The International Journal of Biochemistry & Cell Biology 41 (2009) 323–329

Contents lists available at ScienceDirect

The International Journal of Biochemistry & Cell Biology

journal homepage: www.elsevier.com/locate/biocel

Review

Evolution of cytomotive filaments: The cytoskeleton from prokaryotes to eukaryotes

Jan Löwe*, Linda A. Amos

MRC Laboratory of Molecular Biology, Hills Road, Cambridge CB2 0QH, UK

ARTICLE INFO

Article history:
Available online 13 August 2008

Keywords:
Actin
Tubulin
FtsZ
MreB
WACA
Cytomotive filaments
ParM
Septins

ABSTRACT

The basic features of the active filaments that use nucleotide hydrolysis to organise the cytoplasm are remarkably similar in the majority of all cells and are either actin-like or tubulin-like. Nearly all prokaryotic cells contain at least one form of FtsZ, the prokaryotic homologue of tubulin and some bacterial plasmids use tubulin-like TubZ for segregation. The other main family of active filaments, assembled from actin-like proteins, occurs in a wide range of bacterial species as well as in all eukaryotes. Some bacterial plasmids also use ParM, another actin-like protein. Higher-order filament structures vary from simple to complex depending on the cellular application. Equally, filament-associated proteins vary greatly between species and it is not possible currently to trace their evolution from prokaryotes to eukaryotes. This lack of similarity except in the three-dimensional structures and longitudinal interactions between the filament subunits hints that the most basic cellular function of the filaments is to act as linear motors driven by assembly dynamics and/or bending and hence we term these filament systems 'cytomotive'. The principle of cytomotive filaments seems to have been invented independently for actin- and tubulin-like proteins. Prokaryotes appear to have a third class of cytomotive filaments, typically associated with surfaces such as membranes or DNA: Walker A cytoskeletal ATPases (WACA). A possible evolutionary relationship of WACAs with eukaryotic septins is discussed.

© 2008 Elsevier Ltd. All rights reserved.

Contents

1. Introduction

To reproduce themselves exactly, cells need mechanisms to control their shape during growth and to effect division into two daughter cells, each possessing a copy of the genetic information. Because of the dimensions of cells (whose size in turn is partly dictated by the space taken up by the DNA, from 100 nm up to tens of microns), only a very large superstructure will be able to influence and access all parts. Currently, all the cells that have been studied in detail use dynamic polymeric filaments for these purposes. For many years, a filamentous cytoskeleton was believed to be one of the defining characteristics of eukaryotic as compared with prokaryotic cells. However, researchers have gradually discovered the relatively inconspicuous but still highly active filaments that prokaryotic cells use to control their shapes and to constrict the membrane during cell division (recent reviews: Graumann, 2007; Pogliano, 2008). Now it is clear that cells possessing these filamentous proteins are so successful at reproducing themselves that

* Corresponding author. Tel.: +44 1223 252969.
E-mail address: jyl@mrc-lmb.cam.ac.uk (J. Löwe).

1357-2725/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocel.2008.08.010

natural selection has allowed them to displace life-forms that must have been able to grow and divide before the filaments we now see everywhere could evolve.

Filaments of the tubulin/FtsZ/TubZ family and actin/MreB/MreB-like/ParM family all bind nucleotide (GTP or ATP) and use unidirectional cycles of nucleotide hydrolysis to drive either dynamic instability (stochastic growth and shrinkage) or treadmilling or controlled assembly/disassembly or bending. They appear to be present in all types of cells, with the exception of the crenarchaea (Natale et al., 2000), whose division proteins are currently unknown.

In this review, we focus on the common principles of these filament systems, starting at the molecular level. It appears that the only properties conserved throughout evolution are their nucleotide hydrolysing activities and their structures, including the longitudinal contacts between the subunits that form a filament. The two basic classes of proteins, (actin-like and tubulin-like) exist in a bewildering number of uses in different cellular contexts, going hand in hand with a large number of accessory factors controlling these functions. We include, in this list of optional accessory factors, the molecular motors (kinesin, myosin) that are found in eukaryotes and use the filaments as tracks on which to travel long distances. No such molecular motors have been found in prokaryotes and the recent paper by Osawa et al. (2008) provides convincing evidence that none are required for FtsZ-driven membrane constriction.

Based on the conservation of only the most basic properties, including the longitudinal contacts and nucleotide hydrolysis during assembly, to us, the underlying key to the success of the two filament systems is their function as linear motors. Using energy stored in the nucleotide, the filaments themselves can create linear force. The force can actively push or pull objects or can be used to position objects against concentration gradients or thermal motion. Some filaments remodel membranes, possibly by actively sliding relative to each other. Therefore, we would like to propose the term '*cytomotive filaments*' for the dynamic filaments of actin and tubulin and their homologues that form the heart of the cytoskeleton, having been strongly conserved by natural selection. This will distinguish these proteins from the fibrous cytoskeletal proteins such as eukaryotic intermediate filaments (Oshima, 2007) and various coiled-coil filaments found in bacteria (Hurme et al., 1994; You et al., 1996; Ausmees et al., 2003; Yang et al., 2004; Mazouni et al., 2006), whose function is thought to be purely structural.

