Check for updates

Cell division screens and dynamin

Mary Kate Bonner[1] and Ahna R. Skop[1]
Department of Genetics, University of Wisconsin-Madison, 425-G Henry Mall, Madison, WI 53706, U.S.A.

Abstract

Cell division is the most fundamental process in the development of all living organisms. The generation of cell diversity throughout development, the multiplication of cells during wound repair and the maintenance of stem cells in several tissues and organs all rely on proper progress through cell division. Historically, biochemical studies of cell division proved to be difficult, since mitosis is a moving target. The rapid and dynamic nature of mitosis means necessary proteins often exist in multiple isoforms and some for only brief moments during a particular stage in the cell cycle. The advent of proteomics and the introduction of stage-specific inhibitors have enabled the field to identify numerous factors required at distinct steps in the cell cycle. One such factor identified in many of these screens was the highly conserved protein dynamin. Dynamin, long known for its role in endocytosis, is also necessary for co-ordinating actin assembly at membranes. Our knowledge of its precise cell cycle function and upstream/downstream targets, however, is unclear. Our review will describe current knowledge regarding the impacts of several cell division screens and the multiple roles that dynamin may play during mitosis.

Introduction

Cell division is crucial to the survival of all organisms. The microtubule and microfilament cytoskeletons as well as membrane remodelling factors co-ordinate the morphological changes necessary for furrow progression and completion [1]. Signal(s) originating from the mitotic spindle and the asters initiate furrow formation [2,3]. Ingression of the furrow requires the assembly of the actomyosin contractile ring and the addition and remodelling of new membrane [1,4]. As the contraction of the actomyosin ring compacts the spindle midzone, membrane dynamics increase and the two newly formed cells separate [5]. Unregulated, this process can lead to various cellular abnormalities, including cancer and birth defects [6]. A first step to understanding cell division was to identify the factors involved, and early efforts at isolating mitotic structures from distinct cell cycle stages established a basic parts list [7–11]. The list swelled with the introduction of mass spectrometry and genome-wide RNAi (RNA interference) screens [12–17]. This review highlights important cell division screens in animal cells and focuses on one protein, dynamin, that unexpectedly appeared in several of these screens.

Historical efforts to isolate cell division structures and identify important factors

In the early 1950s, Dan Mazia and Katsuma Dan [7] pioneered efforts in the biochemical characterization of the mitotic spindle when they isolated the mitotic apparatus from sea urchin eggs. Mazia and Dan [7] found that the mitotic apparatus behaved as a single unit and that one protein, tubulin, accounted for most of the mass of the structure. Further modification of their isolation procedure preserved lipids and prevented the modification of lipoproteins, which appeared to stabilize the structure [18]. Mazia and Dan's early experiments were simple yet ground-breaking. Their work was instrumental in understanding how the mitotic machinery works and laid the groundwork for much of the research in the field.

In the early 1970s, there was great excitement in trying to understand the dynamic nature of the spindle structure. Zac Cande et al. [9] isolated spindles in a solution of polymerizable tubulin that retained the ability to separate chromosomes. Yet, in the absence of tubulin, microtubule filaments still increased in length, suggesting that a more complex mechanism existed for chromosome movement [9]. Investigation into what caused this movement spurred the use of *Stephanopyxis turris*, a diatom that lent itself to easy synchronization and isolation of subcellular structures. When ATP was added to isolated diatom spindles, the structure was able to separate completely, supporting the idea that 'motors' functioned along the spindle midzone [19]. Although these first attempts were fruitful and exciting, the field was in need of an experimental approach that would rapidly identify individual proteins that comprise this cellular machine.

The spindle midbody: a resource for cell division proteins

In the 1970s, the spindle midbody became a popular source for spindle proteins. The midbody was first described by Walther Flemming in 1891 as the remnant of cell division and was thought to be analogous to the cell plate in plants [20], yet very few thought it was anything more than 'cellular

Key words: cell division, cleavage furrow, cytokinesis, dynamin, membrane remodelling, midbody.

Abbreviations used: PH domain, pleckstrin homology domain; PRD, proline-rich domain; RNAi, RNA interference.

