asharit
CG3762	125	4	Vacuolar H+ AI Pase 68 kDa subunit
			2
CG17654	123	2	Enolase
CG31137	123	2	twin
CG4700	122	2	Bondulin
004799	122	2	Pendulin
CG11567	122	2	Cytochrome P450 reductase
CG9423	120	2	karyopherin α3
CG7726	119	2	Ribosomal protein I 11
CG7720	110	1	Tamin
CG3024	119	1	1 orsin
CG8532	118	3	liquid facets
CG10630	118	3	blanks
CG2746	117	2	Ribosomal protein I 19
CC2644	117	2	kieendel
005044	110	2	bicaudai
CG17870	116	3	14-3-3ζ
CG3821	115	2	Aspartyl-tRNA synthetase
CG4001	115	1	Phosphofructokinase
CG11888	115	2	Regulatory particle non-ATPase 2
0011000	113		Regulatory particle non-ATT ase 2
CG4821	113	4	Tequila
CG5252	113	2	Ranbp9
CG7834	113	2	CG7834
CG30349	113	2	CG30349
CC6275	112	2	nitahanna
0003/3	115	3	pitchoune
CG7033	112	2	CG7033
CG17611	111	1	eIF6
0011		~	Ubiquinol-cvtochrome c reductase
CG4169	111	3	core protein ?
CC4944	111	2	Dibogenel metair 1.26
CG0840	111	2	Ribosomai protein L26
CG17489	111	3	Ribosomal protein L5
CG7490	110	3	Ribosomal protein LP0
CG4464	110	1	Ribosomal protein S19a
CG8722	110	2	Acyl-CoA cynthataea long chain
CG8732	110	2	Acyi-CoA synthetase long-chain
CG4620	109	1	unkempt
CG15081	109	1	Prohibitin 2
CG1100	109	2	Regulatory particle non-ATPase 5
CG5642	109	3	CG5642
003042	100	5	(2)105016
CG3524	109	2	v(2)k05816
CG11661	108	1	Neural conserved at 73EF
CG2064	108	2	CG2064
CG2803	108	3	Troponin C-akin-1
CG2003	100	5	Hoponini C-akin-1
CG10824	108	5	Common Dpr-interacting protein
CG8266	106	2	Sec31 ortholog (S. cerevisiae)
CG16916	105	2	Regulatory particle triple-A ATPase 3
CG16916	105	2	Regulatory particle triple-A ATPase 3
CG16916 CG13387	105 104	2	Regulatory particle triple-A ATPase 3 embargoed
CG16916 CG13387 CG8439	105 104 103	2 2 3	Regulatory particle triple-A ATPase 3 embargoed T-complex Chaperonin 5
CG16916 CG13387 CG8439	105 104 103	2 2 3	Regulatory particle triple-A ATPase 3 embargoed T-complex Chaperonin 5 Nascent polypeptide associated
CG16916 CG13387 CG8439 CG8759	105 104 103 103	2 2 3 1	Regulatory particle triple-A ATPase 3 embargoed T-complex Chaperonin 5 Nascent polypeptide associated complex protein alpha subunit
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CG16916 CG13387 CG8439 CG8759 CG9916 CG3455 CG4729	105 104 103 103 102 102 102	$ \frac{2}{2} 3 1 1 2 1 $	Regulatory particle triple-A ATPase 3 embargoed T-complex Chaperonin 5 Nascent polypeptide associated complex protein alpha subunit Cyclophilin 1 Regulatory particle triple-A ATPase 4 CG4729
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CG16916 CG13387 CG8439 CG8759 CG9916 CG3455 CG4729 CG6815 CG4145	105 104 103 103 102 102 102 102 100	$ \frac{2}{2} 3 1 1 2 1 2 2 $	Regulatory particle triple-A ATPase 3 embargoed T-complex Chaperonin 5 Nascent polypeptide associated complex protein alpha subunit Cyclophilin 1 Regulatory particle triple-A ATPase 4 CG4729 belphegor Collagen type IV
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CG16916 CG13387 CG8439 CG8759 CG9916 CG3455 CG4729 CG6815 CG4145 CG9999 CG7360	105 104 103 102 102 102 102 102 100 100	$ \begin{array}{r} 2 \\ 2 \\ 3 \\ 1 \\ 2 \\ $	Regulatory particle triple-A ATPase 3 embargoed T-complex Chaperonin 5 Nascent polypeptide associated complex protein alpha subunit Cyclophilin 1 Regulatory particle triple-A ATPase 4 CG4729 belphegor Collagen type IV Ran GTPase activating protein
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CG7404	86	2	estrogen-related receptor
CG/8/8	86	2	CG/8/8
CG15792	85	2	zipper
CG3664	85	1	Rab5
CG6203	85	1	Fmr1
CG8890	85	1	GDP-mannose 4,6-dehydratase
CG9373	85	1	rumpelstiltskin
CG4254	84	1	twinstar
CG6692	84	2	Cysteine proteinase-1
CG9738	84	2	CG9246
CG7920	84	2	CG7920
CG3949	83	1	hoi-polloi
CG6072	83	1	sarah
CG16901	83	1	squid
CG8553	82	1	Selenide, water dikinase
CG1453	81	1	Kinesin-like protein at 10A
CG12202	81	2	NAT1 ortholog (S. cerevisiae)
CG42641	81	3	Regulatory particle pop_ATPase 3
CG1274	80	3	thioredoxin peroxidase 2
CG30122	80	1	CG30122
CG17489	80	1	Ribosomal protein L5
CG7622	79	2	Ribosomal protein L36
CG9148	79	2	supercoiling factor
CG8262	79	1	anastral spindle 2
CG8258	79	1	CG8258 T-cn17
006251	/0	1	Translationally controlled tumor
CG4800	78	1	protein ortholog (H. sapiens)
CG12163	77	2	CG12163
CG16858	76	2	viking
CG8649	76	2	Fimbrin
CG12324	76	2	Ribosomal protein S15Ab
CG3593	75	2	rudimentary-like
CG10077	/5	1	CG10077
CG3902	75	1	CG3902
CG5844	75	1	CG5844
CG15442	74	2	Ribosomal protein L27A
CG12233	74	2	lethal (1) G0156
CG9412	73	1	rasputin
CG1341	73	2	Regulatory particle triple-A ATPase 1
CG7632	73	2	CG7632
CG6143	72	1	Protein on ecdysone puffs
CG2469	72	1	CG2469
CG7375	72	1	Ubiquitin conjugating enzyme 12
CG7375 CG8351	72 72	1	Ubiquitin conjugating enzyme 12 Tcp-1ŋ
CG7375 CG8351 CG8787	72 72 71	1 1 7	Ubiquitin conjugating enzyme 12 Tcp-1η Additional sex combs
CG7375 CG8351 CG8787 CG3395	72 72 71 70	1 1 7 2	Ubiquitin conjugating enzyme 12 Tcp-1η Additional sex combs Ribosomal protein S9
CG7375 CG8351 CG8787 CG3395 CG1081	72 72 71 70 70	1 1 7 2 1	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain
CG7375 CG8351 CG8787 CG3395 CG1081	72 72 71 70 70	1 1 7 2 1	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutzmul argulu 420 A synthetizes
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10160	72 72 71 70 70 69 68	1 1 7 2 1 1 1	Ubiquitin conjugating enzyme 12 Tcp-1η Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamyl-prolyl-tRNA synthetase Ecdwsone-inducible gene 1.3
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10160 CG10596	72 72 71 70 70 69 68 68 68	1 1 7 2 1 1 1 1 1	Ubiquitin conjugating enzyme 12 Tcp-1η Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamy1-proly1-tRNA synthetase Ecdysone-inducible gene L3 Msr-110
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10160 CG10596 CG6708	72 72 71 70 70 69 68 68 68 68 68	1 1 7 2 1 1 1 1 1 1 1	Ubiquitin conjugating enzyme 12 Tcp-1η Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamy1-proly1-tRNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10160 CG10596 CG6708 CG12275	72 72 71 70 70 69 68 68 68 68 68 68	1 1 7 2 1 1 1 1 1 1 1	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamy-proly1-RNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein Ribosomal protein S10a
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10596 CG6708 CG6708 CG12275 CG10306	72 72 71 70 70 69 68 68 68 68 68 68 68 68	1 1 7 2 1 1 1 1 1 1 1 1 1 1	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamyl-prolyl-tRNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein Ribosomal protein S10a CG10306
CG7375 CG8351 CG8377 CG3395 CG1081 CG5394 CG10596 CG10596 CG10275 CG10306 CG12275 CG10306	72 72 71 70 70 69 68 68 68 68 68 68 68 68 68 68	1 1 7 2 1 1 1 1 1 1 1 1 1 1 1 1 2	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamyl-prolyl-tRNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein Ribosomal protein S10a CG10306 Une-76
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10160 CG10596 CG6708 CG12275 CG10306 CG3981 CG3981 CG8922 CG21927	72 72 71 70 70 69 68 68 68 68 68 68 68 68 67 67	1 1 7 2 1 1 1 1 1 1 1 1 1 1 1 2 2	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamyl-prolyl-tRNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein Ribosomal protein S10a CG10306 Unc-76 Ribosomal protein S5a prohd do hydrogrifes aleter UPP
CG7375 CG8351 CG8787 CG3395 CG1081 CG5394 CG10160 CG10596 CG6708 CG12275 CG10306 CG3981 CG8922 CG3022 CG31022 CG4554	72 72 71 70 69 68 68 68 68 68 68 68 68 68 68 68 67 67	1 1 7 2 1 1 1 1 1 1 1 1 1 2 1 1	Ubiquitin conjugating enzyme 12 Tcp-1η Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamyl-prolyl-tRNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein Ribosomal protein S10a CG (10306 Unc-76 Ribosomal protein S5a prolyl-4-hydroxylase-alpha EFB Depoxyniging rinburghetase
CG7375 CG8351 CG8351 CG3395 CG1081 CG5394 CG10160 CG10596 CG6708 CG12275 CG10306 CG6708 CG12275 CG10306 CG3981 CG8922 CG31022 CG3022 CG3022	72 72 71 70 69 68 68 68 68 68 68 68 68 68 68 68 67 67 67	$ \begin{array}{c} 1 \\ 1 \\ 7 \\ 2 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2$	Ubiquitin conjugating enzyme 12 Tcp-1ŋ Additional sex combs Ribosomal protein S9 Ras homolog enriched in brain ortholog (H. sapiens) Glutamyl-prolyl-1RNA synthetase Ecdysone-inducible gene L3 Msr-110 Oxysterol binding protein Ribosomal protein S10a CG10306 Unc-76 Ribosomal protein S5a prolyl-4-hydroxylase-alpha EFB Deoxyuridine triphosphatase Vacuolar H+-ATPase S5kD subunit
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_	CG3074	60	2	Secreted Wa interacting molecule
	CG9756	60	4	vermiform
-	005739	00	4	CC5729
_	CG5728	60	1	CG5728
	CG33129	59	1	CG33129
	CG5931	59	1	lethal (3) 72Ab
	CG13628	58	1	Rpb10
	CG1828	57	1	dre4
	CG1416	57	1	CG1416
	001410	51		Zinc/iron regulated transporter-related
	CG7816	57	1	Zinc/iton regulated transporter-related
_				protein 99C
	CG33456	57	2	muscle wasted
	CG4785	56	3	Integrator 14
	CG12050	56	2	CG12050
-	CG4752	56	4	CG4752
-	CG9674	56	2	CG9674
-	CC18102	55	1	ccojo/4
_	CG18102	35	1	snibire
	CG18076	55	3	short stop
	CC2572	55	1	visceral mesodermal armadillo-
	035572	33	1	repeats
	CG9581	55	1	CG9581
-			-	Actin_related protein 2/3 complex
	CG5972	55	2	aubunit 4
-	00000		1	Subulit 4
_	CG9302	22	1	CG9302
_	CG5641	55	1	CG5641
	CG12512	54	1	CG12512
	CG4016	54	1	Serine palmitoyltransferase subunit I
F	CG3201	53	1	Myosin light chain cytoplasmic
F	CG83/0	53	1	unstream of PnIII129
⊢	CC0174	50	1	upsucani oi kpiii128
F	CG81/4	55	1	SKPK
L	CG11856	53	1	Nucleoporin 358kD
Г	CG7392	53	1	Connector of kinase to AP-1
F	CG11804	52	2	ced-6
F				Rho guanine nucleotide exchange
	CG9635	51	1	factor 2
⊢	005000	E 1	1	adainer binding a stat
F	CG5809	51	1	calcium-binding protein 1
L	CG6778	51	1	Glycyl-tRNA synthetase
Γ	CG2957	51	1	mitochondrial ribosomal protein S9
Γ	CG6987	51	2	SF2
-	CG8977	50	1	Cety
-	CC4012	50	1	-EE18
-	004912	30	1	eEF10
	CG5214	50	1	CG5214
	CG8882	49	1	Trip1
	CG7010	49	2	lethal (1) G0334
	CG6891	49	1	CG6891
-	CG2803	49	1	Troponin C-akin-1
-	CG2863	40	1	CC7852
_	CG/852	49	1	CG/852
	CG4821	48	2	Tequila
	CG6819	48	1	members only
	CG7985	48	3	CG7985
	CG8683	48	1	mon2
-	CG8545	48	1	CG8545
-	CC17404	40	1	Econolommo coccoletad anotain
-	001/494	46	1	Sarcolemina associated protein
	CG2194	48	1	suppressor of rudimentary
		47	1	Protein phosphatase 1 at 87B
	CG5650	47	1	
-	CG5650 CG10130	47	1	Sec61 subunit
_	CG5650 CG10130 CG6743	47 47 47	1 1	Sec61 β subunit Nucleoporin 107kD
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	CG5650 CG10130 CG6743 CG8733 CG8286 CG6042 CG4236 CG4236 CG4236 CG4236 CG4173 CG7610 CG12770 CG6181 CG6181 CG9674 CG33097 CG9674 CG33097 CG9847 CG30498 CG10719 CG61847 CG30498 CG10719 CG6155 CG31794 CG41111 CG8475 CG32528 CG1725 CG32528 CG1725 CG32528 CG11427 CG33258 CG11427 CG33433 CG1936 CG11417 CG8103 CG1936 CG10811 CG8103 CG10811 CG10811 CG10811 CG11324 CG5014	$\begin{array}{c} 47\\ 47\\ 47\\ 47\\ 47\\ 47\\ 47\\ 47\\ 47\\ 47\\$		Sec61 β subunit Nucleoporin 107kD Nucleoporin 107kD PS8IPK Cyp12a4 Chromatin assembly factor 1 subunit Adaptor Protein complex 2, a subunit CG12262 Septin 2 ATP synthase, γ subunit Vacuolar protein sorting 28 Ge-1 ortholog (H, sapiens) CG33097 26-29kD-proteinase boca brain tumor Roe1 Paxillin mitochondrial single stranded DNA- binding protein L15 CG8475 mitochondrial ribosomal protein L11 SC35 putzig parvin discs large 1 ruby Ribosomal protein S13 RNA and export factor binding protein 1 Mi-2 Coproporphyrinogen oxidase Glutathione S transferase E12 BS2 eukaryotic translation initiation factor 4G homer VAMP-associated protein of 33kDa ortholog A
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CG14271	39	2	Growth arrest specific protein 8
CG4320	39	1	raptor
CG7277	39	1	CG7277
CG7003	39	1	Msh6
CG8798	39	1	Lon protease
CG6000	39	1	CG6000
CG31817	38	2	CG31817
CG6450	38	1	lava lamp
CG10194	38	2	CG10194
CG1316	38	1	CG1316
CG33180	38	1	Ranbp16
CG1646	37	1	CG1646
CG8610	36	1	Cell division cycle 27 ortholog
CG5726	36	1	CG5726
CG18519	36	1	Aldehyde oxidase 2
CG1915	36	1	sallimus
CG8014	35	1	Receptor mediated endocytosis 8
CG1210	35	1	Phosphoinositide-dependent kinase 1
CG14786	35	1	Leucine-rich pentatricopeptide repeat containing 2
CG5723	34	1	Tenascin major
CG8355	34	1	slit

