Protein family review

The tektin family of microtubule-stabilizing proteins

Linda A Amos

Address: MRC Laboratory of Molecular Biology, Hills Road, Cambridge, CB2 0QH, UK. Email: laa@mrc-lmb.cam.ac.uk

Published: 29 July 2008

*Genome **Biology*** 2008, **9:**229 (doi:10.1186/gb-2008-9-7-229)

The electronic version of this article is the complete one and can be found online at http://genomebiology.com/2008/9/7/229

Summary

Tektins are insoluble α-helical proteins essential for the construction of cilia and flagella and are found throughout the eukaryotes apart from higher plants. Being almost universal but still fairly free to mutate, their coding sequences have proved useful for estimating the evolutionary relationships between closely related species. Their protein molecular structure, typically consisting of four coiled-coil rod segments connected by linkers, resembles that of intermediate filament (IF) proteins and lamins. Tektins assemble into continuous rods 2 nm in diameter that are probably equivalent to subfilaments of the 10 nm diameter IFs. Tektin and IF rod sequences both have a repeating pattern of charged amino acids superimposed on the seven-amino-acid hydrophobic pattern of coiled-coil proteins. The length of the repeat segment matches that of tubulin subunits, suggesting that tektins and tubulins may have coevolved, and that lamins and IFs may have emerged later as modified forms of tektin. Unlike IFs, tektin sequences include one copy of a conserved peptide of nine amino acids that may bind tubulin. The 2 nm filaments associate closely with tubulin in doublet and triplet microtubules of axonemes and centrioles, respectively, and help to stabilize these structures. Their supply restricts the assembled lengths of cilia and flagella. In doublet microtubules, the 2 nm filaments may also help to organize the longitudinal spacing of accessory structures, such as groups of inner dynein arms and radial spokes.

Gene organization and evolutionary history

Genes for tektins are found throughout the animal kingdom (for example, they have been sequenced in mammals, fish, sea urchins, insects, and nematodes) and also in algal species (for example, the unicellular *Chlamydomonas*) but not in flowering plants; that is, they occur in any eukaryotic organism that develops cilia or flagella [1-30]. Their relationships (Figure 1) suggest a complex evolutionary history involving gene duplications and subsequent losses of unnecessary genes. Some organisms have a single tektin; for example, zebrafish have only tektin 2, a testis protein. Others have several: for example, sea urchins use three in their sperm tails; humans have at least six, some of which are specific to testis whereas others occur also in cilia and centrioles in cells in other tissues. The human tektin genes are all found on different chromosomes. Different tektins from one species vary more than equivalent sequences from different species, suggesting that each type may have specific roles [11,12,14-20]. A limited number of interacting protein partners leaves tektin sequences relatively free to mutate. Thus, an essential testis-specific isoform has been included as one of the nuclear genes used to estimate the evolutionary distances between closely related species [21,30].

Tektins are related to intermediate filament (IF) proteins [1,5,31,32] and nuclear lamins [33-35], whose sequences also show evidence of gene duplication. Within the rod domains of both tektins and IFs, the longitudinal repeating pattern of hydrophobic and charged amino acids suggests that their ancestral protein may have evolved in tandem with tubulin, whose globular monomers polymerize into protofilaments with a 4 nm repeat. This spacing, corresponding to 28 residues along a coiled-coil, would have arisen quite simply in an ancestral tektin as groups of four heptads. However, other coiled-coil proteins do have different patterns of charge, and different superhelix repeats; indeed, the

Figure 1

Distribution of tektin sequences. Phylogenetic tree showing the relationships between known tektin sequences. The three original sequences obtained from the sea urchin *Strongylocentrotus purpuratus* are labeled in pink, mammalian tektins 1-3, and 5 in green, and mammalian tektin 4 (found in dense fibers [45]) in blue. Neoptera is a taxonomic group that includes most of the winged insects. Modified output from pfam: family: tektin (pf03148) [66,67]. Species abbreviations [66]: AEDAE, *Aedes aegypti*; ANOGA, *Anopheles gambiae*; BOVIN, *Bos taurus*; BRARE, *Danio rerio*; CAEBR, *Caenorhabditis briggsae*; CAEEL, *Caenorhabditis elegans*; CANFA, *Canis familiaris*; CHLRE, *Chlamydomonas reinhardtii*; CIOIN, *Ciona intestinalis*; DROER, *Drosophila erecta*; DROME, *Drosophila melanogaster*; DROPS, *Drosophila pseudoobscura*; DROSI, *Drosophila simulans*; MACFA, *Macaca fascicularis*; MESAU, *Mesocricetus auratus* (golden hamster); MOUSE, *Mus musculus*; NEOP, *Neoptera* sp.; RAT, *Rattus norvegicus*; SCHJA, *Schistosoma japonicum*; STRPU, *Strongylocentrotus purpuratus*; TETNG, *Tetraodon nigroviridis*; XENLA, *Xenopus laevis*; XENTR, *Xenopus tropicalis*.

charge pattern of tropomyosin matches the 5.5 nm periodicity of subunits in actin filaments [36]. Thus, it is not clear whether a tubulin-like or a tektin-like protein might have existed first.

