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Education

1979	**BSc in Biochemistry** (University of Nottingham)
1983	**PhD in Protein Biophysics (University of Nottingham)**

Positions

2009-	**Professor of Mechanochemical Cell Biology** University of Warwick
2003-	**Honorary Professor of Molecular Cell Biology** University of Kent at Canterbury
1991-	**Leader, Molecular Motors Group**, MCRI, UK
1988-1991	**Research Staff** MRC LMB, Hills Rd, Cambridge CB2 2QH
1986-1988	**MDA Fellow** MRC LMB, Hills Rd, Cambridge CB2 2QH
1984-1986	**EMBO Fellow** OAW IMB, 5020 Salzburg, Austria

Recent Support

*RCUK has tended not to allow applications from MCRI, Usually we have been able to access research council funding only by applying with a collaborator, and then holding the grant at the collaborating institution (see **grant history** below). The postdoc & two students funded from the EPSRC and BBSRC grants to Andrew Turberfield (Oxford Physics) will spend much of their time in my lab doing optical trapping.*

2009-2012	**EPSRC £0.2M** *Programmable kinesin shuttle (with A. Turberfield, Oxford)*
2009-2012	**BBSRC £0.2M** *Kinesin-DNA chimeras (with A. Turberfield, Oxford)*
2009-2012	**AICR £0.2M** *Single molecule analysis of microtubule tip tracking in vitro*
2004-2009	**MRC Strategic Grant £0.5M** *High resolution structure-function of tubulin*
2006-2009	**CRUK £0.15M** *Reconstitution of S. pombe microtubule dynamics in vitro*
2003-2009	Co-holder on **EPSRC Nanotechnology** network grant **£9M**

At MCRI, I have consistently won core-funding for my group at quinquennial external peer review. Work in my group has consistently been rated Alpha-A on the MRC scales (the highest possible category).

In late 2009 in connection with the shutting down of MCRI, I was awarded 1.23M transitional programme funding from Marie Curie Cancer Care, in a competitive process again involving external peer review. This award is intended to fund startup at Warwick.

*The move to Warwick, completed in Feb 2010, is linked to the founding of a new centre, the **Centre for Mechanochemical Cell Biology**, which we proposed and of which I am director. We are constructing a new building to house the centre, at the entrance to the Gibbett Hill campus of Warwick university (UoW). The designs, planning permission and funding for this building are all in place: UoW is contributing 3.4M, AWM (the regional development agency) is contributing 2M and the Wolfson Trust is contributing 1M. Construction is scheduled to begin in July 2010 and will take one year. UoW is also providing 1.5M towards the purchase of microscopy and other equipment for the new centre.*

Scientific Interests & Current Research

I am interested in mechanochemical coupling in molecular motors, and more generally in mechanotransduction and in the principles and possibilities of motorised molecular self-organisation in biological systems and in synthetic nanosystems. We focus specifically on the mechanochemistry of kinesins and microtubules. We develop our own optical microscopes, in particular for single molecule mechanics.

SCIENTIFIC BIOSKETCH

PhD work

My early contributions were in the mechanisms of myosin self-assembly. This is an important biological mechanism because it prefigures the generation of tension and movement by actomyosin. My PhD work at Nottingham and in Salzburg successfully disproved the then-popular Harrington theory of muscle contraction, which predicted a substantial, force-generating helix-coil melting transition in myosin filaments at physiological temperature. Later, as an EMBO fellow in Salzburg, I found a short C-terminal sequence in the tail region of myosin that is required for self-assembly. Cleavage of this sequence blocks myosin self-assembly (FEBS Lett. **200** 355-360).

MRC-LMB

Back in the UK as an MDA fellow at MRC-LMB I found that this was true of nonmuscle myosins also (J. Cell Biol. **109** 549-556, J. Cell Biol. **118** 1085- 1095). Sticking with the myosin self-assembly reaction, I showed using transient kinetics that formation of a compact folded-up conformer of myosin traps the myosin heads in a specific kinetic state that does not bind actin (EMBO J **5** 2637-2641, J. Mol. Biol. **203** 173-18). The folding reaction turns off ATP turnover and allows a substantial pool of soluble subunits to be built up (J. Mol. Biol. **217** 323-335). At this time I also worked out the packing arrangement of subunits within myosin filaments (J. Mol. Biol. **222** 455-458), proposed a kinetic mechanism for assembly, and showed, contrary to the canon, that the building block is a single myosin molecule (EMBO J. **10** 747-756).