[1]email mbonner@wisc.edu or skop@wisc.edu

©The Authors Journal compilation ©2008 Biochemical Society

Downloaded from http://portlandpress.com/biochemsoctrans/article-pdf/36/3/431/626776/bst0360431.pdf by University of Wisconsin Madison user on 04 September 2024

garbage'. However, the midbody was known to be a rich source of microtubules and microtubule-associated proteins [21].

As the midbody is a transient structure, only appearing in the last moments in cell division, it was particularly difficult to isolate and study. Initial attempts were made in the late 1970s to isolate midbodies by Michael Mullins in Richard McIntosh's laboratory [21]. After several unsuccessful attempts, in 1982, Mullins and McIntosh [8] described the first detailed compositional analysis of the mammalian midbody. Their results indicated that the qualitative protein composition of the midbody and the mitotic spindle are similar and therefore a great source for spindle factors. Tubulin was a major component and detailed examination of tubulin dynamics soon followed [8]. However, identification and characterization of many other individual spindle or midbody components would be slow.

A few years later, in 1984, Ryoko Kuriyama, in Gary Borisy's laboratory, isolated mitotic spindles and midbodies from CHO (Chinese hamster ovary) cells in search for cell division factors [22]. Ryoko's approach was to inject isolated mitotic spindles into mice and isolate monoclonal antibodies [11]. Through a monoclonal antibody screen, she identified a factor that localized to the midbody, CHO1 [11], which is now a well-known midzone-associated kinesin of the centralspindlin complex [23]. CHO1 and the rest of centralspindlin complex are required for RhoA, myosin, and F-actin accumulation at the cleavage furrow [23]. Ryoko's work was largely unappreciated at that time, but inspired many in the field to find new strategies to identify essential cell division factors. With the advent of new technologies like RNAi and proteomics, scores of new proteins would soon be found.

RNAi screens and proteomic approaches

High-throughput screens in *C. elegans* and *Drosophila* enabled the rapid identification of many genes and proteins important to cytokinesis. In 2000, the Hyman laboratory used a reverse-genetics approach in *C. elegans* by using RNAi to screen chromosome III for genes involved in cell division [13]. Their analysis identified 133 genes necessary for cell division and represented the field's movement toward a comprehensive view of cellular processes [13]. By 2004, RNAi screens were successfully used in combination with a variety of chemical genetic approaches to identify new factors. Using a visual screen in *Drosophila* cells, Eggert et al. [16] compared RNAi targets and potential cytokinesis inhibitors and was successful in identifying a small molecule that inhibited the Aurora B pathway. Combining small molecules with RNAi proved to be an effective way to identify new factors and their targets.

With genomic sequencing, the completion of several genomes, and strides in bioinformatics, came proteomics. Proteomics became more amenable to biological samples and was a promising new way to identify cytokinesis factors. Modifying protocols from Dan Mazia, Michael Mullins and Ryoko Kuriyama, proteins from isolated mammalian midbodies were identified using MuDPIT technologies developed in the Yates laboratory at Scripps [15]. Resident midbody proteins were subsequently shown to function in cell division via an RNAi screen in *C. elegans*. This screen was unique in that it combined several assays to determine conserved cytokinesis proteins - the biochemical purification of spindle midbodies, identification of homologues in *C. elegans* and an RNAi screen. Over 103 proteins previously not related to cytokinesis were identified, many of which were membrane remodelling factors [15].

Further work on isolated spindles in *Xenopus* provided insight into cellular processes working together during the cell cycle [14]. The presence of 40 proteins and an abundance of ribosomes bound to the spindle structure suggested that protein translation is important for spindle function during oocyte meiosis [14]. As the number of proteins associated with mitotic structures multiplied, there was a greater need for functional screens and analyses.

Subsequently, multiple genome-wide RNAi screens in *C. elegans* and *Drosophila* led to the discovery of numerous genes necessary for both phases of cytokinesis [17,24], thus adding to the ever growing parts list. Echard et al. [17] performed a genome-wide screen using a library of 7216 conserved dsRNAs (double-stranded RNAs) and live video microscopy and identified many factors, such as NSF (*N*-ethylmaleimide-sensitive fusion protein) and citron-kinase, which contribute to the stability of the intercellular canal. In 2005, a genome-wide RNAi screen in *C. elegans* yielded 327 genes required for cell division and profiled many other genes as functioning during early *C. elegans* development [24].