CG5680	33	1	basket
CG3416	33	1	Regulatory particle non-ATPase 8
CG5105	33	1	Phospholipase A2 activator protein
CG1591	33	1	REG
CG4853	33	1	CG4853
CG3362	33	1	cytosolic 5'-nucleotidase IIIB
CG7014	33	1	Ribosomal protein S5b
CG11148	33	1	Gigyf
CG8189	32	1	ATP synthase, subunit b
CG10869	32	1	CG10869
CG9674	32	1	CG9674
CG12983	32	1	CG12983
CG6420	32	1	CG6420
CG1945	31	1	fat facets
CG4038	31	1	CG4038
CG11943	31	1	Nucleoporin 205kD
CG8360	31	1	CG8360
CG42670	31	1	pasilla
CG9735	30	1	Tryptophanyl-tRNA synthetase
CG10617	30	1	Synaptotagmin 12

C.7 pUb-GFP-Dragon +OA purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG33052	61897	766	CG33052
CG4264	4605	65	Heat shock protein cognate 4
CG7583	3502	47	C-terminal Binding Protein
CG9277	3400	47	β-Tubulin at 56D
CG7583	3329	45	C-terminal Binding Protein
CG9277	3183	44	ß-Tubulin at 56D
CG4027	2005	47	Actin 5C
CG12051	2020	46	Actin 42A
0012051	2930	40	Actili 42A
CG4147	2720	42	Heat snock /0-kDa protein cognate 3
CG1913	2613	41	α-Tubulin at 84B
CG10067	2227	34	Actin 57B
CG8280	2070	34	Elongation factor 1a48D
CG7478	2042	30	Actin 79B
CG5178	1970	31	Actin 88F
CG15524	1961	37	Spindle assembly abnormal 6 ortholog (C. elegans)
CG9476	1738	27	a-Tubulin at 85E
CG2401	1565	26	ß Tubulin at 60D
CG0250	1/79	20	β Tubulin at 85D
CC8027	14/0	12	Hoat shock pretein accrete 1
CG893/	1259	15	Fleat snock protein cognate 1
CG1528	1171	22	Coat Protein (coatomer) γ
CG9748	1115	16	belle
CG15792	1096	20	zipper
CG17949	1077	17	His2B:CG17949
CG4869	1072	21	β-Tubulin at 97EF
CG8937	1070	10	Heat shock protein cognate 1
CG6871	900	11	Catalase
CG1349	874	14	di-16
CG5436	868	10	Heat shock protein 68
CG18743	852	9	Heat-shock-protein-70Ab
CG15702	840	19	zippor
CG13792	047	16	Zippei
CG12065	812	15	CG12065
CG2216	811	16	Ferritin I heavy chain homologue
CG6718	738	7	calcium-independent phospholipase A2 VIA
CG2238	728	13	Elongation factor 2
CG1873	724	12	Elongation factor 1a100E
CG7439	700	11	Argonaute 2
CG3752	685	4	Aldebyde debydrogenase
CG3379	672	15	Histone H4 replacement
CC22626	650	15	A MD doomingood
CG32828	639	13	AMF deaminase
CG33869	659	14	His4:CG33869
CG5261	655	14	midline uncoordinated
CG5502	645	12	Ribosomal protein L4
CG31613	637	11	His3:CG31613
CG12065	619	13	CG12065
CG10701	616	14	Moesin
CG7961	606	13	Coat Protein (coatomer) a
CG7756	604	7	Heat shock protein cognate 2
CG6223	582	9	Cost Protein (costomer) 8
CG5825	572	10	Histone H3 3A
CG10701	542	10	Measin
001250	522	12	INIOESIII
CG1250	532	0	sec23
CG10279	497	8	Rm62
CG5261	497	11	midline uncoordinated
CG31618	486	10	His2A:CG31618
CG8309	461	7	Transport and Golgi organization 7
CG2216	453	10	Ferritin 1 heavy chain homologue
CG5371	451	8	Ribonucleoside diphosphate reductase
002151	444	5	This as dearing a dearter of
CG2151	444	5	Thioredoxin reductase-1
CG1548	441	5	cathD
CG18212	435	6	aluminum tubes
CG14648	403	7	lost
CG9888	402	9	Fibrillarin
CG8542	395	5	Heat shock protein cognate 5
CG12163	368	5	CG12163
		-	

CG489/	367	5	Ribosomal protein L7
CG10944	364	5	Ribosomal protein S6
CG8322	355	5	ATP citrate lyase
CG4799	338	4	Pendulin
CG3612	328	7	bellwether
CG4863	327	5	Ribosomal protein L3
CG10630	327	6	blanks
CG1403	322	3	Septin 1
CG6253	307	4	Ribosomal protein L14
CG8922	304	4	Ribosomal protein S5a
CG2331	299	6	TER94
CG4634	283	3	Nucleosome remodeling factor - 38kD
CG4389	283	7	Mitochondrial trifunctional protein a
CG3265	273	6	Fb1
CG1489	272	4	Regulatory particle triple-A ATPase 6
CG5920	271	5	Ribosomal protein S2
CG1973	269	4	vata
			Glyceraldehyde 3 phosphate
CG8893	267	3	dehydrogenase 2
CG12233	255	4	lethal (1) G0156
CG2050	253	5	modulo
CG3201	250	4	Myosin light chain cytoplasmic
CG8983	247	5	ERp60
CG4199	244	5	CG4199
CG2922	242	5	extra bases
CG6510	240	5	Ribosomal protein L18A
CG11276	239	4	Ribosomal protein S4
CG7808	239	3	Ribosomal protein S8
CG3455	231	4	Regulatory particle triple-A ATPase 4
CG1100	231	4	Regulatory particle non-ATPase 5
CG31363	229	4	Jupiter
CG7430	227	3	CG7430
CG4863	225	3	Ribosomal protein L3
CG8996	222	3	walrus
CG2168	222	6	Ribosomal protein S3A
CG17246	216	3	Succinate dehydrogenase A
CG1341	215	4	Regulatory particle triple-A ATPase 1
CG7977	213	3	Ribosomal protein L23A
CG33206	213	3	Golgi microtubule-associated protein
			Coat Protein (coatomer) B
CG6699	212	3	
CG6699 CG3523	212 212	3 4	Fatty acid synthase 1
CG6699 CG3523 CG5353	212 212 209	3 4 3	Fatty acid synthase 1 Threonyl-tRNA synthetase
CG6699 CG3523 CG5353 CG3661	212 212 209 208	3 4 3 3	Fatty acid synthase 1 Threonyl-tRNA synthetase Ribosomal protein L23
CG66699 CG3523 CG5353 CG3661 CG5520	212 212 209 208 207	3 4 3 3 4	Fatty acid synthase 1 Threonyl-tRNA synthetase Ribosomal protein L23 Glycoprotein 93
CG6699 CG3523 CG5353 CG3661 CG5520 CG5000	212 212 209 208 207 206	3 4 3 4 3	Fatty acid synthase 1 Threonyl-tRNA synthetase Ribosomal protein L23 Glycoprotein 93 mini spindles
CG6699 CG3523 CG5353 CG3661 CG5520 CG5000 CG17420	212 209 208 207 206 206 206	3 4 3 4 3 3 3	Fatty acid synthase 1 Threonyl-tRNA synthetase Ribosomal protein L23 Glycoprotein 93 mini spindles Ribosomal protein L15
CG6699 CG3523 CG5353 CG3661 CG5520 CG5520 CG17420 CG15442	212 212 209 208 207 206 206 206 206	3 4 3 4 3 3 3 3 2	Fatty acid synthase 1 Threonyl-tRNA synthetase Ribosomal protein L23 Glycoprotein 93 mini spindles Ribosomal protein L15 Ribosomal protein L27A
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CG6699 CG3523 CG3523 CG3561 CG5520 CG17420 CG17420 CG17420 CG324 CG2746 CG3024 CG3024 CG3024 CG3024 CG3024 CG3024 CG3024 CG3024 CG3024 CG3024 CG16944 CG16944 CG16944 CG16944 CG16944 CG16946 CG6235 CG10377 CG10990 CG11888 CG8590 CG6831 CG31764 CG3764 CG3888	212 212 209 208 207 206 206 205 204 195 192 191 190 189 189 187 187 187 187 187 187 186 184 184 184 184 180 179 178	$ \begin{array}{r} 3 \\ 4 \\ 3 \\ 3 \\ 4 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 5 \\ 2 \\ 3 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 1 \\ 2 \\ 4 \\ 3 \\ \end{array} $	Fatty acid synthase 1 Threonyl-tRNA synthetase Ribosomal protein L23 Glycoprotein 93 mini spindles Ribosomal protein L15 Ribosomal protein L27A Torsin Ribosomal protein L27A Torsin Network and the synthesis of the syn

CG10161	176	3	Eukaryotic initiation factor 3 p66
CC0075	174	4	subunit
CG4347	174	2	UGP
CG5215	171	2	Zn72D
CG10206	171	3	nop5
CG1475	170	3	Ribosomal protein L13A
CG11856	170	3	Nucleoporin 358kD
CG6543	169	3	CG6543
CG3314	167	3	Ribosomal protein L7A
CG17333	167	2	CG17333
CG8351	16/	2	Icp-In
CG11154	165	3	ATP synthase, p subunit
CG12242	165	3	Ubiquitin activating anyuma 2
CG12389	164	15	Earnesyl pyrophosphate synthase
CG15784	163	3	CG15784
CG32549	163	2	CG32549
CG6988	162	2	Protein disulfide isomerase
CG4581	158	3	Thiolase
CG5654	154	1	ypsilon schachtel
CG5374	153	2	Tcp1-like
CG7490	152	2	Ribosomal protein LP0
CG9412	152	3	rasputin
CG6439	152	4	CG6439
CG10811	151	2	eukaryotic translation initiation factor
CG8877	151	1	pre-mRNA processing factor 8
0	1.51	-	Receptor of activated protein kinase C
CG7111	150	3	1
CC0092	140	2	Heterogeneous nuclear
009983	149	2	ribonucleoprotein at 98DE
CG8900	148	3	Ribosomal protein S18
CG4651	148	3	Ribosomal protein L13
CG1472	147	3	Sec24AB ortholog (H. sapiens)
CG9805	147	4	elF3-S10
CG4916	144	5	Ribonucleosida diphoaphata reductor
CG8975	144	2	small subunit
CG2522	143	2	GTP-binding protein
CG11943	143	2	Nucleoporin 205kD
CG10535	142	1	Elongator complex protein 1
CG7831	141	1	non-claret disjunctional
CG10305	138	3	Ribosomal protein S26
CG18190	138	2	CG18190
CG2098	136	3	Ferrochelatase
CG13389	133	2	Ribosomal protein S13
CG10882	133	3	stenosis
CG5825	130	6	Histone H3.3A
CG0084	150	2	CG0084 Translationally controlled tumor
CG4800	130	2	protein ortholog (H. saniens)
CG7507	130	3	Dynein heavy chain 64C
CG8439	129	2	T-complex Chaperonin 5
CG10223	127	3	Topoisomerase 2
CG31363	126	2	Jupiter
CG14206	126	2	Ribosomal protein S10b
CG10691	125	1	lethal (2) 37Cc
CG12532	125	3	Adaptor Protein complex 1/2, β subunit
CG7185	123	1	CG7185
CG13849	123	2	Nop56
CG0815 CG2169	121	4	Deipnegor Ribosomal protein S2A
CG30176	120	2	within been
CG1483	119	1	Microtubule-associated protein 205
001100	110		Ubiquinol-cytochrome c reductase core
CG4169	119	2	protein 2
CG3902	116	1	CG3902
CG3606	115	2	cabeza
CG8266	115	2	Sec31 ortholog (S. cerevisiae)
CG10922	113	2	La autoantigen-like
CG9124	111	3	Eukaryotic initiation factor 3 p40
CC10140	110	2	Subunit
CG12287	110	2	ecuysone-multicible gene L5
	110	2	cinidal good
CG9012	110	2	Clathrin heavy chain
CG9012 CG7398	110 108 108	2 3 2	Clathrin heavy chain Transportin
CG9012 CG7398 CG11793	110 108 108 107	2 3 2 1	Clathrin heavy chain Transportin Superoxide dismutase
CG9012 CG7398 CG11793 CG3107	110 108 108 107 107	2 3 2 1 2	Clathrin heavy chain Transportin Superoxide dismutase CG3107
CG9012 CG7398 CG11793 CG3107 CG4584	110 108 108 107 107 107	$ \frac{2}{3} \frac{1}{2} \frac{1}{2} $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase
CG9012 CG7398 CG11793 CG3107 CG4584 CG1242	110 108 107 107 107 107 106	$\begin{array}{r} 2\\ 3\\ \hline 2\\ 1\\ \hline 2\\ 2\\ \hline 2\\ 2 \end{array}$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83
CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073	110 108 108 107 107 107 106 106	$ \begin{array}{r} 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 3 \\ 3 \end{array} $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A
CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8571	110 108 108 107 107 107 106 106 106	$ \begin{array}{r} 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ 3 \\ 2 \\ 1 \\ $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded
CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8571 CG4236	110 108 108 107 107 107 106 106 105 105	$ \begin{array}{r} 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \\ 2 \\ 3 \\ 2 \\ 1 \\ $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit
CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8571 CG4236 CG4259 CG4259	$ \begin{array}{r} 110\\ 108\\ 108\\ 107\\ 107\\ 107\\ 106\\ 106\\ 106\\ 105\\ 105\\ 105\\ 104\\ 102 \end{array} $	$ \begin{array}{r} 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259
CG13337 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8571 CG4236 CG4236 CG4259 CG1453	110 108 108 107 107 107 106 106 105 105 104 103 103	$ \begin{array}{r} 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Beneticene und Director 1
CG10336 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8571 CG4236 CG4236 CG4259 CG1453 CG1453	$ \begin{array}{r} 110 \\ 108 \\ 108 \\ 107 \\ 107 \\ 107 \\ 106 \\ 106 \\ 105 \\ 105 \\ 104 \\ 103 \\ 101 $	$ \frac{2}{3} \frac{3}{2} \frac{1}{2} \frac{1}{2} \frac{2}{2} \frac{3}{2} \frac{1}{1} \frac{1}{2} \frac{2}{2} \frac{2}{2} \frac{1}{2} \frac{1}{2} $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9
CG19337 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8571 CG4236 CG4239 CG4259 CG1453 CG10230 CG8615	110 108 108 107 107 107 106 106 105 105 104 103 101 101	$ \frac{2}{3} $ $ \frac{3}{2} $ $ \frac{1}{2} $ $ \frac{2}{2} $ $ \frac{3}{2} $ $ \frac{1}{1} $ $ \frac{2}{2} $ $ \frac{2}{2} $ $ \frac{2}{2} $ $ \frac{3}{2} $ $ \frac{1}{2} $ $ \frac{2}{2} $ $ \frac{2}{2} $ $ \frac{2}{2} $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18
CG19357 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG45871 CG4236 CG4259 CG1453 CG1453 CG10230 CG8615 CG8798 CG18102	110 108 108 107 107 107 106 106 105 105 105 104 103 101 101 101	$ \frac{2}{3} $ $ \frac{3}{2} $ $ \frac{1}{2} $ $ \frac{2}{2} $ $ \frac{3}{2} $ $ \frac{1}{1} $ $ \frac{2}{2} $ $ \frac{2}{2} $ $ \frac{1}{2} $	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibires
CG13337 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG4259 CG1453 CG4259 CG1453 CG1220 CG6257 CG78815 CG8798 CG18102 CG6692	110 108 107 107 107 107 106 105 105 105 104 103 101 101 101 100	2 3 2 1 2 2 2 3 2 1 1 2 2 2 2 2 2 2 2	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibire Cysteine proteines 1
CG13337 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG4259 CG1453 CG4259 CG1453 CG4259 CG1453 CG6929 CG6692 CG6692 CG6857	110 108 107 107 107 107 106 105 105 105 104 101 101 101 101 100 99	$\begin{array}{c} 2\\ 3\\ 2\\ 1\\ 2\\ 2\\ 2\\ 2\\ 3\\ 2\\ 1\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 1\\ 1\\ 1\\ 1\end{array}$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibire Cysteine proteinase-1 Ribosomal protein S11
CG19337 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG8073 CG8073 CG8259 CG1453 CG8259 CG1453 CG8798 CG8798 CG8857 CG7766	110 108 107 107 107 106 106 106 106 105 104 103 101 101 101 100 100 99 98	$\begin{array}{c} 2\\ 3\\ 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 3\\ 2\\ 1\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 1\\ 1\\ 1\\ 1\end{array}$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibire Cysteine proteinase-1 Ribosomal protein S11 CG7766
CG19357 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG4584 CG1242 CG8073 CG4259 CG1453 CG1453 CG1453 CG1453 CG1453 CG1453 CG1453 CG1230 CG8615 CG8798 CG18102 CG6692 CG8857 CG7766 CG78831	110 108 107 107 107 106 106 106 105 105 104 103 101 101 101 100 100 99 98 97	$\begin{array}{c} 2\\ 3\\ 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 3\\ 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ \end{array}$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibire Cysteine proteinase-1 Ribosomal protein S11 CG7766 Nucleoporin S4kD
CG19012 CG7398 CG11793 CG3107 CG4284 CG1242 CG8073 CG8236 CG4236 CG4239 CG1453 CG4236 CG4259 CG1453 CG10230 CG8615 CG8798 CG18102 CG6692 CG8857 CG7766 CG8831 CG4878	110 108 107 107 107 106 106 105 105 104 103 101 101 101 100 100 99 98 97 97	$\begin{array}{c} 2\\ 3\\ 2\\ 1\\ 2\\ 2\\ 2\\ 3\\ 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 3\end{array}$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibire Cysteine proteinase-1 Ribosomal protein S11 CG7766 Nucleoporin 54kD elF3-S9
CG103367 CG9012 CG7398 CG11793 CG3107 CG4584 CG1242 CG8073 CG4259 CG1453 CG4259 CG1453 CG1230 CG8571 CG4259 CG1453 CG10230 CG8815 CG8798 CG18102 CG8857 CG7766 CG8831 CG4878 CG7766	110 108 107 107 107 106 106 105 104 103 101 101 101 101 100 100 99 98 97 97 97	$\begin{array}{c} 2 \\ 3 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 1 \\ 1 \\ 1$	Clathrin heavy chain Transportin Superoxide dismutase CG3107 Deoxyuridine triphosphatase Heat shock protein 83 Phosphomannomutase 45A smallminded Chromatin assembly factor 1 subunit CG4259 Kinesin-like protein at 10A Regulatory particle non-ATPase 9 Ribosomal protein L18 Lon protease shibire Cysteine proteinase-1 Ribosomal protein S11 CG7766 Nucleoporin 54bD elF3-S9 endosulfine