Bacteria have a homolog of tubulin, FtsZ (a protein involved in septum formation during cell division), that also forms linear protofilaments with a similar longitudinal spacing, although the spacing is a little longer, approximately 4.3 nm, and the protofilaments do not associate to form microtubules [37,38]. Is one of FtsZ's protein partners tektin-like? Several of the proteins known to interact with FtsZ [39,40] appear to form coiled-coil dimers (for example, EzrA, SlmA, and ZapA) but it is difficult to draw parallels with the eukaryotic tubulin-tektin association as FtsZ does not assemble into any long-term stable structure. A coiled-coil protein that forms stable filaments in *Caulobacter crescentus* has been investigated and shows a basic similarity to IF proteins [41,42] but this might be coincidental; for example, muscle myosins bundle into filaments but are not considered to be IF-like. The spirochete coiled-coil protein Scc [43] also forms stable filaments, but the molecules seem to be continuous coiled-coils without any of the breaks or 'stutters' (short interruptions in the repeating pattern of residues) characteristic of IFs. Something in *Spirochaeta halophila* was found to react with anti-tektin antibodies [44] but no candidate sequence has been identified in the genome.

Iida *et al*. [45] recently discovered that a testis-specific tektin [46,47] is not located in doublet microtubules but on the surface of structures called dense fibers [48], which augment the elastic strengths of the sperm tails of many animals, including mammals. Dense fibers do not occur in cilia, or in the flagella of unicellular animals, making it likely that tektin acquired its function in the dense fibers secondarily. If tektin and tubulin evolved together first, lamins/IFs may have evolutionarily 'escaped' in a similar fashion, as a form of tektin that no longer binds to tubulin. The alternative scenario is that the lamin/IF group of coiled-coil proteins evolved first and a modified version of one such protein was subsequently co-opted into axoneme formation, with the length of tubulin becoming adapted to fit the tektin periodicity precisely. In either case, both tektin and tubulin may have adapted to enable a eukaryote ancestor to assemble stable axonemal microtubules. Tubulin could later have found ways of assembling into more dynamic microtubules with the aid of new microtubule-associated proteins (MAPs), some of which may be related to tektins [49,50].

Characteristic structural features

Tektin monomers are typically proteins of around 45-60 kDa, consisting, like IF proteins [33-35], of amino- and carboxy-terminal head and tail domains of varying sizes (Figure 2) on each side of a conserved coiled-coil rod domain. Most have similar halves (see Figure 2) and each half is further divided into two, so the original protein was perhaps equivalent to a quarter of a tektin. The four α-helical rod-domain segments, 1A, 1B, 2A, and 2B, are connected by linkers [5-7]. Because of divergence between the half-domains, the tektin signature nonapeptide sequence (usually RPNVELCRD, variations are shown in Figure 2) occurs only in the middle of the second half (only in the linker between the 2A and 2B helices, although there are other conserved cysteines in the loops at either end of 1B and 2B [9], see Figure 2a). The high degree of conservation of the nonapeptide suggests a functionally important tektin-specific domain, most likely for binding to tubulin, but this has not been shown experimentally. At a similar point, IF and lamins have just a stutter in the heptad pattern of hydrophobic amino acids, to show where a connecting link between two stretches of coiled-coil once existed (see the lamin plot in Figure 2b). Superimposed on the hydrophobic heptad repeats, there are longer repeating patterns of charged amino acids. Three charge repeats, of approximately nine residues each, define lengths of IF rod of approximately 4 nm [33]. The charge pattern is actually less clear in tektins [5], but each quarter-rod segment still matches an 8 nm tubulin heterodimer.

Tektins were first isolated from sea urchin sperm tails. Long continuous filaments run along the doublet microtubules of the sperm flagella [1-3,9,51-53], and the initial determination of their protein components was made from insoluble filaments derived from the tails [1-3]. Extraction of doublet microtubules with anionic detergent produces ribbons of tubulin protofilaments (Figure 3b) stabilized with other proteins, including tektins [1-3] and some other coiled-coil proteins [54-56]. Further solubilization yields filamentous co-polymers of tektins A, B and C, and finally 2 nm filaments containing only tektin AB heterodimers, as confirmed by crosslinking experiments [51]. Sequences obtained for sea urchin tektins A, B and C [5-7,10] showed that A and B were closely related and allowed models of dimer molecules and polymers to be devised (see, for example, Figure 3g,h). The probable molecular lengths (32 nm for AB heterodimers and 48 nm for C homodimers) and the periodicities observed on filaments (especially the strong 16 nm repeat seen on purified tektin AB filaments) are all sub-periods of the 96 nm periodicity found on doublet microtubules decorated with accessory structures. The significance of this conserved periodicity (equal to 12 tubulin dimers) in axonemes is unclear, but it is interesting that the supercoil pitch of four-stranded vimentin fibers is also 96 nm [35].

Localization and function

As already indicated, tektins are essential constituents and specific markers for ciliary and flagellar axonemes (containing doublet microtubules) [1-26] and for basal bodies and centrioles (containing triplet microtubules) [25-29]. In the nematode *Caenorhabditis elegans*, for example, the