Membrane trafficking and cytokinesis

Several key experiments have demonstrated the importance of membrane remodelling and trafficking events during animal cell cytokinesis (reviewed in [4,25,26]). During furrow ingression, new membrane is inserted at the apex of the cleavage furrow [27,28]. Preventing the addition of membrane or clathrin-mediated endocytosis leads to failure in cell division [29–31]. The advent of proteomics reinforced these discoveries, revealing that the majority of midbody proteins play key roles in membrane dynamics [15]. Genome-wide RNAi screens identified several other membrane remodelling factors (reviewed in [6]) [17], suggesting that membrane remodelling was key to our understanding of cytokinesis.

One midbody protein associated with membrane remodelling that was also required for cytokinesis was the large GTPase, dynamin [15]. Although long known to be a major protein required for new cell wall formation in plants, its function in animal cytokinesis was unclear. Subsequently, dynamin has been identified in numerous other RNAi screens as functioning during cell division [16,17,32,33], suggesting that dynamin may indeed play a key role in co-ordinating the membrane remodelling events that occur during cytokinesis, similar to its role in plants.

©The Authors Journal compilation ©2008 Biochemical Society

Downloaded from http://portlandpress.com/biochemsoctrans/article-pdf/36/3/431/626776/bst0360431.pdf by University of Wisconsin Madison user on 04 September 2024

Dynamin

The highly conserved dynamin superfamily is composed of dynamin and several dynamin-related proteins. Mammalian dynamin 1, 2 and 3 are the founding members of the dynamin family [34]. Dynamin 1 was originally identified as a microtubule-binding protein [35] and since then a number of dynamin and dynamin-related proteins have been implicated in various processes such as endocytosis, actin nucleation and dynamics, mitochondrial and chloroplast biogenesis and cytokinesis (reviewed in [34]). Dynamin 2 has been shown to play a key role in endocytosis, actin dynamics and membrane trafficking [36] and is the only mammalian isoform that functions during cytokinesis [37].

Dynamin family members and abundant isoforms have dramatically different localization patterns. For instance, Dyn2aa and Dyn2ab differ by only four amino acids, yet Dyn2aa localizes to clathrin-coated pits at the Golgi and plasma membrane, whereas Dyn2ab is restricted to the plasma membrane [38]. In addition, Dyn1 and Dyn2 exhibit redundant functions in endocytosis; however, they are differentially targeted to apical and basal membranes in epithelial cells [39].

The architectural features common to classical dynamins are a large GTPase domain that binds and hydrolyses GTP, a Middle domain, a GED (GTPase-effector domain) that is involved in oligomerization and stimulation of GTPase activity, a PH domain (pleckstrin homology domain) and a PRD (proline-rich domain) at the C-terminus that interacts with SH3 (Src-homology-3) domains [34]. Dynamin has been shown to directly associate with the lipid bilayer via its PH domain. Mutations that abolish the GTPase activity of dynamin, such as in *C. elegans*, have been widely used to characterize its functions [37]. Most dynamins contain additional domains, which may account for the great diversity of cellular activities [40]. For instance, mammalian dynamin 1 and dynamin 2, but not dynamin 3, contain a PH domain, which allows for phospholipid binding and a PRD that interacts with the SH3 domains of various proteins [40]. Although the functions of the structural motifs in dynamin family members have been identified and extensively studied in mammalian cells, the single isoform found in both *Drosophila* and *C. elegans* suggests that these proteins are likely to retain multiple functions. It will be interesting to determine how this is achieved.

Dynamin, actin and membrane dynamics

In addition to its role in vesicle fission during endocytosis and secretion, dynamin can also influence actin and membrane dynamics. Dynamin is physically required for processes involving cytoskeletal reorganization, such as podosome formation, membrane ruffling (reviewed in [41]) and actin-tail-based vesicle trafficking [42,43]. For example, in *S. cerevisiae*, the yeast dynamin-related protein Vps1p is required for normal actin organization. In *vps1* mutants, depolarized and aggregated actin structures as well as random bud site selection and chitin deposition are observed. Vps1p also physically interacts with Sla1p, a key protein required in actin dynamics and endocytosis [44]. Dynamin interacts with actin-regulatory proteins and localizes at actin-rich sites. Dynamin can control actin nucleation from membranes and regulates actin comet formation and movement of both *Listeria monocytogenes* and endocytosed vesicles [42,43,45].