CG17654	95	1	Enclase
CG2251	05	1	mitoshondrial ribosomal protain I 11
663551	93	4	
CG9999	94	2	Ran GTPase activating protein
CG1633	94	1	thioredoxin peroxidase 1
CG2033	93	3	Ribosomal protein S15Aa
CG5170	93	3	Dodeca-satellite-binding protein 1
CG1683	92	2	Adenine nucleotide translocase 2
CG9543	92	2	Coat Protein (coatomer) s
CG1120	02	1	CG1120
CO1129	92	1	C01129
CG2918	91	1	CG2918
CG6180	91	1	CG6180
CG4463	90	1	Heat shock protein 23
CG7637	90	2	CG7637
CG11522	90	1	Ribosomal protein L6
CG4003	90	1	pontin
CC10652	90	1	Bihasamal matain I 20
CG10652	89	1	Ribosomal protein L30
CG4598	89	2	CG4598
CC4257	00	2	Signal-transducer and activator of
0.04237	00	5	transcription protein at 92E
CG8553	88	1	selenide.water dikinase
CG12775	88	2	Ribosomal protein L21
CG0016	87	1	Cyclophilip 1
009910	87	1	
CG33162	8/	1	Signal recognition particle receptor b
CG3320	86	1	Rab1
CG6050	86	1	Elongation factor Tu mitochondrial
CG5175	86	1	kugelkern
CG34407	86	1	Not1
CG3333	86	1	Nucleolar protein at 60B
CG2152	95	2	Trow 1
0010070	0.5	2	Hapi
CG10370	85	2	Regulatory particle triple-A ATPase 5
CG4954	85	1	eIF3-S8
CG3395	84	2	Ribosomal protein S9
CG8882	84	1	Trip1
CG7340	83	1	graphy smith
CG5204	83	1	Chatamad a schol (DNA) smith stars
CG5394	82	1	Glutamyi-proiyi-tKINA synthetase
CG12324	82	2	Ribosomal protein S15Ab
CG10077	82	2	CG10077
CG31196	81	1	14-3-3ε
CG2061	81	1	CG2061
CG5446	81	1	CC5446
CC3008	01	1	Europhiletere
CG2098	80	2	Ferrochelatase
CG2098	80	1	Ferrochelatase
CG1263	79	1	Ribosomal protein L8
CG12275	79	1	Ribosomal protein S10a
			Cullin-associated and neddylation-
CG5366	79	1	dissociated 1
000402	70	1	Dissociated 1
CG9493	79	1	Pez
CG8552	79	1	Phosphatidic Acid Phospholipase A1
CG9373	78	1	rumpelstiltskin
CG3593	77	2	rudimentary-like
CG1837	77	2	pretaporter
CG12013	77	1	PHGPy
CC7022	76	1	CC7022
CG/033	/6	1	CG7033
CG5064	76	1	Signal recognition particle protein 68
CG11579	75	1	armadillo
			Dead box protein 73D
CG9680	75	1	D'I I . 1 104
CG9680 CG9282	75 75	1	Ribosomal protein L24
CG9680 CG9282	75 75	1	Cleavage stimulation factor 64
CG9680 CG9282 CG7697	75 75 74	1 1 1	Cleavage stimulation factor 64
CG9680 CG9282 CG7697	75 75 74	1 1 1	Cleavage stimulation factor 64 kilodalton subunit
CG9680 CG9282 CG7697 CG10504	75 75 74 74	1 1 1	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase
CG9680 CG9282 CG7697 CG10504 CG2331	75 75 74 74 73	1 1 1 1 1	Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111	75 75 74 74 73 73	1 1 1 1 1 1 1	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389	75 75 74 74 73 73 73	1 1 1 1 1 1 1 1	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456	75 75 74 74 73 73 73 73 73	1 1 1 1 1 1 1 1 4	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668	75 75 74 74 73 73 73 73 73 73 73	1 1 1 1 1 1 1 4 1	Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG28442	75 75 74 74 73 73 73 73 73 73 73 73	1 1 1 1 1 1 1 1 4 1 1	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 chulcec
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG8443 CG5410	75 75 74 74 73 73 73 73 73 73 72 72	1 1 1 1 1 1 1 1 4 1 1 1	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polu4 highing protein
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG32668 CG42668 CG8443 CG5119	75 75 74 74 73 73 73 73 73 73 73 73 72 72	$ \frac{1}{1} \frac{1}{1} $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG84268 CG8443 CG5119 CG7144	75 75 74 74 73 73 73 73 73 73 73 72 72 71	$ \frac{1}{1} \frac{1}{1} \frac{1}{1} \frac{1}{1} \frac{1}{1} \frac{1}{1} \frac{1}{1} \frac{1}{2} $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG8443 CG5119 CG7144 CG10198	75 75 74 73 73 73 73 73 73 73 73 72 72 71 71	$ \begin{array}{c} 1 \\ $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 Clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG8443 CG5119 CG7144 CG10198 CG10198	75 75 74 74 73 73 73 73 73 73 72 72 71 71 71	$ \begin{array}{r} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 4 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG42668 CG42668 CG42668 CG5119 CG7144 CG10198 CG11271 CG2637	75 75 74 73 73 73 73 73 72 72 71 71 71	$ \begin{array}{r} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12 Female sterile (2) Ketel
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CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG8443 CG5119 CG7144 CG10198 CG11271 CG2637 CG11661 CG4173 CG4993 CG9148 CG1422 CG8705 CG11661 CG4173 CG4993 CG9148 CG1422 CG8705 CG14996 CG6521 CG10777 CG2064 CG7392 CG7392 CG7392 CG31012 CG3949 CG31012 CG3949 CG31012 CG10992 CG31012 CG10992 CG3231	$\begin{array}{c} 75\\ 75\\ 75\\ 74\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 72\\ 72\\ 72\\ 72\\ 71\\ 71\\ 71\\ 71\\ 71\\ 71\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70$	$\begin{array}{c} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12 Female sterile (2) Ketel Kinesin heavy chain Neural conserved at 73EF Septin 2 PRL-1 supercoiling factor p115 peanut Chd64 Signal transducing adaptor molecule maheshvara CG2064 Connector of kinase to AP-1 Replication protein A2 CG11811 hoi-polloi CIN85 and CD2AP orthologue Cathepsin B1 GDP-mannose 4.6-dehydratase Nucleoporin 50kD Troponin C-akin-1 T-cp1ζ
CG9680 CG9282 CG7697 CG10504 CG2231 CG4111 CG5389 CG33456 CG42668 CG8443 CG5119 CG7144 CG10198 CG7144 CG10198 CG7144 CG107765 CG7165 CG7165 CG7165 CG1461 CG4173 CG7765 CG7165 CG74993 CG9148 CG9148 CG1422 CG8705 CG14996 CG6521 CG10977 CG2064 CG7392 CG2064 CG7392 CG2064 CG7392 CG31012 CG10971 CG2064 CG7392 CG2064 CG7392 CG31012 CG10992 CG31012 CG10992 CG31012 CG10992 CG31012 CG10992 CG31012 CG1092 CG31012 CG1092 CG31012 CG1092 CG31012 CG1092 CG31012 CG1092 CG31012 CG1092 CG205 CG205 CG205 CG205 CG125 CG1092 CG31012 CG1092 CG31012 CG105 CG205 CG205 CG205 CG205 CG125 CG115 CG115 CG115 CG125 CG25 CG25 CG25 CG25 CG25 CG25 CG25 CG	75 75 74 73 73 73 73 72 72 71 71 70 70 70 70 70 70 70 69 68 68 68 66 66 66 66 66 66 66 66 66 66 66 66 66 66 66 65 65	$\begin{array}{c} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 1$	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12 Female sterile (2) Ketel Kinesin heavy chain Neural conserved at 73EF Septin 2 PRL-1 supercoiling factor p115 peanut Chd64 Signal transducing adaptor molecule maheshvara CG2064 Connector of kinase to AP-1 Replication protein A2 CG11811 hoi-polloi CIN85 and CD2AP orthologue Cathepsin B1 GDP-mannose 4,6-dehydratase Nucleoporin 50kD Troponin C-akin-1 T-cpl ² Pyruvate carboxylase
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG8443 CG5119 CG7144 CG10198 CG11271 CG2637 CG7165 CG11661 CG4173 CG7055 CG11661 CG4173 CG993 CG9148 CG1422 CG8705 CG14996 CG1422 CG8705 CG14993 CG1422 CG3049 CG1422 CG3049 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG10992 CG8890 CG2158 CG2803 CG2156 CG2803 CG1516 CG1516 CG9088	$\begin{array}{c} 75\\ 75\\ 75\\ 74\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73$	$\begin{array}{c} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 $	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12 Female sterile (2) Ketel Kinesin heavy chain Neural conserved at 73EF Septin 2 PRL-1 supercoiling factor p115 peanut Ch644 Signal transducing adaptor molecule maheshvara CG2064 Connector of kinase to AP-1 Replication protein A2 CG11811 hoi-polloi CIN85 and CD2AP orthologue Cathepsin B1 GDP-mannose 4,6-dehydratase Nucleoporin S0kD Troponin C-akin-1 T-ep1ζ Pyruvate carboxylase little imaginal discs
CG9680 CG9282 CG7697 CG10504 CG2331 CG4111 CG5389 CG33456 CG42668 CG8443 CG5119 CG7144 CG10198 CG11271 CG2637 CG7165 CG11661 CG4173 CG4993 CG9148 CG1422 CG8705 CG11661 CG4173 CG4993 CG9148 CG1422 CG8705 CG14996 CG6521 CG10777 CG2064 CG3949 CG31012 CG3949 CG31012 CG3949 CG31012 CG1516 CG9088 CG2258 CG2258 CG2258 CG2258 CG2258 CG2258 CG2258 CG2258 CG2257 CG2158 CG2258 CG2257 CG2158 CG2257 CG2578 CG278	$\begin{array}{c} 75\\ 75\\ 75\\ 74\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 73\\ 72\\ 72\\ 72\\ 71\\ 71\\ 71\\ 71\\ 71\\ 71\\ 71\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70\\ 70$	1 1 1 1 1 1 1 1 2 1 2 1 2 1 2 1 2 1 2 1 1 1 <td>Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12 Female sterile (2) Ketel Kinesin heavy chain Neural conserved at 73EF Septin 2 PRL-1 supercoiling factor p115 peanut Chd64 Signal transducing adaptor molecule mabeshvara CG2064 Connector of kinase to AP-1 Replication protein A2 CG11811 hoi-polloi CIN85 and CD2AP orthologue Cathepsin B1 GDP-mannose 4.6-dehydratase Nucleoporin 50kD Troponin C-akin-1 T-cp1ζ Pyruvate carboxylase little imaginal discs Ribosomal protein S3 </td>	Ribosomal protein L24 Cleavage stimulation factor 64 kilodalton subunit Integrin linked kinase TER94 Ribosomal protein L35 male sterile (3) 72Dt muscle wasted CG42668 clueless polyA-binding protein lysine ketoglutarate reductase Nucleoporin 98-96kD Ribosomal protein S12 Female sterile (2) Ketel Kinesin heavy chain Neural conserved at 73EF Septin 2 PRL-1 supercoiling factor p115 peanut Chd64 Signal transducing adaptor molecule mabeshvara CG2064 Connector of kinase to AP-1 Replication protein A2 CG11811 hoi-polloi CIN85 and CD2AP orthologue Cathepsin B1 GDP-mannose 4.6-dehydratase Nucleoporin 50kD Troponin C-akin-1 T-cp1ζ Pyruvate carboxylase little imaginal discs Ribosomal protein S3