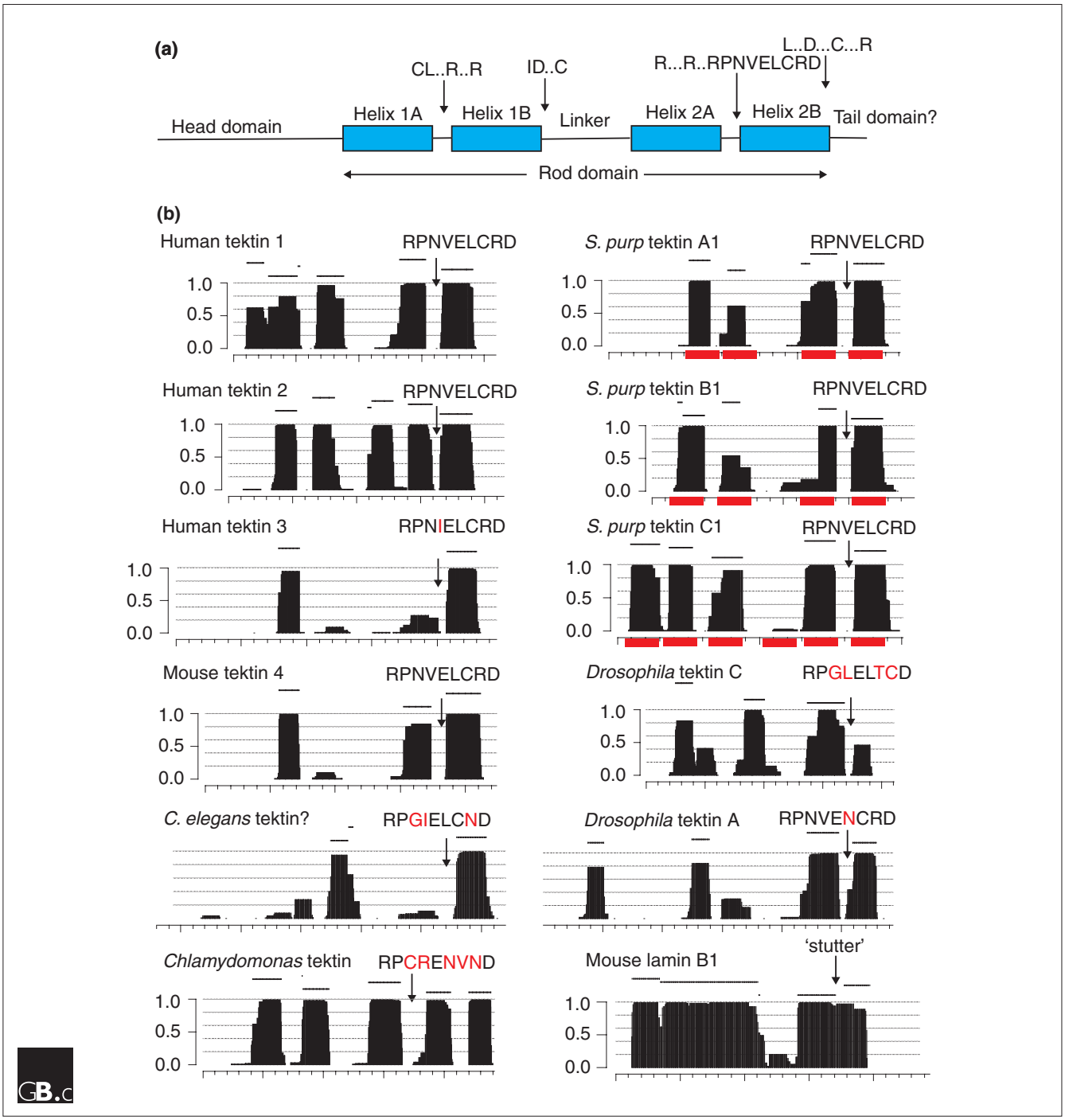

Figure 2

Structure prediction from amino-acid sequences. **(a)** Apparent domain structure within a typical tektin polypeptide. The positions of some conserved residues, including the signature nonapeptide, are indicated in single-letter amino acid code above the diagram. For a detailed comparison of a range of sequences, see NCBI Conserved DOmains pfam03148 [68]. **(b)** Predictions of coiled-coil segments from the amino-acid sequences of various tektins plus a typical lamin for comparison. The vertical scale in each plot is the probability (0.0 to 1.0) of a coiled-coil structure being formed [69,70]. Horizontal lines above each stretch with a high probability indicate the relative phases of the heptad repeats; a 'stutter' thus revealed in the middle of the last coiled-coil of the lamin is a feature of all lamins and IFs [34]. Its position corresponds to that of the tektin loop containing the conserved nonapeptide, whose minor sequence variations are shown in red. For all three sea urchin tektins whose structure has been studied in detail [5-7], predicted 8 nm long (56-residue) segments that may each lie alongside a tubulin heterodimer are indicated by horizontal red bars. Human tektin 1 (NP_444515); human tektin 2 (AAH35620); human tektin 3 (AAH31688); mouse tektin 4 (AAI17527); *C. elegans* tektin (AAA96184); *Chlamydomonas* tektin (BAC77347); *Strongylocentrotus purpuratus* (sea urchin) tektin A1 (NP_999787, GenBank: M97188); *S. purp.* B1 (NP_999789, GenBank: L21838); *S. purp.* tektin C1 (NP_999788, GenBank: U38523); *Drosophila* tektin A (NP_523577); *Drosophila* tektin C (NP_523940); mouse lamin B1 (NP_034851).

expression of tektins correlates spatially with touch receptor cilia [57]. In mammals, tektins occur in testis, brain, retina, and other tissues containing ciliated cells [8]. Of the several types of mammalian tektins, at least two - tektin 2 and tektin 4 - are present in sperm flagella, although tektin 4 is associated with outer dense fibers rather than with outer doublet microtubules [11-20].

While it is clear that tektins are in or next to the partition of outer doublet microtubules (Figure 3a-f), some questions remain about their exact locations and functions. Electron microscope (EM) tomography of sea urchin tubules [58] has revealed a longitudinally continuous thin filament (at the tip of the arrow in Figure 3e) associated with the middle tubulin protofilament of the partition, which would be a good position to provide a central stabilizing element for a sliding and bending doublet microtubule, and is consistent with the proposed role of tektin in regulating the length of an axoneme through a limited supply of one of the tektins [59,60]. However, this thin filament is distanced from the sites of attachment of radial spokes, dynein arms and the regulatory complexes, where the long periodicities inherent in a tektin filament (Figure 3g-h) might serve another useful purpose, as a molecular 'ruler'. Schemes employing both the 32 nm length of tektin AB molecules and 48 nm or 32 nm spaced tektin C molecules (Figure 3i) have been proposed to account for the 96 nm repeating series of accessory proteins on sea urchin doublet microtubules [7,9,10,52]. In species with only one type of tektin, filaments assembled from 32 nm or 48 nm long molecules could still interact with a series of accessory structures to produce a 96 nm repeat. However, there are likely to be length-measuring proteins other than tektins in the axonemes of all species.