MCRI

I left MRC-LMB in 1991 to set up a lab at MCRI to work on the kinesins, then newly-discovered. Working with Ncd, a reverse-directed kinesin, we quickly disproved suggestions that were current at the time that Ncd runs backwards because its kinetic cycle differs radically from that of forwards kinesin (EMBO J. **13** 751-757). Instead, we found that backwards and forwards kinesins compete for the same sites on microtubules (J. Mol. Biol. **249** 763-771), that the mechanism of both involves a cyclic alternation between weak and strong binding states (J. Mol. Biol **257** 66-76, Biochemistry **35** 2365-2373), and that most kinesins are not processive (J. Mol Biol **273** 160-170). In parallel, we obtained in collaboration with Linda Amos and Keiko Hirose of MRC-LMB 3D cryoelectron microscope reconstructions of the structural cycle of kinesins (Nature **376** 277-279, PNAS **93** 9539-9544, J. Mol. Biol. **278** 389-400, EMBO J. **19** 5308-5314). With Joel Vanderkerckhove, we mapped the binding interface between kinesins and tubulin using a novel combination of traditional proteolytic footprinting and mass spec. of the proteolytic digests (EMBO J **17** 945-951).

Besides this latter technique my colleagues and I have developed several other new methods, including a method for labeling single kinesin molecules with an arbitrarily bright fluorescent tag, to allow single molecule tracking using a standard epifluorescence microscope (Current Biology **12** 301-6), and a method for tracking microtubule twisting that revealed a torsion component in the power stroke of kinesin (Nature Chemical Biology **1** 338-341). We designed and used a microtubule-binding molecular roadblock to find out what happens when kinesin molecules hit a barrier (EMBO J **23** 23-32). Using a novel motility assay, we discovered that monastrol, an anti-mitotic, inhibits its target, a kinesin called Eg5, by locking it into a hitherto-undescribed low-friction attached state (Current Biology **14** R411-R412).
My more recent and most influential work has emphasized single molecule approaches to dissect the mechanical cycle of kinesin. My colleague and collaborator Nick Carter built an exceptionally high-resolution optical trap, and together we used it to show processive motility from a kinesin-myosin chimera (FEBS letters **569** 54-58), to discover that a fungal kinesin from Neurospora is processive (EMBO J **18** 5863-5872), and to show that Kif1d, a fast transporter kinesin, is not (EMBO J. **20** 5101-5113).

My best contributions are my most recent (5 key contributions below).

FIVE KEY CONTRIBUTIONS

Mechanics of the kinesin step	**Carter & Cross 2005** (Nature **435** 308-12) revolutionized the motors field with the discovery that kinesin molecules can walk backwards. We showed that the 8nm mechanical step is an extremely fast, unitary process (<30 μs) and we measured the entire force velocity curve for kinesin, from plus 15 pN to -15 pN, at both high and low [ATP]. This paper was accompanied by a Nature *News and Views* and is an F1000 'must read'. Four years on, no one has been able to improve on these data: our optical trap, built on a modest budget at MCRI, has achieved the best spatial and temporal resolution of any instrument in the world – apart from our recently-completed MCRI Mk II optical trap.
A uniquely-powerful model ***reconstituted system for dissecting microtubule dynamics***	**Drummond & Cross 2000** (Current Biology **10** 766-775) made seminal measurements on interphase microtubule dynamics in *S. pombe* that triggered an avalanche of related work on this important model system. Drummond and I realized early on that the key to understanding mechanism was to find a way to express and purify milligram quantities of single-isoform mutant tubulins. We have recently succeeded in this and and are working with Jan Löwe at MRC-LMB to obtain a high resolution crystal structure of a kinesin-tubulin complex.
ATP-gating mechanism of kinesin	**Alonso & Cross 2007** (Science **316** 120-123) found an ATP-gating mechanism governing the walking action of kinesin-1. This model remains the focus of current thinking in the field. This paper was accompanied by a *Perspective* in Science and a *Commentary* in 'The Scientist'. It is an F1000 'must read'.
Low friction attached state of kinesin-5	**Crevel & Cross 2004** (Current Biology **14** 411-412). This short paper revolutionized thinking on monastrol, a new cancer drug, by showing that it locks kinesin-5 into a previously-undescribed low-friction microtubule-attached state. We are continuing to work on the biophysical cell biology of monastrol-like drugs (collaboration with McAinsh lab) and have thereby discovered a cell cycle clock that governs mitotic prophase (submitted to Science).
Mal3 changes microtubule structure	**DesGeorges et al 2008** (Nature Struc Mol Biol **15** 1102-8) showed that Mal3, an abundant cellular protein, forces microtubules to assemble using the A-Lattice packing diagram. This finding calls into serious doubt the very long-held assumption in Cell Biology that microtubules in cells have a B-lattice structure. This paper is an F1000 'must read'.