CG7762	64	2	Regulatory particle non-ATPase 1
CG3714	64	2	CG3714
CG7626	64	1	Spt5
CG1943	63	1	CG1943
CG4817	62	1	Structure specific recognition protein
CG7935	62	1	moleskin
CG11198	62	2	Acetyl-CoA carboxylase
CG8610	61	5	Cell division cycle 27 ortholog
CG12101	61	1	Heat shock protein 60
CG4567	61	1	iconcelect
CC1524	60	1	Dibase mal motoin \$14s
CG1324	60	1	Ribosoniai protein S14a
CG3922	60	1	Ribosomal protein S1/
CG5289	60	2	Regulatory particle triple-A ATPase 2
CG1088	60	1	Vacuolar H+-ATPase 26kD subunit
CG14224	60	2	Ubiquilin
CG4046	60	2	Ribosomal protein S16
CG33180	60	2	Ranbp16
CG3203	58	1	Ribosomal protein L17
CG4679	58	1	CG4679
CG33129	58	2	CG33129
CG10641	57	1	Swiprosin-1
CG7939	56	1	Ribosomal protein L32
CG5838	56	1	DNA replication-related element factor
00000	50	•	Small ribonucleoprotein particle
CG10753	56	1	protein SmD1
CC 4529	56	1	CC4528
CG4558	50	1	004338
CG6907	55	1	CG6907
CG32533	55	2	CG32533
CG4183	54	1	Heat shock protein 26
CG6850	54	1	UDP-glucose-glycoprotein
000000	5.		glucosyltransferase
CG7074	54	1	missing oocyte
CG7581	53	1	Bub3
CG42708	53	1	Glutaminase
CG5931	53	1	lethal (3) 72Ab
CG9244	52	1	Aconitase
CG4457	52	1	Signal recognition particle protein 19
CG9423	52	1	karvopherin α3
CG8683	52	1	mon2
CG5733	52	1	Nucleoporin 75kD
CG17870	51	1	14-3-37
CG2016	51	1	Sentin 5
CC22710	51	1	CC9042
CG0903	51	1	CG0905
CG9325	51	1	hu li tai shao
CG17255	50	2	no circadian temperature entrainment
CG9160	49	1	mitochondrial acyl carrier protein 1
CG4821	49	1	Tequila
CG12030	48	2	UDP-galactose 4'-epimerase
CG8390	48	1	vulcan
CG2674	47	1	S-adenosylmethionine Synthetase
CG11738	47	1	lethal (1) G0004
CG7461	47	1	CG7461
CG1945	46	1	fat facets
CG9577	45	1 i	CG9577
CG8036	45	1	CG8036
CG6042	45	1	Cup12o4
CC22120	4.5	1	CC22120
CG33129	45	1	CG33129
0010596	44	1	Msr-110
CG6375	44	1	pitchoune
CG14792	43	1	stubarista
CG4252	43	1	meiotic 41
CG3395	43	1	Ribosomal protein S9

CG4752	43	2	CG4752
CG10824	43	1	Common Dpr-interacting protein
CG7985	42	2	CG7985
CG15717	42	1	CG15717
CG3262	42	1	CG3262
CG5723	41	1	Tenascin major
CG8609	41	1	Mediator complex subunit 4
CG4931	41	1	specifically Rac1-associated protein 1
CG2171	40	1	Triose phosphate isomerase
CG6226	40	1	FK506-binding protein 1
CG16827	40	2	Integrin alphaPS4 subunit
CG8787	40	2	Additional sex combs
CG4211	39	1	no on or off transient A
CG7404	38	1	estrogen-related receptor
CG5642	38	1	CG5642
CG31739	37	1	Aspartyl-tRNA synthetase, mitochondrial
CG3821	36	1	Aspartyl-tRNA synthetase
CG1071	36	1	E2F transcription factor 2
CG6546	36	1	Brahma associated protein 55kD
CG4785	36	1	Integrator 14
CG10194	36	1	CG10194
CG12223	35	1	Dorsal switch protein 1
CG9854	35	1	hiiragi
CG6339	35	1	rad50
CG5916	35	1	CG5916
CG15697	35	1	Ribosomal protein S30
CG7834	35	1	CG7834
CG31550	35	1	CG31550
CG7558	35	1	Actin-related protein 3
CG4035	34	1	Eukaryotic initiation factor 4E
CG7917	34	1	Nucleoplasmin
CG12264	34	1	CG12264
CG5728	34	1	CG5728
CG6946	34	1	glorund
CG15811	33	1	Ras opposite
CG30349	33	1	CG30349
CG15822	32	1	CG15822
CG7546	32	1	CG7546
CG6418	32	1	CG6418
CG5519	32	1	Prp19
CG4032	31	1	Abl tyrosine kinase
CG9553	31	1	chickadee
CG7070	31	1	Pyruvate kinase
CG7434	31	1	Ribosomal protein L22
CG2658	31	1	CG2658
CG8677	31	1	CG8677
CG10863	31	1	CG10863
CG3328	31	1	CG3328
CG13708	31	1	CG13708
CG10289	31	1	CG10289
CG4747	31	1	CG4747
CG31367	31	1	CG31367
CG6790	30	1	CG6790
CG14317	30	1	CG14317
CG31794	30	1	Paxillin

C.8 pMT-Dragon-GFP purification from *Drosophila* cells

CG #	Size	#pep	Full name
CG15792	227633	701	zipper
CG15792	237395	696	zipper
CG15792	232241	696	zipper
CG15792	228521	696	zipper
CG15792	233676	696	zipper
CG15792	227529	695	zipper
CG33052	37855	253	CG33052
CG4027	42194	173	Actin 5C
CG12051	42196	172	Actin 42A
CG10067	42207	157	Actin 57B
CG7478	42159	126	Actin 79B
CG5178	42072	129	Actin 88F
CG1484	144959	40	flightless I
CG9155	119657	44	Myosin 61F
CG3201	16717	41	Myosin light chain cytoplasmic
CG4898	29336	42	Tropomyosin 1
CG7438	117649	35	Myosin 31DF
CG4898	29248	39	Tropomyosin 1
CG4898	32537	37	Tropomyosin 1
CG4898	32795	34	Tropomyosin 1
CG8280	50561	25	Elongation factor 1a48D
CG4898	80290	32	Tropomyosin 1
CG4898	53394	32	Tropomyosin 1
CG4898	32783	32	Tropomyosin 1
CG4898	32783	32	Tropomyosin 1
CG4898	54666	32	Tropomyosin 1

CG4898	32783	32	Tropomyosin 1
CG4898	32783	32	Tropomyosin 1
CG10540	32853	18	capping protein alpha
CG1913	50561	28	α-Tubulin at 84B
CG2146	138912	22	dilute class unconventional myosin
CG4264	71372	17	Heat shock protein cognate 4
CG7595	251804	16	crinkled
CG1539	41524	19	tropomodulin
CG5825	15376	14	Histone H3.3A
CG6450	316451	21	lava lamp
CG5695	144349	20	jaguar
CG7583	42738	22	C-terminal Binding Protein
CG9476	50619	19	α-Tubulin at 85E
CG4145	175391	13	Collagen type IV
CG5502	45112	12	Ribosomal protein L4
CG12008	472720	9	karst
CG16858	194685	14	viking
CG3595	19999	16	spaghetti squash
CG4897	29591	10	Ribosomal protein L7
CG5409	42459	11	Actin-related protein 53D
CG4898	48168	9	Tropomyosin 1
CG4898	74950	9	Tropomyosin 1
CG4898	48168	9	Tropomyosin 1
CG4898	18518	9	Tropomyosin 1
CG8937	70871	5	Heat shock protein cognate 1
CG8937	61480	5	Heat shock protein cognate 1
CG8937	61480	5	Heat shock protein cognate 1

CG18572	248796	3	rudimentary
CG9277	51720	11	B-Tubulin at 56D
CG14702	20266	6	p-1 ubunii at 50D
C014/92	30200	0	Haat she sh 70 kDe protein
CG4147	72330	11	Heat snock /0-kDa protein
	00110	10	cognate 3
CG1106	82648	12	Gelsolin
CG31613	15436	11	His3:CG31613
CG9277	42619	10	β-Tubulin at 56D
CG9277	42619	10	β-Tubulin at 56D
CG18212	95266	5	aluminum tubes
CG3401	51387	7	ß Tubulin at 60D
CG1077	270101	5	p-1 douin at 00D
001977	279101	5	a spectrili
CG1883	22156	6	Ribosomal protein S7
CG8014	274770	5	Receptor mediated endocytosis 8
CG6699	103618	4	Coat Protein (coatomer) b'
CG1973	97727	6	CG1973
CG32138	133702	4	CG32138
CG0001	44050	2	Actin related protein 2
CC9/15	21922		Diharana protein 2
CG8615	21822	0	Ribosomai protein L18
CG1/158	31572	0	capping protein beta
CG3/52	57325	3	Aldehyde dehydrogenase
CG9359	50408	8	β-Tubulin at 85D
CG3751	15095	7	Ribosomal protein S24
CG7765	110901	4	Kinesin heavy chain
CG7558	47459	6	Actin-related protein 66B
			Transport and Golgi organization
CG8309	44515	3	
CC10170	25000	4	Foducone indusible I 2
0010160	55800	4	Ecuysone-inducible gene L3
CG10938	27094	1	Proteasome α5 subunit
CG15693	13593	4	Ribosomal protein S20
CG3379	11374	8	Histone H4 replacement
CG8578	45489	6	CG8578
CG6223	108308	4	Coat Protein (coatomer) B
CG33869	11356	7	His4·CG33869
CG32977	11256	7	High-CC22077
CC33877	11255	7	HIS4.CC336//
00338/9	11356	/	HIS4:CG338/9
CG33881	11356	7	H1s4:CG33881
CG1873	51030	10	Elongation factor 1a100E
CG1873	51030	10	Elongation factor 1a100E
CG1873	51030	10	Elongation factor 1a100E
CG1873	51030	10	Elongation factor 1g100E
CG5436	70043	4	Heat shock protein 68
CG8022	25760	4	Pibosomal protain \$5a
005922	23760	4	Ribosofilar protein 55a
CG5825	1368/	10	Histone H3.3A
CG6831	308914	2	rhea
CG7762	103010	1	Regulatory particle non-ATPase 1
CG10223	165034	5	Topoisomerase 2
CG2168	30549	7	Ribosomal protein S3A
CC21619	13355	8	His2A:CG31618
0.0151016			
0031018	10000	0	Regulatory particle triple-A
CG3455	45111	4	Regulatory particle triple-A
CG3455	45111	4	Regulatory particle triple-A ATPase 4
CG3455 CG4863	45111 47285	4	Regulatory particle triple-A ATPase 4 Ribosomal protein L3
CG3455 CG4863 CG17489	45111 47285 34244	4 3 7	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5
CG3455 CG4863 CG17489	45111 47285 34244 36109	4 3 7 3	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein
CG31618 CG3455 CG4863 CG17489 CG7111	45111 47285 34244 36109	4 3 7 3	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1
CG31618 CG3455 CG4863 CG17489 CG7111 CG1691	45111 47285 34244 36109 62376	4 3 7 3 2	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein
CG31613 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937	45111 47285 34244 36109 62376 240799	$\begin{array}{r} 3 \\ 4 \\ \hline 3 \\ \hline 7 \\ \hline 3 \\ \hline 2 \\ \hline 5 \\ \end{array}$	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein cheerio
CG31613 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253	45111 47285 34244 36109 62376 240799 19219		Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein cheerio Ribosomal protein L14
CG31613 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253 CG15099	45111 47285 34244 36109 62376 240799 19219 293740		Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein cheerio Ribosomal protein L14 CGI 5099
CG31613 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253 CG15099 CG5920	45111 47285 34244 36109 62376 240799 19219 293740 29110	$ \begin{array}{r} 3 \\ 4 \\ $	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein cheerio Ribosomal protein L14 CGI 5099 Ribosomal protein S2
CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253 CG15099 CG5920 CG3920	45111 47285 34244 36109 62376 240799 19219 293740 293740 29110 18545	$ \begin{array}{r} $	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein cheerio Ribosomal protein L14 CG15099 Ribosomal protein S2 Pibosomal protein S2
CG31618 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253 CG15099 CG5920 CG2168	45111 47285 34244 36109 62376 240799 19219 293740 29110 18546 18546	4 3 7 3 2 5 3 3 5 6 6	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein Cheerio Ribosomal protein L14 CG15099 Ribosomal protein S2 Ribosomal protein S3A Dibensid protein S2
CG31618 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253 CG15099 CG5920 CG2168 CG4863 CG4863	45111 47285 34244 36109 62376 240799 19219 293740 29110 18546 18295	4 3 7 3 2 5 3 3 5 6 2	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein cheerio Ribosomal protein L14 CG15099 Ribosomal protein S2 Ribosomal protein S3A Ribosomal protein L3
CG31618 CG3455 CG4863 CG17489 CG7111 CG1691 CG3937 CG6253 CG15099 CG5920 CG2168 CG4863 CG4863	45111 47285 34244 36109 62376 240799 19219 293740 29110 18546 18295 15772	$ \begin{array}{r} 3 \\ 4 \\ $	Regulatory particle triple-A ATPase 4 Ribosomal protein L3 Ribosomal protein L5 Receptor of activated protein kinase C 1 IGF-II mRNA-binding protein Cheerio Ribosomal protein L14 CG15099 Ribosomal protein S2 Ribosomal protein S3A Ribosomal protein L3 Ribosomal protein L3
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CG7626	1		
	120226	1	Spt5
CG6779	27682	4	Ribosomal protein S3
CG5289	19161	2	Regulatory particle triple-A
CU3289	47404	2	ATPase 2
CG13388	88252	1	A kinase anchor protein 200
CG5482	45005	1	CG5482
CG5000	227956	2	mini spindles
CG7756	70078	2	Haat shock protein cognete 2
CG7750	107024	2 5	Minute Stock protein cognate 2
CG3299	10/034	5	Vinculin
CG6846	17270	3	Ribosomal protein L26
CG9325	128772	2	hu li tai shao
CG1569	242390	3	rough deal
CG1994	113659	1	lethal (1) G0020
CG1528	08470	2	Coat Protain (contomor) v
C01528	56470	3	Coat Flotenii (coatoniei) y
CG2050	60387	3	modulo
CG17521	26024	2	Ribosomal protein L10
CG14996	20859	2	Chd64
0010077	4.4070		Heterogeneous nuclear
CG10377	44970	1	ribonucleoprotein at 27C
CG9012	102037	2	Clathrin heavy chain
000012	172757	2	Difference la sectoria C15
CG8552	17026	2	Ribosomal protein S15
CG1/291	66067	3	Protein phosphatase 2A at 29B
CG4651	25050	4	Ribosomal protein L13
CG10305	13543	3	Ribosomal protein S26
CG8705	60448	1	peanut
CG1115	24361	1	CG1115
CG7977	29445	2	Ribosomal protein I 23 A
0021704	25443	1	Ribosofilai proteini E23A
CG31/94	66128	1	Paxillin
CG12030	39071	2	UDP-galactose 4'-epimerase
CG3164	79017	2	CG3164
CG4463	20730	1	Heat shock protein 23
			eukarvotic translation initiation
CG10811	184570	2	factor 4G
CG15524	55135	2	Spindle assembly abnormal 6
			ortholog (C. elegans)
CG2238	95424	4	Elongation factor 2
CG4464	17394	3	Ribosomal protein S19a
CG8715	135935	1	lingerer
CG3074	50124	1	Secreted Wg-interacting molecule
CG14206	17967	2	Pibosomal protain \$10b
C014200	17807	3	Kibosolilai proteili 3100
CG12532	101914	1	Adaptor Protein complex $1/2$, β
			subunit
CG18076	624270	1	short stop
CG18076	620997	1	short stop
CG18076	590626	1	short stop
CG18076	992421	1	short stop
CG18076	623815	1	short stop
CC18076	500722	1	short stop
CG18076	590735	1	short stop
CG18076	620997	1	short stop
CG18076	623898	1	short stop
CG6684	13193	3	Ribosomal protein S25
CG3661	15041	2	Ribosomal protein L23
CG1559	131256	1	Upf1
CG18102	03371	1	chibire
CC4046	16070	2	Dihosomal matein \$16
CG4040	10878	2	Ribosoniai proteini 310
CG8900	17658	2	Ribosomal protein S18
(1(1)1000)	76610		hinno
CG11228	75518	1	mppo
CG11228 CG6757	63584	1	SH3PX1
CG11228 CG6757 CG15697	63584 14633	1 1 2	SH3PX1 Ribosomal protein S30
CG11228 CG6757 CG15697 CG2621	63584 14633 59192	1 1 2 1	SH3PX1 Ribosomal protein S30 shaggy
CG11228 CG6757 CG15697 CG2621 CG5499	73318 63584 14633 59192 14972	1 1 2 1 5	SH3PX1 Ribosomal protein S30 shaggy Histone H2A variant
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CG4111	14498	2	Ribosomal protein L35
CG6815	68489	2	belphegor
CG3195	17891	1	Ribosomal protein L12
CG10535	143580	1	Elongator complex protein 1
CG2033	14933	2	Ribosomal protein S15Aa
CG6522	91901	2	Testin ortholog
CG17272	17239	1	CG17272
CG6439	40698	1	CG6439
CG42611	548180	1	Megalin
CG8571	105000	1	smallminded
CG3529	57852	1	CG3529
CG6199	82914	1	procollagen lysyl hydroxylase
CG9805	134425	1	eIF3-S10
CG17489	15603	2	Ribosomal protein L5
CG6944	71371	2	Lamin
CG3178	75045	1	Recombination repair protein 1
CG2998	7529	1	Ribosomal protein S28b
CG32086	56258	3	CG32086
CG42668	70815	1	CG42668
CG4602	58673	1	Srp54
CG12324	14903	1	Ribosomal protein S15Ab
CG14549	26223	3	Sld5
CG3587	33919	1	CG3587
CG42595	93624	1	unextended
CG6143	11598	1	Protein on ecdysone puffs
CG1399	69173	1	Leucine-rich repeat
CG6476	72926	1	Suppressor of variegation 3-9
CG1945	314766	1	fat facets
CG17766	170592	1	Rabconnectin-3B
CG15899	354966	1	Ca^{2+} -channel protein α_1 subunit
CG16932	134507	1	Epidermal growth factor receptor
			pathway substrate clone 15
CG12292	42714	1	spichthyin
CG15100	113269	1	Methionyl-tRNA synthetase
CG11981	23618	1	Proteasome β3 subunit
CG1263	27989	1	Ribosomal protein L8
CG10840	127638	2	elF5B
CG31012	57268	1	CIN85 and CD2AP orthologue
CG1059	125078	1	Karyopherin ß 3
CG10501	57555	4	α methyl dopa-resistant
CG1524	16312	1	Ribosomal protein S14a
CG4079	22135	1	TBP-associated factor 11
CG14804	52794	1	Vacuolar protein sorting 26
CG3210	83085	1	Dynamin related protein I
CG15784	62634	1	CG15/84
CG4217	29945	1	mitochondrial transcription factor
CC5515	28702	1	A CC5515
CG3515	28702	1	CG5515 Dibasamal matain L D2
C04918	11/30	1	Glutamine fructore 6 phoephete
CG1345	77403	1	aminotraneforaça 2
CG6076	245267	1	Myosin 28B1
CG6976	245258	1	Myosin 28B1
CG6076	120117	1	Myosin 20D1
CG6076	120117	1	Myosin 28B1
CG32075	62202	1	CG32075
CG8857	18262	1	Ribosomal protein \$11
CG6077	218051	1	Cadherin 87A
CG42318	83573	1	approximated
CG12065	76897	1	CG12065
CG1810	75461	2	mRNA-capping-enzyme
CG14224	58798	1	Ibiquilin
CG15398	35388	2	CG15398
CG5525	57764	1	CG5525
CG18467	28173	1	CG18467
0010407	20175	1	Regulatory particle triple-A
CG2241	45255	1	ATPase 6-related
CG8472	16800	1	Calmodulin