Linck has proposed that tektins bundle to form one of the protofilaments close to the inner junction between tubules A and B [10,52,61], which would be consistent with evidence that tektins are stably connected to the accessory structures [62]. However, the EM tomographic image (Figure 3c-f) does not indicate any protofilament with a radically different internal composition. In contrast, the unique thin filament on the partition has the appearance expected for a simple tektin AB polymer, such as that seen by Pirner and Linck [52] and modeled in Figure 3i,j, and the long sideways projections reaching out as far as the junctions might explain the association of tektin with dynein. These long strands projecting sideways from the thin filament may be amino-terminal domains, for example, from tektin A (see Figure 3g), or could be separate coiled-coil proteins (possibly tektin C or related to the *Chlamydomonas* 'rib' proteins [54-56]). The additional proteins that co-purify with the insoluble tektins are presumably associated with the partition, rather than with regions of the A- and B-tubules that disintegrate early (see Figure 3b); in addition to the continuous filament and associated projections on the A-tubule side of the partition, the tomogram (Figure 3c-f) shows a considerable amount of material on the B-tubule side.

It is also possible that tektins can form more than a single filament; the crosslinking experiments [10,52] proved the existence of tektin AB heterodimers and continuous polymers, and tektin C homodimers and tetramers, but not necessarily complexes of all three proteins. For example, the partition filament might be tektin AB while tektin C tetramers could associate with accessory attachment sites (Figure 3a,e). Alternatively, there could be more than one heteropolymeric filament per doublet, if the reported quantitation [29] turns out to be accurate. Data for *Chlamydomas* flagella (which apparently contain a soluble tektin that is not retained in the insoluble ribbon fraction [63]) also suggest two separate roles and sites for tektin in the doublet. The flagella of mutants lacking inner dynein arms contain only 20% of the normal amount of this tektin, suggesting that the other 80% may co-assemble with inner dynein arms. Thus, in species making only one type of tektin, one protein might occupy both types of sites, forming a continuous filament on the partition and a more soluble complex at the base of the inner dynein arms or radial spokes.

Frontiers

Many details remain to be resolved regarding the structural arrangement of tektins, ribs and other proteins that co-purify with the stable ribbons of axonemal doublet microtubules. Filaments from a range of sources other than sea urchin sperm [53] and *Chlamydomonas* [54-56] flagella need to be isolated to investigate their compositions and structural characteristics. Similarly, there is more to be learned from three-dimensional EM cryo-tomography [58], including images to be reconstructed with 48 nm or 96 nm rather than 16 nm longitudinal averaging. The possibilities of identifying different proteins in sea urchin axonemes by labeling are limited (antibodies are unlikely to reach sites located inside the doublets) but better methods are available for microorganisms such as *Chlamydomonas* and *Tetrahymena*, which can be genetically modified to add labels or remove components. Initially, it will probably be rewarding to compare tomograms of wild-type *Chlamydomonas* and the mutants mentioned above [63].

The precise function of the tektin signature sequence, RPNVELCRD, remains to be determined. This question may be approached using peptides or small segments of tektin produced by recombinant expression systems. It may be possible to determine whether the conserved loop binds directly to tubulin and, if so, what types of mutations eliminate binding. A related question is why mammalian tektin 4 locates to dense fibers rather than to doublet tubules [45], even though it has the standard signature sequence. Is there any tubulin in the outer dense fibers?