International Conferences I have Organised

2008	**MCRI Spring Workshop** *Microtubule Dynamics*
2005	**EMBO workshop** / **Harden Conference** *Molecular Motors* Cambridge
1993-2008	**Marie Curie** annual workshops on *Molecular Motors*
1998	**FEBS Advanced Course** at MCRI, *Molecular Motors*
1993	**EMBO workshop** in Cambridge, UK *Molecular Motors*
1991	**Wellcome Trust Frontiers in Science** congress *Molecular Motors*
1990	**EMBO workshop** in Maria Alm, *Smooth Muscle Contraction*

Recent Invitations

15 03 10	Institut Curie, Paris *2010 External reviewer for CNRS unit*
02 05 10	EMBL *2010 EMBO Microtubule Workshop*

Publications

2009

Katsuki,M., Drummond, D.R., Osei, M. & Cross, R.A. (2009)
Mal3 masks catastrophe events in Schizosacharomyces pombe microtubules by inhibiting shrinkage and promoting rescue
Journal of Biological Chemistry. **23** 29246-50

Braun, M., Drummond,D.R., Cross, R.A. & McAinsh, A.D. (2009)
Klp2 organises microtubules into parallel bundles by an ATP-dependent sorting mechanism
Nature Cell Biol. **11** 724-30

2008

DesGeorges, A., Katsuki, M., Drummond, D.R., Osei, M., Cross, R.A. & Amos, L.A. (2008)
Mal3, the S. pombe homologue of EB1, changes the microtubule lattice
Nature Struc. Mol. Biol.**15** 1102-8

Cross R.A. (2008)
Single molecule for the people (review of *Single molecule techniques*, a laboratory manual eds Selvin & Ha)
Nature Cell Biol. **10** 1014

Dunn, S., Morrison, E., Liverpool,T., Molina-Paris, C., Cross, R., Alonso, M. & Peckham, M. (2008)
Differential trafficking of kinesin-1 (Kif5c) on tyrosinated and detyrosinated microtubules in live cells
J.Cell Sci **121** 1085-95

Kaseda,K., Crevel, I., Hirose, K., Cross, R. (2008)
Single-headed mode of kinesin-5
EMBO Reports **9** 761-76

2007

Alonso,M.C., Drummond, D.R., Kain, S., Hoeng, J., Amos, L.A. & Cross, R.A. (2007)
An ATP-gate controls tubulin binding by the tethered head of kinesin-1
Science **316** 120-123

Grant, B., McCammon,A., Caves, L.S. & Cross, R.A. (2007)
Multivariate analysis of conserved sequence-structure relationships in kinesins: coupling of the active site and a tubulin-binding subdomain
J.Mol.Biol. **368** 1231-1248

2006

Moores, C.A., Perderiset,M., Kappeler,C., Kain,S., Drummond, D., Perkins,S.J., Chelly, J., Cross, R.A., Houdusse,A. & Francis,F. (2006)
Distinct roles of doublecortin in modulating the microtubule cytoskeleton
EMBO J **25** 4448-4457