Despite the intriguing list of interacting proteins, the functional significance of the physical associations of dynamin with the actin cytoskeleton is unclear, specifically during mitosis. How does dynamin function during cytokinesis? Dynamin could direct actin assembly at specific sites within equatorial and furrow membranes during cytokinesis, similar to the function of dynamin in vesicle fission and cytoplasmic transport during endocytosis [15,46]. Dynamin may also function as a link between the plasma membrane and actin filaments through interactions with proteins like Abp1, profilin or cortactin [41]. Alternatively, dynamin assembled on plasma membranes could act a structural component that organizes and stabilizes actin filaments at the furrow membrane, therefore being a platform from which the contractile ring would form.

Dynamin and microtubule dynamics

Dynamin was originally identified as a microtubule-associated protein and was proposed to mediate microtubule sliding [35]. However, there is little evidence that microtubules are involved in the initial events of endocytosis in which dynamin has been implicated [47]. Several studies in plants have suggested that dynamin may serve as a linker between cargo and microtubules, similar to the function of molecular motors, such as kinesin and dynein. The dynamin homologue in plants, DRP1a, associates with microtubules and has been suggested to serve as an anchor for Golgi-derived vesicles found on microtubules destined for the cell plate as Golgi-derived material is improperly targeted to the cell plate in DRP1a mutants [36]. In addition, focal adhesion disassembly involves both microtubules and dynamin, and depletion of dynamin prevents cell migration [48]. Using a GST-tagged Dyn2, Dyn2 pulled down actin, alpha-tubulin and gamma-tubulin and was also shown to be required for centrosome cohesion [49], suggesting that the role of dynamin in regulating microtubule dynamics might be genuine. Interestingly, phosphorylation of dynamin by cdc2 kinase leads to the reduced binding affinity of dynamin for microtubules [50], suggesting that dynamin might in part function in microtubule regulation during the cell cycle. However, the role of dynamin in regulating microtubule bundling or dynamics has not been addressed, specifically during furrow formation and completion.

A conserved role for dynamin in cytokinesis

A few experiments in animal cells have linked dynamin directly to cytokinesis [37,51,52], and its role in cytokinesis appears to be conserved. In *C. elegans* and in zebrafish, dynamin is necessary for completion of cytokinesis and

©The Authors Journal compilation ©2008 Biochemical Society

Downloaded from http://portlandpress.com/biochemsoctrans/article-pdf/36/3/431/626776/bst0360431.pdf by University of Wisconsin Madison user on 04 September 2024

localizes to only newly formed membranes [15,52]. In *Dictyostelium*, dynamin depletion leads to cytokinesis defects, but its localization is primarily in cytoplasmic vesicles [51], suggesting a role for dynamin in endocytic pathways during cell division. In plants, dynamin-related proteins ADL1A and ADL1E are required for cell plate formation, plasma membrane recycling and the completion of cytokinesis. ADL1A distribution is similar to *C. elegans* DYN-1 in that it is highly dynamic and primarily localizes to the plasma membrane of newly formed cells [53].

Dynamin's localization to the new cleavage furrow during cell division, role in endocytic events and actin nucleation are still unknown, but clearly the role of dynamin in cytokinesis is a crucial one. Several unanswered questions about dynamin exist. What are the distinct roles of dynamin during the cell cycle? Does dynamin function in actin nucleation and dynamics during furrow formation? Does dynamin regulate endocytic pathways required during furrow formation? Does dynamin regulate the mitotic spindle? What factors influence dynamin during furrow formation and completion? Determining the roles of dynamin and its associated factors during the cell cycle will probably reveal mechanistic connections between cytokinesis and membrane remodelling events.