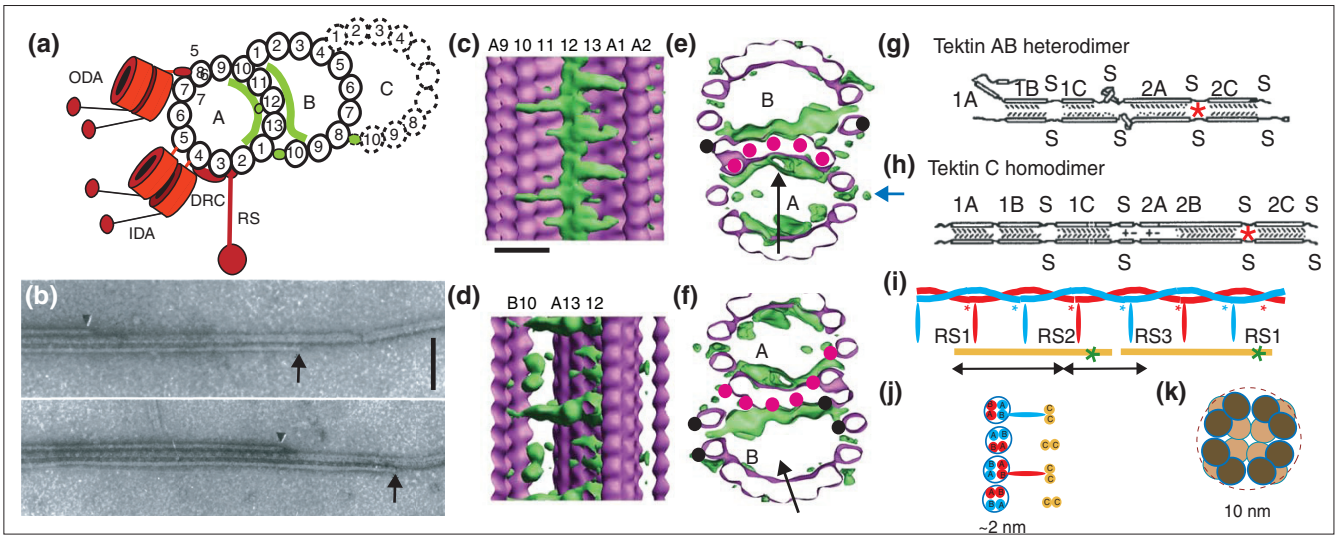

Figure 3

Filament structure and interactions based on electron microscopy. **(a)** Diagram of the cross-section of a doublet or triplet microtubule, with the tubulin protofilaments numbered as in [71]. Attached to the complete A-tubule are rows of outer dynein arms (ODA), inner dynein arms (IDA), radial spokes (RS), dynein regulatory complexes (DRC) and the incomplete B-tubule. The outer A-B junction is a direct interaction between two tubulin protofilaments but, at the inner junction, the so-called 11th protofilament of the B-tubule [72] turned out to be a row of non-tubulin crosslinks (d). In the case of a triplet microtubule, the C-tubule is probably attached in a similar way to the outside of the B-tubule. Green material on either surface of the shared partition between A- and B-tubules in (a) represents that seen in (c-f). **(b)** Electron microscope (EM) images of disintegrating doublet microtubules isolated from sea urchin sperm tails and contrasted with uranyl acetate negative stain (reproduced with permission from [1]). The A-tubule and B-tubule [73] can be distinguished even after the loss of accessory structures. An arrowhead indicates the loss of the B-tubule, an arrow shows where most of the A-tubule ends, leaving just the partition. After continued extraction, SDS gels of the remaining ribbons showed that the main proteins present, in addition to some tubulin, were three tektins plus two or three other bands [1,2]. The scale bar represents 100 nm. **(c-f)** Images obtained by EM tomography of frozen doublet microtubules (reproduced with permission from [58]). Tubulin has been colored purple and all other material green. (e,f) End-on views, with the tubulin protofilaments cut through, of the side view of the A-tubule shown in (c) and the junction between the A-tubule and B-tubule shown in (d), respectively. Magenta and black circles in (e,f) denote the groups of A-tubule and B-tubule protofilaments viewed in (c,d), respectively, and the black arrows indicate the directions in which they are viewed. At the tip of the black arrow in (e) is a small hole representing the core of an axially continuous thin filament whose outer surface is seen running down the middle of (c). Projections from this filament extend across the protofilaments on either side of the thin filament. To improve the signal-to-noise ratio, the 3D image was averaged in the axial direction at 16 nm intervals, so any longer periodicities have been lost. The blue arrow in (e) indicates material between protofilaments of the A-tubule that may be involved in the attachment and organization of the radial spokes and sets of inner dynein arms. (c,d) Scale bar = 10 nm. **(g,h)** Models of tektin dimers proposed in [7] (reproduced with permission from [7]). (g) 32 nm long tektin AB heterodimer with amino-terminal segment of tektin A that may form a sideways projection from a filament composed of heterodimers. S S indicates the position of disulfide bonds. (h) 40-48 nm long tektin C homodimer. Colored asterisks in (g,h) show the predicted positions of the nonapeptide loops that may bind strongly to tubulin. (i) Model of a 2 nm tektin AB 'core' filament, consisting of heterodimers joined end-to-end to form two strands (coloured red or cyan; they may differ slightly, as there are two isoforms of tektin A [10]). Colored asterisks show the predicted positions of the nonapeptide loops. Heterodimers in the two strands are shown half-staggered to explain the prominent 16 nm periodicity seen in (b). The red and cyan projections represent the amino-terminal headers of tektin A monomers (see g) in each strand. A strand made up of tektin C homodimers (yellow) is drawn alongside, although the exact relationship between tektin C dimers/tetramers and tektin AB filaments is not clear at present. A pair of 48 nm long tektin C molecules might organize a group of radial spokes (RS1, RS2 and RS3) to give an overall longitudinal repeat distance of 96 nm. The 32 nm spacing between RS1 and RS2 and the 24 nm spacing between RS2 and RS3 are indicated by double-headed arrows. **(j)** The same 2 nm filament as in (i) shown in cross-section at four successive positions to indicate how four individual α-helical strands (two AB dimers) might twist smoothly around each other. In this model, tektin C C homodimers (yellow circles) are shown associated with, but not integrated into, the filament (unlike the model in [10]), as it is hard to account for crosslinking evidence that tektin C forms tetramers but not filaments [52]. **(k)** Cross-section through a possible model of an intermediate filament in which pairs of 2 nm filaments are twisted to form 4 nm filaments and four of these are bundled to form a 10 nm filament; each light-brown or dark-brown circle represents a 2 nm filament; thus, each circle here corresponds to the larger circles in (j). IFs have been proposed to be tubes built from eight 2 nm filaments [34] or supercoils of four 4 nm filaments, each with a pitch of 96 nm [35]; a cross-section through the latter at some levels might appear to be a ring of eight smaller filaments (dark brown), while slices at other levels would show 4 nm filaments arranged as a cross (light brown). Each subfilament of an IF is thought to be bipolar, whereas tektin filaments are most probably polar to match the polar tubulin protofilaments.