$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	CG2746	24154	1 1	Ribosomal protein I 19
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	CG9281	70085	1	CG9281
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	CG1702	27130	1	Glutathione S transferase T3
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	CG12740	16019	1	Ribosomal protein I 28
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	0012/40	10017		Vesicle-associated membrane
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CG1599	25211	1	protein 7
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	CG13813	49728	3	CG13813
$\begin{array}{c cccc} CG33079 & 45975 & 1 & capulet \\ CG15249 & 21072 & 1 & CG15249 \\ CG9188 & 69081 & 1 & septin interacting protein 2 \\ CG8258 & 59795 & 1 & CG8258 \\ CG1475 & 23803 & 1 & Ribosomal protein L13A \\ CG4560 & 20349 & 1 & Actin-related protein 2/3 complex, subunit 3A \\ CG5378 & 45524 & 1 & Regulatory particle non-ATPase 7 \\ CG17209 & 156467 & 1 & CG17209 \\ CG7380 & 10338 & 1 & barrier to autointegration factor \\ CG18437 & 369614 & 1 & CG18437 \\ CG7808 & 23859 & 1 & Cytochrome c oxidase subunit 7A \\ CG7324 & 147970 & 1 & CG7324 \\ CG7808 & 23859 & 1 & Ribosomal protein S8 \\ CG30115 & 172806 & 1 & Guanine nucleotide exchange factor in mesoderm \\ CG3724 & 52971 & 1 & Phosphogluconate dehydrogenase \\ CG5371 & 92889 & 1 & Ribonucleoside diphosphate reductase large subunit \\ CG9124 & 38725 & 1 & Subunit 3D \\ CG4633 & 114629 & 3 & synthetase \\ CG4054 & 106158 & 1 & eIF3-58 \\ CG13809 & 198915 & 1 & osm-1 \\ CG1529 & 16959 & 1 & BETS ortholog \\ CG18026 & 173429 & 1 & glorund \\ CG4214 & 51818 & 1 & Syntaxin 5 \\ CG76368 & 26279 & 1 & BETS ortholog \\ CG16802 & 60164 & 1 & aarF domain containing kinase \\ CG3671 & 153384 & 1 & Atg17 \\ CG9983 & 39014 & 1 & Heterogeneous nuclear ribonucleoprotein at 98DE \\ CG16880 & 26279 & 1 & Nimrod C3 \\ CG1683 & 4007 & 1 & Adenine nucleotide translocase 2 \\ CG32649 & 88166 & 2 & CG32643 \\ CG32549 & 82093 & 1 & CG32549 \\ CG32643 & 88166 & 2 & CG32683 \\ CG4257 & 71722 & 1 & Signal-transducer and activator of transcription protein at 92E \\ CG9945 & 58896 & 1 & CG9945 \\ CG32649 & 70002 & 1 & CG32549 \\ CG32649 & 77002 & 1 & CG32643 \\ CG1249 & 239542 & 1 & CG12499 \\ CG6059 & 1004113 & 1 & CG6059 \\ CG17514 & 296460 & 1 & CG17514 \\ CG1422 & 93094 & 1 & p115 \\ CG32743 & 366260 & 1 & no-on-and-no-off transient C \\ CG1214 & 57687 & 1 & CG2121 \\ \end{array}$	CG5870	266316	1	ß Spectrin
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	CG33979	45975	1	capulet
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$\begin{array}{c ccccc} CG30115 & 172806 & 1 & Guanine nucleotide exchange factor in mesoderm \\ CG3724 & 52971 & 1 & Phosphogluconate dehydrogenase \\ CG5371 & 92889 & 1 & Ribonucleoside diphosphate reductase large subunit \\ CG9124 & 38725 & 1 & Eukaryotic initiation factor 3 p40 \\ subunit & subunit \\ CG4633 & 114629 & 3 & mitochondrial alanyl-tRNA \\ CG4633 & 114629 & 3 & synthetase \\ CG4954 & 106158 & 1 & eIF3-58 \\ CG13809 & 198915 & 1 & osm-1 \\ CG1359 & 16959 & 1 & BETS ortholog \\ CG18026 & 173429 & 1 & glorund \\ CG46214 & 51818 & 1 & Syntaxin 5 \\ CG7843 & 107612 & 1 & Ars2 \\ CG3608 & 60164 & 1 & aarf domain containing kinase \\ CG1480 & 26279 & 1 & Heterogeneous nuclear ribonucleoprotein at 98DE \\ CG16880 & 26279 & 1 & Nimrod C3 \\ CG1683 & 34007 & 1 & Adenine nucleotide translocase 2 \\ CG32649 & 88166 & 2 & CG32643 \\ CG32549 & 82093 & 1 & CG32643 \\ CG32549 & 82093 & 1 & CG32643 \\ CG32549 & 82093 & 1 & CG32549 \\ CG32683 & 88166 & 2 & CG32683 \\ CG4257 & 71722 & 1 & Signal-transducer and activator of transcription protein at 92E \\ CG9945 & 58896 & 1 & CG9945 \\ CG32649 & 72002 & 1 & CG12499 \\ CG32743 & 366260 & 1 & no-on-and-no-off transient C \\ CG41618 & 81739 & 1 & Zasp67 \\ CG32741 & 57687 & 1 & CG2121 \\ \end{array}$	CG7808	23859	1	Ribosomal protein S8
$\begin{array}{cccccccccccccccccccccccccccccccccccc$				Guanine nucleotide exchange
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	CG30115	172806	1	factor in mesoderm
$\begin{array}{c cccccc} CG5371 & 92889 & 1 & Ribonucleoside diphosphate reductase large subunit \\ \hline CG9124 & 38725 & 1 & Eukaryotic initiation factor 3 p40 \\ subunit \\ \hline CG4633 & 114629 & 3 & synthetase \\ \hline CG4633 & 114629 & 3 & synthetase \\ \hline CG4954 & 106158 & 1 & e1F3-58 \\ \hline CG13809 & 198915 & 1 & osm-1 \\ \hline CG1359 & 16959 & 1 & BET5 ortholog \\ \hline CG18026 & 173429 & 1 & calcium activated protein for secretion \\ \hline CG6946 & 61359 & 1 & glorund \\ \hline CG46214 & 51818 & 1 & Syntaxin 5 \\ \hline CG7843 & 107612 & 1 & Ars2 \\ \hline CG3608 & 60164 & 1 & aarF domain containing kinase \\ \hline CG1880 & 26279 & 1 & Nimrod C3 \\ \hline CG16880 & 26279 & 1 & Nimrod C3 \\ \hline CG16880 & 26279 & 1 & Nimrod C3 \\ \hline CG3661 & 79621 & 1 & CG3961 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 82093 & 1 & CG32643 \\ \hline CG32649 & 71002 & 1 & CG32643 \\ \hline CG4257 & 71722 & 1 & Signal-transducer and activator of transcription protein at 92E \\ \hline CG9945 & 58896 & 1 & CG9945 \\ \hline CG32743 & 366260 & 1 & no-on-and-no-off transient C \\ \hline CG32743 & 366260 & 1 & menage a trois \\ \hline CG2121 & 57687 & 1 & CG2121 \\ \hline \end{array}$	CG3724	52971	1	Phosphogluconate dehydrogenase
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CG4033 114029 5 synthetase CG4954 106158 1 eIF3-S8 CG13809 198915 1 osm-1 CG1359 16959 1 BET5 ortholog CG18026 173429 1 Calcium activated protein for secretion CG6946 61359 1 glorund CG4214 51818 1 Syntaxin 5 CG7843 107612 1 Ars2 CG3008 60164 1 aarF domain containing kinase CG1847 153384 1 Atg17 CG9983 39014 1 Heterogeneous nuclear ribonucleoprotein at 98DE CG16880 26279 1 Nimrod C3 CG1683 34007 1 Adenine nucleotide translocase 2 CG3961 79621 1 CG3961 CG32549 82093 1 CG32643 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9934	CC4622	114620	2	mitochondrial alanyl-tRNA
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CG3608 60164 1 aarF domain containing kinase CG1347 153384 1 Atg17 CG9983 39014 1 Heterogeneous nuclear ribonucleoprotein at 98DE CG16880 26279 1 Nimrod C3 CG1683 34007 1 Adenine nucleotide translocase 2 CG3661 79621 1 CG3961 CG32549 82093 1 CG32549 CG3263 88166 2 CG32549 CG3263 88166 2 CG32549 CG3263 88166 2 CG32549 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG12499 239542 1 CG12499 CG12499 239542 1 CG12499 CG12414 296460 1 CG17514 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67	CG7843	107612	1	Ars2
CG1347 153384 1 Atg17 CG9983 39014 1 Heterogeneous nuclear ribonucleoprotein at 98DE CG16880 26279 1 Nimrod C3 CG1683 34007 1 Adenine nucleotide translocase 2 CG3961 79621 1 CG3961 CG32549 82093 1 CG32549 CG32643 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG12499 239542 1 CG6059 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG1249 239542 1 CG17514 CG1249 239542 1 CG17514 CG1242 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG302	CG3608	60164	1	aarF domain containing kinase
CG9983 39014 1 Heterogeneous nuclear ribonucleoprotein at 98DE CG16880 26279 1 Nimrod C3 CG1683 34007 1 Adenine nucleotide translocase 2 CG3961 79621 1 CG3961 CG31617 26400 1 His1:CG31617 CG32683 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9345 58896 1 CG32494 CG12499 239542 1 CG12499 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG3001 67089 1 menage a trois CG2121 57687 1 CG2121	CG1347	153384	1	Atg17
CG16880 26279 1 ribonucleoprotein at 98DE CG16880 26279 1 Nimrod C3 CG1683 34007 1 Adenine nucleotide translocase 2 CG3961 79621 1 CG3961 CG32549 82093 1 CG32549 CG32549 82093 1 CG32549 CG32683 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9394 77002 1 CG9394 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG1249 239542 1 CG12499 CG6059 104413 1 CG6059 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-mo-off transient C CG14168 81739 1 Zasp67 CG3002 67089 1 menage a trois CG2121	CG0083	30014	1	Heterogeneous nuclear
CG16880 26279 1 Ninrod C3 CG1683 34007 1 Adenine nucleotide translocase 2 CG3961 79621 1 CG3961 CG32617 26400 1 His1:CG31617 CG32649 82093 1 CG32649 CG32649 82093 1 CG32649 CG32649 82093 1 CG32643 CG32653 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG12499 239542 1 CG12499 CG12499 239542 1 CG12499 CG12499 239542 1 CG12499 CG12414 296460 1 CG17514 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 <t< td=""><td>66//05</td><td>55014</td><td>•</td><td>ribonucleoprotein at 98DE</td></t<>	66//05	55014	•	ribonucleoprotein at 98DE
CG1683 34007 1 Adenine nucleotide translocase 2 CG3961 79621 1 CG3961 CG31617 26400 1 His1:CG31617 CG32549 82093 1 CG32549 CG32683 88166 2 CG32683 CG4257 71722 1 Signal-translucer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG32549 77002 1 CG12499 CG6059 104413 1 CG6059 CG17514 294600 1 CG17514 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG3021 67089 1 menage a trois CG3221 57687 1 CG2121	CG16880	26279	1	Nimrod C3
CG3961 79621 1 CG3961 CG31617 26400 1 His1:CG31617 CG32649 82093 1 CG32549 CG32683 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG9394 77002 1 CG9394 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG3001 7689 1 menage a trois CG2121 57687 1 CG2121	CG1683	34007	1	Adenine nucleotide translocase 2
CG31617 26400 1 His1:CG31617 CG32549 82093 1 CG32549 CG3263 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG9394 77002 1 CG9394 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG12414 296400 1 CG17514 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG3961	79621	1	CG3961
CG32549 82093 1 CG32549 CG32683 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG9945 58896 1 CG9394 CG12499 239542 1 CG12499 CG17514 266605 104413 1 CG6059 CG17514 296460 1 CG17514 CG12499 CG322743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30201 67089 1 menage a trois CG2121 57687 1 CG2121	CG31617	26400	1	His1:CG31617
CG32683 88166 2 CG32683 CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG9394 77002 1 CG9394 CG12499 239542 1 CG12499 CG17514 296460 1 CG17514 CG1422 93094 1 p115 CG2743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG32549	82093	1	CG32549
CG4257 71722 1 Signal-transducer and activator of transcription protein at 92E CG9945 58896 1 CG9945 CG9394 77002 1 CG9945 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG1242 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG32683	88166	2	CG32683
CG9945 58896 transcription protein at 92E CG9945 58896 CG9945 CG9394 77002 CG9394 CG12499 239542 CG12499 CG6059 1004413 CG6059 CG17514 296400 1 CG122 93094 1 CG1242 93094 1 CG1242 93094 1 CG1422 93094 1 CG1423 366260 1 CG3021 67089 1 CG3021 67089 1 CG3021 57687 1 CG2121 57687 1	CG4257	71722	1	Signal-transducer and activator of
CG9945 58896 1 CG9945 CG9394 77002 1 CG9394 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG122 93094 1 p115 CG32743 366260 1 no-on-and-no-fit transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	004257	71722	•	transcription protein at 92E
CG9394 77002 1 CG9394 CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG9945	58896	1	CG9945
CG12499 239542 1 CG12499 CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG1242 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG3021 67089 1 menage a trois CG2121 57687 1 CG2121	CG9394	77002	1	CG9394
CG6059 104413 1 CG6059 CG17514 296460 1 CG17514 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30201 67089 1 menage a trois CG2121 57687 1 CG2121	CG12499	239542	1	CG12499
CG17514 296460 1 CG17514 CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG6059	104413	1	CG6059
CG1422 93094 1 p115 CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG17514	296460	1	CG17514
CG32743 366260 1 no-on-and-no-off transient C CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG1422	93094	1	p115
CG14168 81739 1 Zasp67 CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG32743	366260	1	no-on-and-no-off transient C
CG30021 67089 1 menage a trois CG2121 57687 1 CG2121	CG14168	81739	1	Zasp67
CG2121 57687 1 CG2121	CG30021	67089	1	menage a trois
	CG2121	57687	1	CG2121