The many uses of cytomotive filaments, with or without accessory motors, are somewhat analogous to the very widespread use of motors in engineering where many different tasks are performed with the same device. In accordance with the idea that the only truly conserved function of cytomotive filaments is their longitudinal dynamic assembly, none of the large number of accessory factors that control the filaments seems to be conserved between prokaryotes and eukaryotes or even across all groups of prokaryotes (Michie and Löwe, 2006).

2. The tubulin/FtsZ/TubZ family of cytomotive filaments

This family of cytomotive filaments is almost ubiquitous in living cells. It now appears that the feature conserved during evolution of tubulin-like filaments is the longitudinal contact between adjacent 40–50 kDa protein subunits (Fig. 1A). Tubulin-like proteins consist of two conserved domains with the N-terminal domain providing nucleotide-binding and one interface of the active contact, whereas the C-terminal domain provides the other interface (Nogales et al., 1998a). After the contact is made during filament assembly, residues on the second interface directly activate the nucleotide, thus linking nucleotide hydrolysis with polymerisation. The two-domain structure and distribution of functions across the domains has led to the hypothesis that tubulin-like proteins once were two separate molecules with nucleotide-binding and hydrolysis-activation activity, respectively (Oliva et al., 2004). Generally, filament assembly (and not the nucleotide state of the subunits) is thought to cause a conformational change that in turn increases the hydrolysis rate in subunits other than the last one (Oliva et al., 2007; Huecas et al., 2008; Rice et al., 2008). This important feature and the ability to 'trap' the nucleotide in the filament, with no exchange (Romberg and Mitchison, 2004), enables the filaments to have dynamic instability (Mitchison and Kirschner, 1984), although it is currently thought FtsZ does not use this feature.

Clearly, FtsZ is an ancient protein (Erickson, 2007). Nevertheless, it is a multi-domain molecule with a sophisticated mode of activation. Almost certainly, cells were able to divide, by some unknown means, before this protein fold was perfected. The widespread occurrence of FtsZ and its homologues is proof of the superiority of this design, with its conserved three-dimensional structure and conserved longitudinal interaction around the GTP-binding pocket. Several different implementations of tubulin-like proteins exist in nature: FtsZ, TubZ, tubulins and BtubAB. We are confident that more will appear with more genome sequencing and others will also have existed, including intermediates that have gone extinct. Vaughan et al. (2004) have made a comprehensive survey of tubulin/FtsZ like sequences currently known in prokaryotic genomes, while FtsZ and eukaryotic tubulin sequences are compared by Erickson (2007).

FtsZ filaments consist of one type of subunit and they are involved in bacterial cell division, where the protein forms the Z-ring around the middle of the cell (Bi and Lutkenhaus, 1991) that, together with other proteins, brings about division of a cell into two daughter cells (Haeusser and Levin, 2008). A number of accessory proteins have been identified (review: Löwe et al., 2004), but their exact mode of action remains unclear at this moment (SulA is the only exception, (Cordell et al., 2003; Dajkovic et al., 2008)). It seems that at least part of the division process, namely the generation of a constrictive force on the membrane can be accomplished by FtsZ alone (Osawa et al., 2008), provided it has a means of linking to the membrane (normally provided by an accessory protein but Osawa et al. engineered their FtsZ to have its own membrane-binding peptide). It is thought that the nucleotide in these filaments is freely available, making it impossible for FtsZ filaments to be controlled by GTP-bound 'caps' at their ends as in microtubule dynamic instability (Romberg and Mitchison, 2004). *In vitro* under certain conditions, FtsZ shows complex dynamics (Chen and Erickson, 2005) and there is a continual turnover of GTP.

In vivo, the Z-ring seen by light microscopy displays strong dynamic behaviour (Anderson et al., 2004). However, it is currently unclear what mechanism the filaments use to constrict the membrane. Tomographic images of the division site in cells (Li et al., 2007) have shown isolated short filaments in contact with the membrane and the authors have suggested that GTPase-dependent bending of initially straight FtsZ protofilaments leads to a gradual cumulative constriction. However, structural data do not support the concept of nucleotide-dependent bending ((Oliva et al., 2004, 2007); see Rice et al. (2008) for a similar conclusion about tubulin). An alternative possibility to active bending by individual filaments is that pairs or small bundles of filaments interact transiently (for too short a time to be trapped in the tomographic specimens) and constrict the membrane through some form of relative sliding. Such a mechanism might explain FtsZ's high turnover of GTP.

TubZ was recently discovered and is a bacterial plasmid-borne protein (Larsen et al., 2007) that displays a highly dynamic implementation of the tubulin-like cytomotive filaments (Larsen et al.,

Download English Version:

https://daneshyari.com/en/article/1984278

Download Persian Version:

https://daneshyari.com/article/1984278

Daneshyari.com