It would also be interesting to know what makes some tektins insoluble after the assembly of doublet tubules, although, presumably, only soluble complexes are transported into the flagellum. Is there a post-translational modification, similar to the phosphorylation that allows vimentin to remain soluble until it is assembled into IFs and allows it to be resolubilized during disassembly [64]? As tektins are unlikely to be reused [59,60], they might be phosphorylated immediately after translation, dephosphorylated in the course of axoneme assembly but then degraded by proteolysis during flagellar retraction. Such events will probably be most conveniently studied in *Chlamydomonas* or *Tetrahymena*.

The cause of the differential solubility of tektins that are assumed to be in different locations in triplet microtubules [29] might also be investigated.

A continued search for prokaryotic ancestors of tektins and IF proteins is expected. The *Escherichia coli* protein SlmA [65] is of possible interest because it apparently supports FtsZ assembly (possible tektin-like behavior) and also associates with the bacterial nucleoid (possible lamin-like behavior), although its coiled-coil is so short as to correspond to just one of the *Strongylocentrotus purpuratus* (sea urchin) tektin coiled-coil segments in Figure 2. However, there may be a related protein in other bacterial species that has grown longer through gene duplication.

It is likely that many such questions will be answered as new researchers take an interest in tektins. After many years of being regarded as an obscure group of specialized proteins, they have become important, as related genes are found in every newly sequenced eukaryotic genome. Tektins will increasingly be used in phylogenetic studies [21-23,30] and may turn out to vary even among human beings and be useful, for example, in tracking population movements.

Acknowledgements

I thank Dick Linck for introducing me to tektins long ago and for reading this review and making helpful comments.

References

1. Linck RW: **Flagellar doublet microtubules: fractionation of minor components and alpha-tubulin from specific regions of the A-tubule.** *J Cell Sci* 1976, **20:**405-439.
2. Linck RW, Langevin G: **Structure and chemical composition of insoluble filamentous components of sperm flagellar microtubules.** *J Cell Sci* 1982, **58:**1-22.
3. Linck RW, Stephens RE: **Biochemical characterization of tektins from sperm flagellar doublet microtubules.** *J Cell Biol* 1987, **104:**1069-1075.
4. Amos WB, Amos LA, Linck RW: **Proteins closely similar to flagellar tektins are detected in cilia but not in cytoplasmic microtubules.** *Cell Motil* 1985, **5:**239-249.
5. Norrander JM, Amos LA, Linck RW: **Primary structure of tektin A1: comparison with intermediate-filament proteins and a model for its association with tubulin.** *Proc Natl Acad Sci USA* 1992, **89:**8567-8571.
6. Chen R, Perrone CA, Amos LA, Linck RW: **Tektin B from ciliary microtubules: primary structure as deduced from the cDNA sequence and comparison with tektin A.** *J Cell Sci* 1993, **106:**909-918.
7. Norrander JM, Perrone CA, Amos LA, Linck RW: **Structural comparison of tektins and evidence for their determination of complex spacings in flagellar microtubules.** *J Mol Biol* 1996, **257:**385-397.
8. Norrander J, Larsson M, Stahl S, Höög C, Linck R: **Expression of ciliary tektins in brain and sensory development.** *J Neurosci* 1998, **18:**8912-8918.
9. Linck R, Norrander JM: **Protofilament ribbon compartments of ciliary and flagellar microtubules.** *Protist* 2003, **154:**299-311.
10. Setter PW, Malvey-Dorn E, Steffen W, Stephens RE, Linck RW: **Tektin interactions and a model for molecular functions.** *Exp Cell Res* 2006, **312:**2880-2896.
11. Iguchi N, Tanaka H, Fujii T, Tamura K, Kaneko Y, Nojima H, Nishimune Y: **Molecular cloning of haploid germ cell-specific tektin cDNA and analysis of the protein in mouse testis.** *FEBS Lett* 1999, **456:**315-321.
12. Larsson M, Norrander J, Gräslund S, Brundell E, Linck R, Ståhl S, Höög C: **The spatial and temporal expression of Tekt1, a mouse tektin C homologue, during spermatogenesis suggest that it is involved in the development of the sperm tail basal body and axoneme.** *Eur J Cell Biol* 2000, **79:**718-725.
13. Ma Z, Khatlani TS, Sasaki K, Inokuma H, Onishi T: **Cloning of canine cDNA encoding tektin.** *J Vet Med Sci* 2000, **62:**1013-1016.