C.9 pMT-Dragon-GFP +OA purification from *Drosophila* cells

CG #	Score	#pep	Full name
CG15792	36530	566	zipper
CG15792	36311	564	zipper
CG15792	36311	564	zipper
CG15792	36311	564	zipper
CG15792	36311	564	zipper
CG15792	36266	563	zipper
CG33052	24140	337	CG33052
CG4027	9568	145	Actin 5C
CG12051	9532	143	Actin 42A
CG10067	7953	122	Actin 57B
CG7478	7380	103	Actin 79B
CG5178	5060	100	Actin 88F
CG3201	2730	51	Myosin light chain cytoplasmic
CG9155	2495	47	Myosin 61F
CG9155	2483	46	Myosin 61F
CG9155	2483	46	Myosin 61F
CG9155	2483	46	Myosin 61F
CG7583	2262	40	C-terminal Binding Protein
CG7583	1984	38	C-terminal Binding Protein
CG4264	1796	35	Heat shock protein cognate 4
CG1973	1584	20	yata

CG5695	1513	29	jaguar
CG4898	1404	33	Tropomyosin 1
CG5695	1401	26	jaguar
CG8280	1367	31	Elongation factor 1a48D
CG9012	1347	22	Clathrin heavy chain
CG4898	1313	31	Tropomyosin 1
CG7438	1280	26	Myosin 31DF
CG9277	1220	18	β-Tubulin at 56D
CG1913	1201	25	α-Tubulin at 84B
CG9277	1176	17	β-Tubulin at 56D
CG3595	1144	27	spaghetti squash
CG9277	1117	16	β-Tubulin at 56D
CG9277	1117	16	β-Tubulin at 56D
CG4898	1113	25	Tropomyosin 1
CG1484	1107	21	flightless I
CG4898	1022	23	Tropomyosin 1
CG16858	1014	16	viking
CG4145	984	15	Collagen type IV
CG5825	748	6	Histone H3.3A
CG9476	747	16	α-Tubulin at 85E
CG17158	745	12	capping protein beta
CG12065	708	15	CG12065

CG4898	697	16	Tropomyosin 1
CG4898	697	16	Tropomyosin 1
CG4898	697	16	Tropomyosin 1
CC4808	607	16	Tropomyosin 1
CC4898	697	10	Tiopolityosiii 1
CG4898	697	16	Tropomyosin 1
CG4898	697	16	Tropomyosin 1
CG4898	697	16	Tropomyosin 1
CG2146	673	20	dilute class unconventional myosin
CG18743	628	9	Heat-shock-protein-70Ab
005426	620	,	Heat-shock-protein-70A0
CG5456	600	8	Heat shock protein 68
CG31449	600	8	Heat-shock-protein-70Ba
CG31359	600	8	Heat-shock-protein-70Bb
CG6489	600	8	Heat-shock-protein-70Bc
CG5824	600	0	Hon70Phb
C03834	500	0	TISP/0B00
CG6223	590	12	Coat Protein (coatomer) B
CG10938	566	2	Proteasome α5 subunit
CG4898	549	10	Tropomyosin 1
CG4898	549	10	Tropomyosin 1
CC4000	540	10	Tropolityosin 1
CG4898	549	10	1 ropomyosin 1
CG4898	549	10	Tropomyosin 1
CG5502	548	11	Ribosomal protein L4
CG1539	548	10	tropomodulin
CG2146	522	16	dilute class unconventional muccin
002140	323	10	unute class unconventional myosin
CG4634	508	5	Nucleosome remodeling factor - 38kD
CG3752	506	2	Aldehyde dehydrogenase
CG1528	488	8	Coat Protein (coatomer) y
CG2331	481	10	TER94
CG31619	/181	8	His2A-CC31619
0031010	+01	0	DNA nolumenter H 221 D
CG/885	4/0	2	KINA polymerase II 33KD subunit
CG9325	463	5	hu li tai shao
CG3401	458	7	β-Tubulin at 60D
CG6699	441	6	Coat Protein (coatomer) B'
CG0350	428	10	B-Tubulin at 85D
CC12052	+20	10	p-1 uouiii at 65D
CG12052	425	2	longitudinals lacking
CG8937	410	4	Heat shock protein cognate 1
CG8937	410	4	Heat shock protein cognate 1
CG8937	410	4	Heat shock protein cognate 1
CC1972	407	15	Elongation fastor 1=100E
001875	407	13	Elongation factor 10100E
CG1873	407	15	Elongation factor 1a100E
CG1873	407	15	Elongation factor 1a100E
CG1873	407	15	Elongation factor 1a100E
CG1242	378	8	Heat shock protein 83
CC6921	279	2	where
000851	378	3	mea
CG3016	3/3	4	Ubiquitin specific protease 30
CG6871	372	5	Catalase
CG10160	365	5	Ecdysone-inducible gene L3
CG7595	363	6	crinkled
0010070	333	4	Regulatory particle triple A ATPase 5
((til)))/()		-	
CG10370	330	3	karet
CG10370 CG12008	330	3	karst
CG10370 CG12008 CG7961	330 329	3	karst Coat Protein (coatomer) α
CG10370 CG12008 CG7961 CG32549	330 329 317	3 11 7	karst Coat Protein (coatomer) α CG32549
CG10370 CG12008 CG7961 CG32549 CG10540	330 329 317 301	3 11 7 6	karst Coat Protein (coatomer) α CG32549 capping protein alpha
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499	330 329 317 301 294	3 11 7 6 6	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996	330 329 317 301 294 294	3 11 7 6 6 8	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148	330 329 317 301 294 294 294 289	3 11 7 6 6 8 4	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG1106	330 329 317 301 294 294 289 287	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin
CG10370 CG12008 CG7961 CG32549 CG10540 CG14996 CG6148 CG1106 CG11143	330 329 317 301 294 294 289 287 285	$3 \\ 11 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 4$	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG1106 CG11143	330 329 317 301 294 294 289 287 285 285	3 11 7 6 6 8 4 7 4 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Electric factor 2
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG1106 CG11143 CG2238	330 329 317 301 294 294 289 287 285 284	3 11 7 6 8 4 7 4 7 7	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14896 CG14896 CG1106 CG11143 CG2238 CG6815	330 329 317 301 294 294 289 287 285 284 276	3 11 7 6 8 4 7 4 7 7 7	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG6148 CG1106 CG11143 CG2238 CG6815 CG3937	330 329 317 301 294 294 289 287 285 284 276 275	3 11 7 6 8 4 7 4 7 7 7 7	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG1106 CG11143 CG2238 CG6815 CG3937 CG8014	330 329 317 301 294 294 289 287 285 284 276 275 274	$ \begin{array}{r} 3 \\ 111 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG14996 CG1143 CG238 CG61143 CG2238 CG6815 CG3937 CG8014 CG6439	330 329 317 301 294 294 289 287 285 284 276 275 274 272	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG14996 CG1106 CG11143 CG2238 CG1066 CG6815 CG3937 CG8014 CG6439 CG6439 CG6439	330 329 317 301 294 294 289 287 285 284 276 275 274 275 274 272 265	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439 Ribosomal protein L7
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG1106 CG11143 CG2238 CG6815 CG3937 CG8014 CG6439 CG6439 CG64397	330 329 317 301 294 289 287 285 284 276 275 274 275 274 272 265	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439 Ribosomal protein L7 belphegor
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG6148 CG6148 CG6148 CG6148 CG6815 CG3937 CG8014 CG6439 CG4	330 329 317 301 294 289 287 285 284 275 274 275 274 272 265 265 265	$ \begin{array}{r} 3 \\ 111 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439 Ribosomal protein L7 belle
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG14896 CG1106 CG11143 CG2238 CG6815 CG3937 CG8014 CG6439 CG64397 CG9748 CG9748 CG9748	330 329 317 301 294 294 289 287 285 284 276 275 274 275 274 275 274 275 265 262 265	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 6 \\ 8 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 8 \\ 7 \\ $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439 Ribosomal protein L7 belle Calamodulin
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG1106 CG11143 CG2238 CG6815 CG3937 CG8014 CG6439 CG4897 CG8014 CG6439 CG4887 CG8748 CG8472 CG4147	330 329 317 301 294 289 287 285 284 276 275 284 276 275 265 265 265 265 261 261	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 8 \\ 4 \\ 7 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ 7 \\ 5 \\ \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439 Ribosomal protein L7 belle Calmodulin Heat shock 70-kDa protein cognate 3
CG10370 CG12008 CG7961 CG32549 CG10540 CG5499 CG14996 CG6148 CG6148 CG6148 CG6148 CG6148 CG6149 CG64147 CG6439 CG6472 CG9748 CG8472 CG9748 CG8472 CG9748	330 329 317 301 294 289 287 285 284 276 275 274 272 265 262 265 262 261 259	$ \begin{array}{r} 3 \\ 11 \\ 7 \\ 6 \\ 8 \\ 4 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 4 \\ 6 \\ 4 \\ 8 \\ 7 \\ 7 \\ 5 \\ 2 \\ \end{array} $	karst Coat Protein (coatomer) α CG32549 capping protein alpha Histone H2A variant Chd64 Putative Achaete Scute Target 1 Gelsolin Inos Elongation factor 2 belphegor cheerio Receptor mediated endocytosis 8 CG6439 Ribosomal protein L7 belle Calmodulin Heat shock 70-kDa protein cognate 3 CG7878
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CG4634	190	2	Nucleosome remodeling factor - 38kD
CG2621	189	2	shaggy
CG12280	199	-	Dibosomel protein \$12
0015589	100	4	Ribosoniai proteini 515
CG11943	188	2	Nucleoporin 205kD
CG17333	178	2	CG17333
CG18740	177	3	moira
002714	177	2	002714
CG3/14	1//	2	CG3/14
CG18572	176	1	rudimentary
CG1782	175	2	Ubiquitin activating enzyme 1
0020102	175	2	CC20122
CG30122	173	3	0030122
CG8578	173	4	CG8578
CG1064	172	1	Snf5-related 1
CG2252	171	2	famala starila (1) homaatia
CG2252	171	2	Temate sterile (1) homeone
CG3379	171	5	Histone H4 replacement
CG5289	171	2	Regulatory particle triple-A ATPase 2
CG16944	170	8	stress-sensitive B
000004	1/0	0	Sites sensitive b
CG8036	168	2	CG8036
CG7726	167	3	Ribosomal protein L11
CG18190	167	4	CG18190
000015	107		Diharanal anatala L 19
C08015	107	3	Ribosoniai protein L18
CC16022	165	2	Epidermal growth factor receptor
C010932	105	2	pathway substrate clone 15
CG4878	163	4	aIE3-SQ
004070	103	4	en 5-37
CG6339	163	2	rad50
CG31048	162	1	sponge
CG6617	160	2	06617
CC14200	100	1	0014000
CG14299	15/	1	CG14299
CG7756	154	2	Heat shock protein cognate 2
			Ribonucleoside diphosphate reductase
CG5371	154	2	lorgo enhunit
L			large subunit
CG12522	152	4	Adaptor Protein complex 1/2, β
0012002	135	4	subunit
CG8/130	153	1	T-complex Chaperonin 5
0010001	155	1	1-complex Chaperonnii 5
CG10986	152	1	garnet
CG1548	151	4	cathD
CG9805	151	3	eIF3-S10
005000	1.40	2	Diherand i 02
CG5920	149	5	Kibosomai protein S2
CG1683	147	6	Adenine nucleotide translocase 2
CG1683	147	6	Adenine nucleotide translocase 2
0017654	146	1	Parlan
CG1/654	146	1	Enolase
CG9888	146	4	Fibrillarin
CG18102	146	3	shihire
CC11056	140	2	Nuclear siz 2591-D
CG11856	146	2	Nucleoporin 358kD
CG16916	145	1	Regulatory particle triple-A ATPase 3
CG5378	144	3	Regulatory particle non-ATPase 7
CC0292	144	2	Dibacamal matain I 24
009282	144	2	Kibosofiai protein L24
CC1245	144	2	Glutamine:fructose-6-phosphate
C01545	144	2	aminotransferase 2
	142	2	Dihaa1 0000
CG15693	143		Kiposomal protein S20
CG15693	145	2	Ribosomal protein S20
CG15693 CG9901	143	1	Actin-related protein 2
CG15693 CG9901 CG1403	143 141 139	2 1 1	Actin-related protein 2 Septin 1
CG15693 CG9901 CG1403 CG9543	143 141 139 138	2 1 1 1	KIDOSOMAI protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε
CG15693 CG9901 CG1403 CG9543 CG10306	145 141 139 138	2 1 1 1 2	Actin-related protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) c
CG15693 CG9901 CG1403 CG9543 CG10306	143 141 139 138 138	2 1 1 2	Kinosomai protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169	143 141 139 138 138		Kinosomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169	143 141 139 138 138 138	2 1 1 2 2	κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG17949	143 141 139 138 138 138 138	$ \begin{array}{r} 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \end{array} $	Kinosomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG17949 CG2416	143 141 139 138 138 138 138	$\begin{array}{c} 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\end{array}$	Kitoosomai protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Bauulguru particle zen ΔTPace 9
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG17949 CG3416	143 141 139 138 138 138 138 138	$\begin{array}{c} 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\$	Kinosomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691	143 141 139 138 138 138 138 138 138 135 135	$\begin{array}{c} 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\$	Kioosomai protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954	143 141 139 138 138 138 138 138 138 135 135 135		κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smo5
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG3416 CG17949 CG3416 CG1691 CG8954	143 141 139 138 138 138 138 138 135 135 135 134		Kioosomai protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Dibogenuel neutrice 117
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG17949 CG37949 CG3416 CG1691 CG8954 CG3203	143 141 139 138 138 138 138 138 138 135 135 135 134 134	$ \frac{2}{1} $ 1 2 2 2 2 2 1 3 3	κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG4169 CG3416 CG1691 CG8954 CG3203 CG3821	143 141 139 138 138 138 138 138 138 138 135 135 135 134 134 134	$ \begin{array}{r} 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 1 \\ 3 \\ 1 \\ \end{array} $	Kitoosomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) s CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase
CG15693 CG9901 CG1403 CG9543 CG10306 CG4169 CG4169 CG3416 CG1691 CG8954 CG3203 CG3821 CG6258	143 141 139 138 138 138 138 138 135 135 135 134 134 133 132	$ \frac{2}{1} $ 1 1 2 2 2 2 2 2 1 3 1 3 1 3 1 3 1 3 1 3 1 3 1 3 1 3 1 1	Kuosomai protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit
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CG15693 CG9901 CG1403 CG9543 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954 CG3203 CG3821 CG6258 CG4003 CG2216	143 141 139 138 138 138 138 135 135 135 135 135 134 134 133 132 131 130	$ \begin{array}{c} 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 1 \\ 3 \\ 1 \\ 3 \\ 1 \\ 3 \\ 1 \end{array} $	κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue
CG15693 CG9901 CG1403 CG9543 CG9543 CG17949 CG17949 CG3416 CG1691 CG8954 CG3203 CG3203 CG3203 CG2206 CG2206 CG2206	143 141 139 138 138 138 138 138 138 138 138 138 138 131 130 129	$ \begin{array}{c} 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 1\\ 3\\ 1\\ 3\\ 1\\ 3\\ 1\\ 3\\ 1 \end{array} $	κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue CG5704
CG15693 CG9901 CG1403 CG9543 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954 CG3203 CG3821 CG6258 CG4003 CG2216 CG5704 CG5704	143 141 139 138 138 138 138 135 135 135 135 134 134 133 132 131 130 129 129	$ \begin{array}{c} 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 1 \\ 3 \\ 1 \\ 3 \\ 1 \\ $	κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue CG5704 Chalese
CG15693 CG9901 CG1403 CG9543 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954 CG3203 CG3203 CG3203 CG3203 CG32216 CG6258 CG4003 CG2216 CG5704 CG8443 CG5704	143 141 139 138 138 138 138 138 138 135 135 134 134 133 132 131 130 129 129		κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue CG5704 clueless CG1 roop
CG15693 CG9901 CG1403 CG9543 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954 CG3203 CG3203 CG32216 CG6258 CG4003 CG2216 CG5704 CG5704 CG5704	143 141 139 138 138 138 138 138 135 134 135 134 133 131 130 129 129 129	$ \begin{array}{c} 2\\ 1\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 1\\ 3\\ 1\\ 3\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	Kuosomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue CG5704 clueless CG15820
CG15693 CG9901 CG1403 CG9543 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954 CG3203 CG3203 CG3821 CG6258 CG4003 CG2216 CG5704 CG5704 CG8443 CG15820 CG15820	143 141 139 138 138 138 138 138 138 131 131 130 129 129 129 129 129 129 129 127	$ \begin{array}{c} 2 \\ 1 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1$	Actin-related protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ɛ CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue CG5704 clueless CG15820 Ribosomal protein S9
CG15693 CG9901 CG1403 CG9543 CG9543 CG10306 CG4169 CG17949 CG3416 CG1691 CG8954 CG3203 CG3821 CG6258 CG4003 CG3821 CG6258 CG4003 CG5704 CG5704 CG3395 CG3395	143 141 139 138 138 138 138 138 138 135 134 135 134 133 132 131 130 129 129 129 129 127	$ \begin{array}{c} 2\\ 1\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 1\\ 3\\ 1\\ 1\\ 3\\ 1\\ 1\\ 1\\ 3\\ 3\\ 3\\ 1 \end{array} $	κισοsomal protein S20 Actin-related protein 2 Septin 1 Coat Protein (coatomer) ε CG10306 Ubiquinol-cytochrome c reductase core protein 2 His2B:CG17949 Regulatory particle non-ATPase 8 IGF-II mRNA-binding protein Smg5 Ribosomal protein L17 Aspartyl-tRNA synthetase Replication factor C 38kD subunit pontin Ferritin 1 heavy chain homologue CG5704 clueless CG15820 Ribosomal protein S9 Sec13 ortholog (S cerevisine)
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Appendix C