Conclusion

Although the study of cell division has a long history, the mechanisms and biological networks that orchestrate this elaborate cellular event is still unclear. Numerous genomic and proteomic screens have generated a myriad of proteins necessary for cytokinesis, but the roles of many of them remain vague. The importance of membrane remodelling factors during cell division is just beginning to be understood. Dynamin, probably a major player in membrane remodelling events, is a perfect candidate for the co-ordination of membrane-cytoskeletal events that occur. Our knowledge of the roles of membrane remodelling factors will increase in the years to come and probably bridge connections between our understanding of the actin and microtubule cytoskeletons during cytokinesis.

References

1 Barr, F.A. and Gruneberg, U. (2007) Cytokinesis: placing and making the final cut. Cell **131**, 847–860
2 Rappaport, R. (1961) Experiments concerning the cleavage stimulus in sand dollar eggs. J. Exp. Zool. **148**, 81–89
3 Bringmann, H. and Hyman, A.A. (2005) A cytokinesis furrow is positioned by two consecutive signals. Nature **436**, 731–734
4 Matheson, J., Yu, X., Fielding, A.B. and Gould, G.W. (2005) Membrane traffic in cytokinesis. Biochem. Soc. Trans. **33**, 1290–1294
5 Schweitzer, J.K., Burke, E.E., Goodson, H.V. and D'Souza-Schorey, C. (2005) Endocytosis resumes during late mitosis and is required for cytokinesis. J. Biol. Chem. **280**, 41628–41635
6 Eggert, U.S., Mitchison, T.J. and Field, C.M. (2006) Animal cytokinesis: From parts list to mechanisms. Ann. Rev. Biochem. **75**, 543–566
7 Mazia, D. and Dan, K. (1952) The isolation and biochemical characterization of the mitotic apparatus of dividing cells. Proc. Nat. Acad. Sci. U.S.A. **38**, 826–838
8 Mullins, J.M. and McIntosh, J.R. (1982) Isolation and initial characterization of the mammalian mid-body. J. Cell Biol. **94**, 654–661
9 Cande, W.Z., Snyder, J., Smith, D., Summers, K. and McIntosh, J.R. (1974) Functional mitotic spindle prepared from mammalian cells in culture. Proc. Natl. Acad. Sci. U.S.A. **71**, 1559–1563
10 Kuriyama, R. and Borisy, G.G. (1985) Identification of molecular components of the centrosphere in the mitotic spindle of sea-urchin eggs. J. Cell Biol. **101**, 524–530
11 Sellitto, C. and Kuriyama, R. (1988) Distribution of a matrix component of the midbody during the cell-cycle in Chinese hamster ovary cells. J. Cell Biol. **106**, 431–439
12 Yoon, H.J., Feoktistova, A., Wolfe, B.A., Jennings, J.L., Link, A.J. and Gould, K.L. (2002) Proteomics analysis identifies new components of the fission and budding yeast anaphase-promoting complexes. Curr. Biol. **12**, 2048–2054
13 Gonczy, P., Echeverri, C., Oegema, K., Coulson, A., Jones, S.J.M., Copley, R.R., Duperon, J., Oegema, J., Brehm, M., Cassin, E. et al. (2000) Functional genomic analysis of cell division in *C. elegans* using RNAi of genes on chromosome III. Nature **408**, 331–336
14 Liska, A.J., Popov, A.V., Sunyaev, S., Coughlin, P., Habermann, B., Shevchenko, A., Bork, P., Karsenti, E. and Shevchenko, A. (2004) Homology-based functional proteomics by mass spectrometry: Application to the *Xenopus* microtubule-associated proteome. Proteomics **4**, 2707–2721