14. Xu M, Zhou Z, Cheng C, Zhao W, Tang R, Huang Y, Wang W, Xu J, Zeng L, Xie Y, Mao Y: **Cloning and characterization of a novel human tektin1 gene.** *Int J Biochem Cell Biol* 2001, **33:**1172-1182.
15. Inoue K, Dewar K, Katsanis N, Reiter LT, Lander ES, Devon KL, Wyman DW, Lupski JR, Birren B: **The 1.4-Mb CMT1A duplication/HNPP deletion genomic region reveals unique genome architectural features and provides insights into the recent evolution of new genes.** *Genome Res* 2001, **11:**1013-1033.
16. Iguchi N, Tanaka H, Nakamura Y, Nozaki M, Fujiwara T, Nishimune Y: **Cloning and characterization of the human tektin-t gene.** *Mol Hum Reprod* 2002, **8:**525-530.
17. Wolkowicz MJ, Naaby-Hansen S, Gamble AR, Reddi PP, Flickinger CJ, Herr JC: **Tektin B1 demonstrates flagellar localization in human sperm.** *Biol Reprod* 2002, **66:**241-250.
18. Roy A, Yan W, Burns KH, Matzuk MM: **Tektin3 encodes an evolutionarily conserved putative testicular microtubules-related protein expressed preferentially in male germ cells.** *Mol Reprod Dev* 2004, **67:**295-302.
19. Matsuyama T, Honda Y, Doiguchi M, Iida H: **Molecular cloning of a new member of tektin family, Tektin4, located to the flagella of rat spermatozoa.** *Mol Reprod Dev* 2005, **72:**120-128.
20. Murayama E, Yamamoto E, Kaneko T, Shibata Y, Inai T, Iida H: **Tektin5, a new tektin family member, is a component of the middle piece of flagella in rat spermatozoa.** *Mol Reprod Dev* 2008, **75:**650-658.
21. Ota A, Kusakabe T, Sugimoto Y, Takahashi M, Nakajima Y, Kawaguchi Y, Koga K: **Cloning and characterization of testis-specific tektin in *Bombyx mori*.** *Comp Biochem Physiol B: Biochem Mol Biol* 2002, **133:**371-382.
22. Whinnett A, Brower AVZ, Lee M-M, Willmott KR, Mallett J: **Phylogenetic utility of tektin, a novel region for inferring systematic relationships among Lepidoptera.** *Ann Entomol Soc Am* 2005, **98:**873-886.
23. Ogino K, Tsuneki K, Furuya H: **The expression of tubulin and tektin genes in dicyemid mesozoans (Phylum: Dicyemida).** *J Parasitol* 2007, **93:**608-618.
24. Arenas-Mena C, Wong KS-Y, Arandi-Forosani N: **Ciliary band gene expression patterns in the embryo and trochophore larva of an indirectly developing polychaete.** *Gene Expr Patt* 2007, **7:**544-549.
25. Linck RW, Goggin MJ, Norrander JM, Steffen W: **Characterization of antibodies as probes for structural and biochemical studies of tektins from ciliary and flagellar microtubules.** *J Cell Sci* 1987, **88:**453-466.
26. Steffen W, Linck RW: **Evidence for tektins in centrioles and axonemal microtubules.** *Proc Natl Acad Sci USA* 1988, **85:**2643-2647.
27. Steffen W, Fajer E, Linck R: **Centrosomal components immunologically related to tektins from ciliary and flagellar microtubules.** *J Cell Sci* 1994, **107:**2095-2105.
28. Hinchcliffe E, Linck R: **Two proteins isolated from sea urchin sperm flagella: structural components common to the stable microtubules of axonemes and centrioles.** *J Cell Sci* 1998, **111:**585-595.
29. Stephens RE, Lemieux NA: **Tektins as structural determinants in basal bodies.** *Cell Motil Cytoskel* 1998, **40:**379-392.
30. Mallarino R, Bermingham E, Willmott KR, Whinnett A, Jiggins CD: **Molecular systematics of the butterfly genus *Ithomia* (Lepidoptera: Ithomiinae): a composite phylogenetic hypothesis based on seven genes.** *Mol Phylog Evol* 2005, **34:** 625-644.
31. Chang XJ, Piperno G: **Cross-reactivity of antibodies specific for flagellar tektin and intermediate filament subunits.** *J Cell Biol* 1987, **104:**1563-1568.
32. Steffen W, Linck RW: **Relationship between tektins and intermediate filament proteins: an immunological study.** *Cell Motil Cytoskel* 1989, **14:**359-371.
33. McLachlan AD, Stewart M: **Periodic charge distribution in the intermediate filament proteins desmin and vimentin.** *J Mol Biol* 1982, **162:**693-698.
34. Parry DA, Strelkov SV, Burkhard P, Aebi U, Herrmann H: **Towards a molecular description of intermediate filament structure and assembly.** *Exp Cell Res* 2007, **313:**2204-2216.
35. Goldie KN, Wedig T, Mitra A, Aebi U, Herrmann H, Hoenger A: **Dissecting the 3-D structure of vimentin intermediate filaments by cryo-electron tomography.** *J. Struct Biol* 2007, **158:**378-385.
36. Stewart M, McLachlan AD: **Fourteen actin-binding sites on tropomyosin?** *Nature* 1975, **257:**331-333.