CG8332	107	2	Ribosomal protein S15
CG1646	107	2	CG1646
CG7808	106	5 4	mad2 Ribosomal protein SS
CG7762	100	2	Regulatory particle non-ATPase 1
CG4429	103	4	RNA-binding protein 2
CG9281	103	2	CG9281
CG9881	103	1	Actin-related protein 2/3 complex,
CG4869	102	2	ß-Tubulin at 97EF
CG4869	102	2	B-Tubulin at 97EF
CG5434	102	1	Signal recognition particle protein 72
CG6779	101	4	Ribosomal protein S3
CG8542	100	3	Heat shock protein cognate 5
CG7558	100	2	Actin-related protein 66B
CG12030	100	2	UDP-galactose 4 -epimerase
CG1633	98	3	thioredoxin peroxidase 1
CG4260	98	1	Adaptor Protein complex 2, a subunit
CG3922	97	2	Ribosomal protein S17
CG43119	97	3	Ectoderm-expressed 4
CG4046	96	3	Ribosomal protein S16
CG1349	96	3	di-18
007111		2	Receptor of activated protein kinase C
CG/III	94	2	1
CG10944	92	2	Ribosomal protein S6
CG6948	92	2	Clathrin light chain
CG3455 CC2751	91	2	Ribosomal protoin \$24
CG1250	91	1	Sec23 ortholog (S. cerevisiae)
CG4157	90	1	Regulatory particle non-ATPase 12
CG12262	90	1	<u>CG12262</u>
CG7283	90	1	Ribosomal protein L10Ab
CG2905	90	1	Nipped-A
CG6315	89	1	female lethal d
CG5119	89 88	2	polyA-binding protein
CG4033	88	2	RNA polymerase I 135kD subunit
CG3523	88	3	Fatty acid synthase 1
CG5261	88	2	midline uncoordinated
CG4931	88	1	specifically Rac1-associated protein 1
CG17420	87	4	Ribosomal protein L15
CG3612	86	3	bellwether
CG14792	85 84	2	Studarista Histone H3 34
CG31613	84	2	His3:CG31613
CG33803	84	2	His3:CG33803
CG33806	84	2	His3:CG33806
CG33809	84	2	His3:CG33809
CG33812	84	2	His3:CG33812
CG33815	84	2	His3:CG33815
CG33821	84	2	His3:CG33821
CG33824	84	2	His3:CG33824
CG33827	84	2	His3:CG33827
CG33830	84	2	His3:CG33830
CG33833	84	2	His3:CG33833
CG33836	84	2	His3:CG33836
CG33842	84	2	His3:CG33842
CG33845	84	2	His3:CG33845
CG33848	84	2	His3:CG33848
CG33851	84	2	His3:CG33851
CG33854	84	2	His3:CG33854
CG33857	84	2	His3:CG33857
CG33863	04	4	11155:CC555600
2333005	84	2	His3.CG33863
CG33866	84 84	2	His3:CG33863 His3:CG33866
CG33866 CG4863	84 84 82	2 2 1	His3:CG33863 His3:CG33866 Ribosomal protein L3
CG33866 CG4863 CG10423	84 84 82 82	2 2 1 2	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27
CG33866 CG4863 CG10423 CG3724	84 82 82 81	2 2 1 2 1	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase
CG33866 CG4863 CG10423 CG3724 CG17611	84 84 82 82 81 81 81	2 2 1 2 1 1	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase EIF6 B22C1D
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CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG8947 CG3314	84 84 82 81 81 80 80 79	2 2 1 2 1 1 1 1 1 1 1	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG8947 CG3314 CG8231	84 84 82 81 81 80 80 80 79 79 79	2 2 1 2 1 1 1 1 1 1 2	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ
CG33866 CG4863 CG10423 CG3724 CG3724 CG7724 CG2699 CG7324 CG8947 CG3314 CG8231 CG1994	84 84 82 81 81 80 80 80 79 79 79 79	$ \begin{array}{c} 2 \\ 2 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 1 \\ 2 \\ 2 \\ 1 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1 lethal (1) G0020
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG8947 CG3314 CG8231 CG1994 CG5028 CG5028	84 84 82 81 81 80 80 80 79 79 79 79 79 79	2 2 1 2 1 1 1 1 1 2 1 2 1 3 3	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp15 lethal (1) G0020 CG5028
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG8947 CG3314 CG8231 CG1994 CG5028 CG5330 CG774	84 84 82 81 81 80 80 80 79 79 79 79 79 79 79 79 79 78	$ \begin{array}{r} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 3\\ 1\\ 1 \end{array} $	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting new in 1
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG8947 CG3314 CG8231 CG1994 CG5028 CG5320 CG2774 CG3587	84 84 82 82 81 81 80 80 80 79 79 79 79 79 79 79 79 78 78 78	$ \begin{array}{r} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp15 lethal (1) 60020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG8947 CG3314 CG8231 CG1994 CG5028 CG5330 CG2774 CG3587 CG16817	84 84 82 82 81 80 80 80 79 79 79 79 79 79 79 79 79 79 79 79 79	$ \begin{array}{r} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 3\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 2\\ 1\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG3314 CG8231 CG1994 CG5028 CG5330 CG2774 CG3587 CG16817 CG5726	84 84 82 82 81 81 80 80 80 80 79 79 79 79 79 79 79 79 79 79 77 77 77	$ \begin{array}{c} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 3\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG5726
CG33866 CG4863 CG10423 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3947 CG3314 CG8947 CG3314 CG8231 CG1994 CG5028 CG5330 CG2774 CG3587 CG16817 CG5726 CG8351	84 84 82 82 81 81 80 80 80 80 79 79 79 79 79 79 79 79 78 78 77 77 76 76	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG6726 Tcp-1η
CG33866 CG4863 CG10423 CG3724 CG3724 CG3724 CG2699 CG7324 CG8947 CG3314 CG8947 CG3314 CG8947 CG5028 CG5330 CG2774 CG5526 CG3587 CG16817 CG5726 CG8726 CG8351 CG41733	84 84 82 81 81 80 80 80 80 80 80 80 80 79 79 79 79 79 79 79 79 79 79 79 79 79	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1 lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG5726 Tcp-1η Septin 2
CG33866 CG4863 CG10423 CG3724 CG3724 CG2699 CG7324 CG8947 CG3314 CG8947 CG3314 CG8231 CG1994 CG5028 CG5028 CG5028 CG330 CG2774 CG3587 CG16817 CG5726 CG3587 CG16817 CG16817 CG4173 CG12512 CG4173	84 84 82 81 81 80 80 79 79 79 79 79 79 79 79 79 79 79 79 79	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp15 lethal (1) 60020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG5726 Tcp-1ŋ Septin 2 CG12512
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG3314 CG8947 CG3314 CG994 CG5028 CG5028 CG5028 CG2774 CG3587 CG16817 CG5726 CG8351 CG4173 CG12512 CG4217 CG333070	84 84 82 81 81 80 80 79 79 79 79 79 79 79 79 79 79 79 79 79	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 3\\ 3\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 3\\ 3\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG3587 CG16817 CG5726 Tcp-1η Septin 2 CG12512 mitochondrial transcription factor A
CG33866 CG4863 CG10423 CG3724 CG17611 CG2699 CG7324 CG3314 CG8231 CG1994 CG5028 CG5330 CG2774 CG3587 CG16817 CG3587 CG16817 CG3526 CG4512 CG4217 CG33979 CG6476	84 84 82 81 81 80 80 80 80 80 80 79 79 79 79 79 79 79 79 79 79 79 79 79	2 2 1 1 1 1 1 1 1 2 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 2 1 1 1 2 1 1 2 1	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG3587 CG16817 CG5726 Tcp-1η Septin 2 CG12512 mitochondrial transcription factor A capulet Suppressor of variegation 3-9
CG33866 CG4863 CG10423 CG3724 CG3724 CG2699 CG7324 CG8947 CG3314 CG8947 CG3314 CG8947 CG5028 CG5330 CG2774 CG3587 CG16817 CG726 CG8351 CG12512 CG4217 CG33979 CG6476 CG7439	84 84 82 81 81 80 80 80 80 80 79 79 79 79 79 79 79 79 79 79 79 79 79	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\ 3\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG5726 Tcp-1η Septin 2 CG12512 mitochondrial transcription factor A capulet Suppressor of variegation 3-9 Argonaute 2
CG33866 CG4863 CG10423 CG17611 CG2699 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG394 CG528 CG5330 CG2774 CG3587 CG16817 CG3587 CG41631 CG4173 CG42171 CG33979 CG4464	84 82 81 80 80 79 79 79 79 78 78 77 76 76 75 74 73 72	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 3\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG5726 Tcp-1η Septin 2 CG12512 mitochondrial transcription factor A capulet Suppressor of variegation 3-9 Argonaute 2 Ribosomal protein 519a
CG33866 CG4863 CG10423 CG17611 CG2699 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG3724 CG8947 CG3314 CG929 CG5320 CG5330 CG2774 CG3587 CG16817 CG5726 CG4173 CG12512 CG4217 CG33979 CG6476 CG7439 CG426 CG3226	84 82 81 80 80 79 79 79 78 77 76 75 74 73 72 72	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 3\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase eIF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) G0020 CG5028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG6817 CG6817 CG6726 Tcp-1η Septin 2 CG12512 mitochondrial transcription factor A capulet Suppressor of variegation 3-9 Argonaute 2 Ribosomal protein S19a CG3226
CG33866 CG4863 CG10423 CG3724 CG3724 CG3724 CG2699 CG7324 CG8947 CG3314 CG8947 CG3314 CG1994 CG5028 CG330 CG2774 CG5028 CG3387 CG16817 CG16817 CG5726 CG4217 CG12512 CG4217 CG33979 CG6476 CG7439 CG4464 CG3226 CG4226 CG4226 CG14206	84 82 81 80 80 79 79 79 79 79 78 77 76 75 75 74 73 72 72 72	$\begin{array}{c} 2\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 3\\ 1\\ 1\\ 2\\ 3\\ 1\\ 1\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 1\\ 2\\ 2\\ 3\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	His3:CG33863 His3:CG33866 Ribosomal protein L3 Ribosomal protein S27 Phosphogluconate dehydrogenase elF6 Pi3K21B CG7324 26-29kD-proteinase Ribosomal protein L7A T-cp1ζ lethal (1) 60020 CG3028 Nucleosome assembly protein 1 Sorting nexin 1 CG3587 CG16817 CG65726 TCp-1η Septin 2 CG65726 TCp-1η Septin 2 CG12512 mitochondrial transcription factor A capulet Suppressor of variegation 3-9 Argonaute 2 Ribosomal protein S19a CG3226 Ribosomal protein S19b