15 Skop, A.R., Liu, H.B., Yates, J., Meyer, B.J. and Heald, R. (2004) Dissection of the mammalian midbody proteome reveals conserved cytokinesis mechanisms. Science **305**, 61–66
16 Eggert, U.S., Kiger, A.A., Richter, C., Perlman, Z.E., Perrimon, N., Mitchison, T.J. and Field, C.M. (2004) Parallel chemical genetic and genome-wide RNAi screens identify cytokinesis inhibitors and targets. PLoS Biol. **2**, 2135–2143
17 Echard, A., Hickson, G.R., Foley, E. and O'Farrell, P.H. (2004) Terminal cytokinesis events uncovered after an RNAi screen. Curr. Biol. **14**, 1685–1693
18 Mazia, D., Mitchison, J.M., Medina, H. and Harris, P. (1961) The direct isolation of the mitotic apparatus. J. Biophys. Biochem. Cytol. **10**, 467–474
19 Cande, W.Z. and McDonald, K.L. (1985) *In vitro* reactivation of anaphase spindle elongation using isolated diatom spindles. Nature **316**, 168–170
20 Paweletz, N. (2001) Walther Flemming: pioneer of mitosis research. Nat. Rev. Mol. Cell Biol. **2**, 72–75
21 Mullins, J.M. and McIntosh, J.R. (1979) Birefringence of the mammalian midbody. Exp. Cell Res. **121**, 395–399
22 Kuriyama, R., Keryer, G. and Borisy, G.G. (1984) The mitotic spindle of Chinese hamster ovary cells isolated in taxol-containing medium. J. Cell Sci. **66**, 265–275
23 Glotzer, M. (2005) The molecular requirements for cytokinesis. Science **307**, 1735–1739
24 Sonnichsen, B., Koski, L.B., Walsh, A., Marschall, P., Neumann, B., Brehm, M., Alleaume, A.M., Artelt, J., Bettencourt, P., Cassin, E. et al. (2005) Full-genome RNAi profiling of early embryogenesis in *Caenorhabditis elegans*. Nature **434**, 462–469
25 Baluska, F., Menzel, D. and Barlow, P.W. (2006) Cytokinesis in plant and animal cells: endosomes 'shut the door'. Dev. Biol. **294**, 1–10
26 Albertson, R., Riggs, B. and Sullivan, W. (2005) Membrane traffic: a driving force in cytokinesis. Trends Cell Biol. **15**, 92–101
27 Danilchik, M.V., Bedrick, S.D., Brown, E.E. and Ray, K. (2003) Furrow microtubules and localized exocytosis in cleaving *Xenopus laevis* embryos. J. Cell Sci. **116**, 273–283
28 Lecuit, T. and Wieschaus, E. (2000) Polarized insertion of new membrane from a cytoplasmic reservoir during cleavage of the *Drosophila* embryo. J. Cell Biol. **150**, 849–860
29 Skop, A.R., Bergmann, D., Mohler, W.A. and White, J.G. (2001) Completion of cytokinesis in *C. elegans* requires a brefeldin A-sensitive membrane accumulation at the cleavage furrow apex. Curr. Biol. **11**, 735–746
30 Sisson, J.C., Field, C., Ventura, R., Royou, A. and Sullivan, W. (2000) Lava lamp, a novel peripheral golgi protein, is required for *Drosophila melanogaster* cellularization. J. Cell Biol. **151**, 905–918
31 Boucrot, E. and Kirchhausen, T. (2007) Endosomal recycling controls plasma membrane area during mitosis. Proc. Natl. Acad. Sci. U.S.A. **104**, 7939–7944
32 Kiger, A.A., Baum, B., Jones, S., Jones, M.R., Coulson, A., Echeverri, C. and Perrimon, N. (2003) A functional genomic analysis of cell morphology using RNA interference. J. Biol. **2**, 27