37. Erickson HP: **FtsZ, a prokaryotic homolog of tubulin?** *Cell* 1995, **80:**367-370.
38. Löwe J, Amos LA: **Tubulin-like protofilaments in Ca^{2+}-induced FtsZ sheets.** *EMBO J* 1999, **18:**2364-2371.
39. Goehring NW, Beckwith J: **Diverse paths to midcell: assembly of the bacterial cell division machinery.** *Curr Biol* 2005, **15:**R514-R526.
40. Michie KA, Löwe J: **Dynamic filaments of the bacterial cytoskeleton.** *Annu Rev Biochem* 2006, **75:**467-492.
41. Ausmees N, Kuhn JR, Jacobs-Wagner C: **The bacterial cytoskeleton: an intermediate filament-like function in cell shape.** *Cell* 2003, **115:**705-713.
42. Ausmees N: **Intermediate filament-like cytoskeleton of *Caulobacter crescentus*.** *J Mol Microbiol Biotechnol* 2006, **11:**152-158.
43. Mazouni K, Pehau-Arnaudet G, England P, Bourhy P, Saint Girons I, Picardeau M: **The Scc spirochetal coiled-coil protein forms helix-like filaments and binds to nucleic acids generating nucleoprotein structures.** *J Bacteriol* 2006, **188:**469-476.
44. Barth AL, Stricker JA, Margulis L: **Search for eukaryotic motility proteins in spirochetes: immunological detection of a tektin-like protein in *Spirochaeta halophila*.** *Biosystems* 1991, **24:**313-319.
45. Iida H, Honda Y, Matsuyama T, Shibata Y, Inai T: **Tektin 4 is located on outer dense fibers, not associated with axonemal tubulins of flagella in rodent spermatozoa.** *Mol Reprod Dev* 2006, **73:**929-936.
46. Tanaka H, Iguchi N, Toyama Y, Kitamura K, Takahashi T, Kaseda K, Maekawa M, Nishimune Y: **Mice deficient in the axonemal protein tektin-t exhibit male infertility and immotile-cilium syndrome due to impaired inner arm dynein function.** *Mol Cell Biol* 2004, **24:**7958-7964.
47. Roy A, Lin Y-N, Agno JE, DeMayo FJ, Matzuk MM: **Absence of tektin 4 causes asthenozoospermia and subfertility in male mice.** *FASEB J* 2007, **21:**1013-1025.
48. Nakagawa Y, Yamane Y, Okanoue T, Tsukita S, Tsukita S: **Outer dense fiber 2 is a widespread centrosome scaffold component preferentially associated with mother centrioles: its identification from isolated centrosomes.** *Mol Biol Cell* 2001, **12:**1687–1697.
49. Steffen W, Linck RW: **Evidence for a non-tubulin spindle matrix and for spindle components immunologically related to tektin filaments.** *J Cell Sci* **101:**809-822.
50. Durcan TM, Jalpin ES, Rao T, Collins NS, Tribble EK, Hornick JE, Hinchcliffe EH. **Tektin 2 is required for central spindle microtubule organization and the completion of cytokinesis.** *J Cell Biol* 2008, **181:**595-603.
51. Linck RW, Amos LA, Amos WB: **Localization of tektin filaments in microtubules of sea urchin sperm flagella by immunoelectron microscopy.** *J Cell Biol* 1985, **100:**126-135.
52. Pirner M, Linck R: **Tektins are heterodimeric polymers in flagellar microtubules with axial periodicities matching the tubulin lattice.** *J Biol Chem* 1994, **269:**31800-31806.
53. Pirner MA, Linck RW: **Methods for the isolation of tektins and sarkosyl-insoluble protofilament ribbons.** *Meth Cell Biol* 1995, **47:** 373-380.
54. Norrander JM, deCathelineau AM, Brown JA, Porter ME, Linck RW: **The rib43a protein is associated with forming the specialized protofilament ribbons of flagellar microtubules in *Chlamydomonas*.** *Mol Biol Cell* 2000, **11:**201-215.
55. **NCBI CDD pfam 05914** [http://www.ncbi.nlm.nih.gov/Structure/cdd/cddsrv.cgi?uid=69437]
56. Ikeda K, Brown JA, Yagi T, Norrander JM, Hirono M, Eccleston E, Kamiya R, Linck RW: **Rib72, a conserved protein associated with the ribbon compartment of flagellar A-microtubules and potentially involved in the linkage between outer doublet microtubules.** *J Biol Chem* 2003, **278:**7725-7734.
57. **Gene summary for R02E12.4** [http://www.wormbase.org/db/gene/gene?name=WBGene00019828;class=Gene]
58. Siu H, Downing KH: **Molecular architecture of axonemal microtubule doublets revealed by cryo-electron tomography.** *Nature* 2006, **442:**475-478.
59. Stephens R: **Quantal tektin synthesis and ciliary length in sea-urchin embryos.** *J Cell Sci* 1989, **92:**403-413.
60. Norrander J, Linck R, Stephens R: **Transcriptional control of tektin A mRNA correlates with cilia development and length determination during sea urchin embryogenesis.** *Development* 1995, **121:**1615-1623.
61. Nojima D, Linck RW, Egelman EH: **At least one of the protofilaments in flagellar microtubules is not composed of tubulin.** *Curr Biol* 1995, **5:**158-167.
62. Stephens RE, Oleszko-Szuts S, Linck RW: **Retention of ciliary ninefold structure after removal of microtubules.** *J Cell Sci* 1989, **92:**391-402.
63. Yanagisawa H-A, Kamiya R: **A tektin homologue is decreased in *Chlamydomonas* mutants lacking an axonemal inner-arm dynein.** *Mol Biol Cell* 2004, **15:**2105-2115.
64. Eriksson JE, He T, Trejo-Skalli AV, Harmala-Brasken AS, Hellman J, Chou YH, Goldman RD: **Specific *in vivo* phosphorylation sites determine the assembly dynamics of vimentin intermediate filaments.** *J Cell Sci* 2004, **117:**919-932.
65. Bernhardt TG, de Boer PAJ: **SlmA, a nucleoid-associated, FtsZ binding protein required for blocking septal ring assembly over chromosomes in *E. coli*.** *Mol Cell* 2005, **18:**555-564.
66. **pfam: Family: Tektin (PF03148)** [http://pfam.janelia.org/family?acc=PF03148]
67. **pfam: Family: Tektin (PF03148)** [http://pfam.sanger.ac.uk/family?acc=PF03148]
68. **NCBI CDD pfam03148** [http://www.ncbi.nlm.nih.gov/Structure/cdd/cddsrv.cgi?uid=66800]
69. Lupas A. Van Dyke M, Stock J: **Predicting coiled coils from protein sequences.** *Science* 1991, **252:**1162–1164.
70. **COILS** [http://www.ch.embnet.org/software/COILS_form.html]
71. Linck RW, Stephens RE: **Functional protofilament numbering of ciliary, flagellar, and centriolar microtubules.** *Cell Motil Cytoskel* 2007, **64:**489-495.
72. Tilney LG, Bryan J, Bush DJ, Fujiwara K, Mooseker MS, Murphy DB, Snyder DH: **Microtubules: evidence for 13 protofilaments.** *J Cell Biol* 1973, **59:**267-275.
73. Amos LA, Klug A: **Arrangement of subunits in flagellar microtubules.** *J Cell Sci* 1974, **14:**523-549.