CG4364	70	1	CG4364
CG6684	69	2	Ribosomal protein S25
CG3333	69	1	Nucleolar protein at 60B
CG6/82 CG5028	69	2	scheggia
CG11901	68	1	EG3028
CG13349	68	1	Regulatory particle non-ATPase 13
CG14549	68	4	Sld5
CG16973	67	2	misshapen
CG3210	67	1	Dynamin related protein 1
CG5366	67	1	Cullin-associated and neddylation-
CG6203	67	1	Emr1
CG3539	66	1	SLY-1 homologous
CG6543	66	1	CG6543
CG5174	66	1	CG5174
CG6646	65	1	DJ-1a
CG2050	64	1	modulo
CG11228	64	1	hippo
CG12306	63	2	polo
CG8977	63	2	Cety Difference in 62.4
CG11276	62	2	Ribosomal protein S3A Ribosomal protein S4
CG18212	62	1	aluminum tubes
CG6937	62	1	CG6937
CG2216	61	2	Ferritin 1 heavy chain homologue
CG6842	61	1	Vacuolar protein sorting 4
CG16901	61	1	squid
CG7490	60	1	Ribosomal protein LP0
CG10701	60	2	Moesin
CG2508	60	1	Cell division cycle 23 ortholog
CG10944	58	1	Kibosomal protein S6
CG3067	58	1	Elongation factor 1 p
CO3907	- 20	1	calcium-independent phospholipase
CG6718	58	1	A2 VIA
CG9769	58	1	CG9769
CG31617	58	1	His1:CG31617
CG32066	58	1	CG32066
CG6603	56	1	Hsc70Cb
CG7843	56	3	Ars2
CG4211	55	1	no on or off transient A
CG8103	55	2	Mi 2
CG2982	55	1	CG2982
CG6846	55	1	Ribosomal protein L26
CG8649	54	2	Fimbrin
CG1911	54	1	CAP-D2 condensin subunit
CG10161	54	1	Eukaryotic initiation factor 3 p66
COIOIOI	54	1	subunit
CG12163	54	2	CG12163
CG38/9	53	2	Dead how protein 72D
CG7269	51	1	Helicase at 25E
007207	51	1	Eukarvotic initiation factor 3 p40
CG9124	51	1	subunit
CG6084	51	1	CG6084
CG6854	51	1	CTP synthase
CG7070	50	1	Pyruvate kinase
CG12775	50	1	Ribosomal protein L21
CG8/28	50	1	CG8728
CG4994	49	1	mitochondriai phosphate carrier
CG6582	49	1	Aac11
CG1406	49	1	U2A
CG4954	49	1	eIF3-S8
CG34126	49	1	CG34126
CG10279	48	1	Rm62
CG3320	48	1	Rab1
CG3162	48	1	Large Subunit 2
CG4800	47	1	protein ortholog (H. saniens)
CG5433	46	1	Kinesin light chain
CG14472	46	1	purity of essence
CG1821	46	2	Ribosomal protein L31
CG4043	46	1	Rrp46
CG5602	46	1	DNA ligase I
CG15784	45	1	CG15784
CG10354	45	1	Rat1
CG1945 CG2061	44	3	Tat facets
CG2001 CG6907	44	1	CG2001 CG6907
CG6199	44	1	procollagen lysyl hydroxylase
CG4759	44	1	Ribosomal protein L27
CC20004	44	1	Z band alternatively spliced PDZ-
CG30084	44	1	motif protein 52
CG8882	43	1	Trip1
CG15899	43	3	Ca^{2+} -channel protein α_1 subunit T
CG6876	43	1	Prp31
CG4651	42	1	Ribosomal protein L13
CG11715	41	1	Kibosomai protein S14a
CG0446	41	1	Cyp4g15
CG7057	40	1	AP-50
CG5642	40	1	CG5642
CC9222	39	1	Reduction in Cnn dots 1
CG8255			

CG32086	39	2	CG32086
CG6944	38	1	Lamin
CG8340	38	1	upstream of RpIII128
CC4257	29	1	Signal-transducer and activator of
0.04237	20	1	transcription protein at 92E
CG17023	38	1	Dead box protein 80
CG11888	38	1	Regulatory particle non-ATPase 2
CG9940	38	1	CG9940
CG5348	38	3	CG5348
CG4079	37	1	TBP-associated factor 11
CG3585	37	1	Rabconnectin-3A
CG9677	37	1	Int6 homologue
CG17280	37	1	levy
CG10587	37	2	CG10587
CG6946	37	2	glorund
CG5515	37	1	ČG5515
CG16880	36	3	Nimrod C3
CG31045	36	1	Myosin heavy chain-like
CG14648	36	1	lost
CG5374	35	1	Tcp1-like
CG17766	35	1	Rabconnectin-3B
		-	TAR DNA-binding protein-43
CG10327	35	1	homolog
CG12264	35	1	CG12264
CG16868	35	1	CG16868
CG9712	35	1	tumor suppressor protein 101
CG1943	35	1	CG1943
CG6213	34	1	Vacuolar H+ ATPase 13kD subunit
CG15523	34	1	Vacuolar protein sorting 13B
CG10539	33	1	PPS6_p70_protein kinase
CG8571	33	1	smallminded
CG4820	22	1	CG4820
CG0188	22	1	contin interacting protein 2
CG10501	33	2	a methyl dopa-resistant
CG7467	32	2	u metnyi dopa-resistant
CC2807	22	1	05a
CG2807	22	1	cG2807
CG0008	32	1	atlastin
CG31188	32	1	CG18/49
CG32854	32	1	mitochondrial ribosomal protein S21
CG9191	31	1	Kinesin-like protein at 61F
CG11064	31	1	Retinoid- and fatty-acid binding
0010840	21	1	protein
CG10840	51	1	eifsb
CG15249	31	1	CG15249
CG4/44	31	1	CG4/44
CG12/34	51	1	Girdin
CG10630	31	1	blanks
CG13601	31	1	CG13601
CG2112	31	1	CG2112
CG3762	31	1	Vacuolar H+ ATPase 68 kDa subunit 2
CG6476	31	1	Suppressor of variegation 3-9
CG2904	30	2	echinus
CG8975	30	2	Ribonucleoside diphosphate reductase small subunit

CG9635	30	1	Rho guanine nucleotide exchange
CG4004	30	2	CG4004
CG6279	30	2	CG6279
CG13813	30	1	CG13813
CG15442	30	1	Ribosomal protein L 27A
CG10305	29	1	Ribosomal protein S26
0010505	2)	1	mitochondrial single stranded DNA-
CG4337	29	1	binding protein
CG32809	29	2	CG32809
CG6092	29	1	Dak1
			Golgi-localized, y-adaptin ear
CG3002	29	1	containing, ARF binding protein
CG9406	29	1	CG9406
CG14168	29	2	Zasp67
CG1347	29	1	Atg17
CG43318	29	1	CG43318
CG1554	28	1	RNA polymerase II 215kD subunit
CG10922	28	1	La autoantigen-like
CG11020	28	1	no mechanoreceptor potential C
0015949	20	1	Sarcoplasmic calcium-binding protein
CG15848	28	1	1
CG11471	28	1	Isoleucyl-tRNA synthetase
CG5252	28	1	Ranbp9
CG2522	27	1	GTP-binding protein
CG5183	27	1	KDEL receptor
CG4633	27	1	mitochondrial alanyl-tRNA synthetase
CG12499	27	1	CG12499
CG17510	27	1	Fis1
CG32146	27	1	dally-like
CG32683	27	1	CG32683
CG31175	27	1	Dystrophin
CG17870	26	1	14-3-3ζ
000740	26	1	small ribonucleoprotein particle U1
CG8/49	20	1	subunit 70K
CG7405	26	1	Cyclin H
CG17838	26	1	Syncrip
CG33233	26	1	CG33233
CG8793	26	1	lethal (3) 76BDm
CG4001	25	1	Phosphofructokinase
CG10859	25	1	CG10859
CG32016	25	1	eIF4E-Transporter
CG43063	25	1	CG43063
CG14816	23	1	Phosphoglycerate mutase 5
CG31116	23	2	Chloride channel-a
CG32210	23	1	Listerin E3 ubiquitin protein ligase 1
CG42327	23	1	CG42327
CG18176	21	1	deflated
CG1716	20	1	Set2

C.10 pUb-GFP-Dragon purification from syncytial *Drosophila* embryos

CG #	Score	#pep	Full name
CG33052	2764	50	CG33052
CG4264	1590	25	Heat shock protein cognate 4
CG8280	1028	15	Elongation factor 1a48D
0015524	750	10	Spindle assembly abnormal 6 ortholog
C015524	152	10	(C. elegans)
CG9277	731	17	β-Tubulin at 56D
CG9277	656	14	β-Tubulin at 56D
CG9359	506	11	β-Tubulin at 85D
CG4147	439	6	Heat shock 70-kDa protein cognate 3
CG8937	438	5	Heat shock protein cognate 1
CG8937	389	4	Heat shock protein cognate 1
CG18743	386	4	Heat-shock-protein-70Ab
CG2979	345	6	Yolk protein 2
CG4466	321	6	Heat shock protein 27
CG11129	315	7	Yolk protein 3
CG3401	308	9	β-Tubulin at 60D
CG1349	307	4	dj-1β
CG1873	300	6	Elongation factor 1a100E
CG7756	277	3	Heat shock protein cognate 2
004160	254	4	Ubiquinol-cytochrome c reductase core
CG4109	254		protein 2
CG10521	241	58	Netrin-B
CG4869	233	7	β-Tubulin at 97EF
CG7660	232	3	Peroxinectin-like
CG1913	215	5	α-Tubulin at 84B
CG17246	179	2	Succinate dehydrogenase A
CG9476	177	4	α-Tubulin at 85E
CG17291	173	3	Protein phosphatase 2A at 29B
CG3283	169	4	Succinate dehydrogenase B
005266	161	2	Cullin-associated and neddylation-
CG5366			dissociated 1
CG4916	141	3	maternal expression at 31B
CG8863	139	2	DnaJ-like-2
CG4183	133	2	Heat shock protein 26

CG33129	129	19	CG33129
CG4634	126	2	Nucleosome remodeling factor - 38kD
CG15825	121	1	fondue
CG10377	118	1	Heterogeneous nuclear ribonucleoprotein at 27C
CG12233	116	3	lethal (1) G0156
CG1263	114	1	Ribosomal protein L8
CG12306	113	1	polo
CG16944	110	6	stress-sensitive B
CG7349	104	2	Succinate dehydrogenase, subunit B (iron-sulfur)-like
CG6235	101	2	twins
CG14648	100	3	lost
CG1548	97	2	cathD
CG5371	94	2	Ribonucleoside diphosphate reductase large subunit
CG5499	88	2	Histone H2A variant
CG5261	87	2	midline uncoordinated
CG13422	87	1	GNBP-like 3
CG12262	83	1	CG12262
CG11181	80	1	cup
CG2985	80	4	Yolk protein 1
CG2168	77	1	Ribosomal protein S3A
CG8947	77	1	26-29kD-proteinase
CG11793	69	2	Superoxide dismutase
CG4916	69	2	maternal expression at 31B
CG1372	67	1	yolkless
CG15693	66	1	Ribosomal protein S20
CG8308	64	2	α-Tubulin at 67C
CG1683	64	1	Adenine nucleotide translocase 2
CG3203	64	1	Ribosomal protein L17
CG1242	59	1	Heat shock protein 83
CG1782	59	2	Ubiquitin activating enzyme 1
CG12244	58	2	licorne
CG7361	57	1	Rieske iron-sulfur protein

CG4193	56	1	deadhead
CG4863	56	1	Ribosomal protein L3
CG5504	53	1	lethal (2) tumorous imaginal discs
CG11276	53	1	Ribosomal protein S4
CG5502	52	1	Ribosomal protein L4
CG3024	52	1	Torsin
CG4651	51	1	Ribosomal protein L13
CG12052	50	1	longitudinals lacking
CG8415	50	1	Ribosomal protein S23
CG33456	50	2	muscle wasted
CG12369	49	12	Lachesin
CG6782	49	1	scheggia
CG5252	47	1	Ranbp9
CG9738	44	1	MAP kinase kinase 4
CG7977	44	1	Ribosomal protein L23A
CG13671	44	9	CG13671
CG1633	42	1	thioredoxin peroxidase 1
CG31884	41	1	thioredoxin-2
CG32164	40	1	CG32164
CG8905	37	1	Superoxide dismutase 2 (Mn)
CG5261	37	1	midline uncoordinated
CG4752	37	5	CG4752
CG31038	35	3	CG31038
CG2048	34	1	discs overgrown
CG4683	34	2	Testis EndoG-Like 4
CG10718	33	1	nebbish
CG9012	32	1	Clathrin heavy chain
CG6453	32	1	Glucosidase 2 β subunit
CG1821	31	1	Ribosomal protein L31
CG12163	31	1	CG12163
CG5263	30	1	smaug
CG2982	29	1	CG2982
CG9769	29	1	CG9769
CG7985	28	1	CG7985
CG33322	28	1	CG33322
CG32599	28	1	CG32599
CG42333	28	1	Synaptotagmin β
CG8246	27	1	Pox neuro
0040478	27	1	Dual-specificity tyrosine
CG40478			phosphorylation-regulated kinase 3
CG14961	27	2	CG14961
CG10617	27	1	Synaptotagmin 12
CG8900	26	1	Ribosomal protein S18
CG2179	26	1	Xe7

CG16827	26	1	Integrin alphaPS4 subunit
CG31029	26	1	CG31029
CG12079	26	1	NADH dehydrogenase (ubiquinone)
CG10594	25	2	spook
CG12164	25	1	CG12164
CG8907	25	2	CG8907
CG7413	23	1	Retinoblastoma-family protein
CG9809	24	1	spargel
CG8201	24	2	par_1
CG16983	23	1	skpA
CG5762	22	2	CG5762
CG2050	21	1	modulo
CG9537	21	2	Dayy-like protein
CG7260	21	1	CG7260
CG34434	21	1	CG34434
0004404	21	1	Clycoroldobydo 2 phoephoto
CG12055	20	1	dehvdrogenase 1
CG9081	20	1	Cyp4s3
CG10021	19	1	brother of odd with entrails limited
CG9674	19	1	CG9674
CG1842	18	1	Dynein heavy chain at 89D
CG9159	18	2	Kruppel homolog 2
CG15744	18	1	CG15744
CG42346	18	1	CG42346
CG8817	17	1	lilliputian
CG30281	17	1	CG30281
CG7378	16	1	CG7378
CG12836	16	1	CG12836
CG3350	16	1	bigmax
CG17632	15	1	brown
CG11387	15	1	cut
CG11254	15	1	maelstrom
CG8322	15	1	ATP citrate lyase
CG6509	15	1	Discs large 5
CG11107	15	1	DHX15 ortholog
CG9168	15	1	CG9168
CG30484	15	1	CG30484
CG10375	14	1	CG10375
2010373	14		010373

Appendix D



D.1 Original autoradiogram of four gels with indicated boxes that were cropped for Figure 5-12C. Numbers are explained in figure legend on the right. Domains of Sas6 in aa (amino acids); 1% input of ³⁵S-Methionine-labelled Sas6 fragment that was used for each binding assay; binding assays of ³⁵S-Methionine-labelled Sas6 fragment with GST-alone immobilised on resin (::GST) or GST-N-terminally tagged Dragon immobilised on resin (::GST-Dragon).