©The Authors Journal compilation ©2008 Biochemical Society

Downloaded from http://portlandpress.com/biochemsoctrans/article-pdf/36/3/431/626776/bst0360431.pdf by University of Wisconsin Madison user on 04 September 2024

33 Kamath, R.S., Fraser, A.G., Dong, Y., Poulin, G., Durbin, R., Gotta, M., Kanapin, A., Le Bot, N., Moreno, S., Sohrmann, M. et al. (2003) Systematic functional analysis of the *Caenorhabditis elegans* genome using RNAi. Nature **421**, 231–237
34 Praefcke, G.J. and McMahon, H.T. (2004) The dynamin superfamily: universal membrane tubulation and fission molecules? Nat. Rev. Mol. Cell Biol. **5**, 133–147
35 Shpetner, H.S. and Vallee, R.B. (1989) Identification of dynamin, a novel mechanochemical enzyme that mediates interactions between microtubules. Cell **59**, 421–432
36 Konopka, C.A., Schleede, J.B., Skop, A.R. and Bednarek, S.Y. (2006) Dynamin and cytokinesis. Traffic **7**, 239–247
37 Thompson, H.M., Skop, A.R., Euteneuer, U., Meyer, B.J. and McNiven, M.A. (2002) The large GTPase dynamin associates with the spindle midzone and is required for cytokinesis. Curr. Biol. **12**, 2111–2117
38 McNiven, M.A., Kim, L., Krueger, E.W., Orth, J.D., Cao, H. and Wong, T.W. (2000) Regulated interactions between dynamin and the actin-binding protein cortactin modulate cell shape. J. Cell Biol. **151**, 187–198
39 Altschuler, Y., Barbas, S.M., Terlecky, L.J., Tang, K., Hardy, S., Mostov, K.E. and Schmid, S.L. (1998) Redundant and distinct functions for dynamin-1 and dynamin-2 isoforms. J. Cell Biol. **143**, 1871–1881
40 Hinshaw, J.E. (2000) Dynamin and its role in membrane fission. Annu. Rev. Cell Dev. Biol. **16**, 483–519
41 Schafer, D.A. (2004) Regulating actin dynamics at membranes: a focus on dynamin. Traffic **5**, 463–469
42 Lee, E. and De Camilli, P. (2002) Dynamin at actin tails. Proc. Natl. Acad. Sci. U.S.A. **99**, 161–166
43 Orth, J.D., Krueger, E.W., Cao, H. and McNiven, M.A. (2002) The large GTPase dynamin regulates actin comet formation and movement in living cells. Proc. Natl. Acad. Sci. U.S.A. **99**, 167–172
44 Yu, X. and Cai, M. (2004) The yeast dynamin-related GTPase Vps1p functions in the organization of the actin cytoskeleton via interaction with Sla1p. J. Cell Sci. **117**, 3839–3853
45 Merrifield, C.J., Feldman, M.E., Wan, L. and Almers, W. (2002) Imaging actin and dynamin recruitment during invagination of single clathrin-coated pits. Nat. Cell Biol. **4**, 691–698
46 Otsuki, M., Itoh, T. and Takenawa, T. (2003) Neural Wiskott-Aldrich syndrome protein is recruited to rafts and associates with endophilin A in response to epidermal growth factor. J. Biol. Chem. **278**, 6461–6469
47 Vallee, R.B. and Okamoto, P.M. (1995) The regulation of endocytosis: identifying dynamin's binding partners. Trends Cell Biol. **5**, 43–47
48 Ezratty, E.J., Partridge, M.A. and Gundersen, G.G. (2005) Microtubule-induced focal adhesion disassembly is mediated by dynamin and focal adhesion kinase. Nat. Cell Biol. **7**, 581–590
49 Thompson, H.M., Cao, H., Chen, J., Euteneuer, U. and McNiven, M.A. (2004) Dynamin 2 binds γ-tubulin and participates in centrosome cohesion. Nat. Cell Biol. **6**, 335–342
50 Hosoya, H., Komatsu, S., Shimizu, T., Inagaki, M., Ikegami, M. and Yazaki, K. (1994) Phosphorylation of dynamin by cdc2 kinase. Biochem. Biophys. Res. Commun. **202**, 1127–1133
51 Wienke, D.C., Knetsch, M.L., Neuhaus, E.M., Reedy, M.C. and Manstein, D.J. (1999) Disruption of a dynamin homologue affects endocytosis, organelle morphology, and cytokinesis in *Dictyostelium discoideum*. Mol. Biol. Cell **10**, 225–243
52 Feng, B., Schwarz, H. and Jesuthasan, S. (2002) Furrow-specific endocytosis during cytokinesis of zebrafish blastomeres. Exp. Cell Res. **279**, 14–20
53 Otegui, M.S., Verbrugghe, K.J. and Skop, A.R. (2005) Midbodies and phragmoplasts: analogous structures involved in cytokinesis. Trends Cell Biol. **15**, 404–413

Received 7 January 2008
doi:10.1042/BST0360431

Downloaded from http://portlandpress.com/biochemsoctrans/article-pdf/36/3/431/626776/bst0360431.pdf by University of Wisconsin Madison user on 04 September 2024

©The Authors Journal compilation ©2008 Biochemical Society