Cross R.A. (2006)
Myosin's mechanical ratchet *review*
PNAS **103** 8911-8912

Carter N.J. & Cross R.A. (2006)
Kinesin's moonwalk *peer-reviewed review*
Current Opinion in Cell Biology **18** 61-67

Skoufias, D.A., DeBonis, S., Saoudi, Y., Lebeau, L., Crevel, I., Cross, R., Wade, . Hackney, D. & Kozielski, F. (2006)
S-Trityl-L-cysteine is a reversible tight binding inhibitor of the hunan kinesin Eg5 that specifically blocks mitotic progression
J. Biol Chem **281** 17559-17569

2005

Yajima J. & Cross R.A. (2005)
A torque component in the kinesin-1 power stroke
Nature Chemical Biology **1** 338-341

Carter N.J. & Cross R.A. (2005)
Mechanics of the kinesin step
Nature **435** 308-12

Cross R.A. (2005)
Intracellular transport *peer-reviewed review*
Encyclopaedia of the Life Sciences http://www.els.net Wiley

Carter N.J. & Cross R.A. (2005)
Microtubule Motility Assays
in Celis J (ed) Cell Biology a laboratory manual
Academic Press

2004

Cross R.A. (2004)
The kinetic mechanism of kinesin *peer-reviewed review*
Trends in Biochemical Sciences **89** 301-309

Crevel I. M-T. C. Alonso M. & Cross R.A. (2004)
Monastrol stabilizes an attached low-friction state of Eg5
Current Biology **14** R411-R412

Crevel, I, Nyitray M., Weiss, S., Geeves, MA, Cross, RA (2004)
What kinesin does at roadblocks: the coordination mechanism for molecular walking
EMBO J **23** 23-32

Eickel V. Drummond D. Kendrick-Jones J. & Cross R.A. (2004)
Kinesin heads fused to hinge-free myosin tails drive efficient motility
FEBS letters **569** 54-58

Cross R.A. (2004)
Dynein's gearbox (Dispatch)
Current Biology **14** R355-R356

Cross R.A. (2004)
Kinesin's interesting limp (Dispatch)
Current Biology **14** R158-R159

2003

DeBonis S, Simorre JP, Crevel I, Lebeau L, Skoufias DA, Blangy A, Ebel C, Gans P, Cross R, Hackney DD, Wade RH, Kozielski F. (2003)
Interaction of the mitotic inhibitor monastrol with human kinesin Eg5.
Biochemistry **42** 338-49

2002

Drummond D.R. & Cross R.A. (2002)
Multiphoton versus confocal high resolution z-sectioning of eGFP microtubules. Increased multiphoton photobleaching within the focal plane can be compensated using a Pockels cell and dual widefield detectors
J. Microscopy **206** 161-169

Olga Krylyshkina, Irina Kaverina, Wolfgang Kranewitter, Walter Steffen, Maria C. Alonso, Robert A. Cross and J. Victor Small (2002)
Modulation of substrate adhesion dynamics via microtubule targeting requires kinesin-1
J. Cell Biol **156** 349-60

Yajima J., Alonso M.C., Cross R.A. & Toyoshima Y.Y (2002)
Direct long-term observation of kinesin processivity at zero load
Current Biology **12** 301-6

2001

Kallipolitou A., Deluca D., Majdic,U., Laksemper S., Cross R.A., Meyhofer E, Moroder L., Schliwa,M., Woehlke G. (2001)
Unusual properties of the fungal conventional kinesin neck domain from Neurospora crassa
EMBO J. **20** 6226-6235

Rogers K.R., Weiss S., Crevel, I., Brophy, P.J., Geeves, M.A. & Cross, R.A. (2001)
Kif1d is a fast nonprocessive kinesin that demonstrates novel K-loop-dependent mechanochemistry
EMBO J. **20** 5101-5113
Cross R.A. (2001)
Kinesin's string variable (dispatch)
Current Biology **11** R147-R149

2000

Hirose K., Henningsen, U., Schliwa M., Toyoshima C., Shimizu T., Alonso M., Cross R.A. and Amos L.A. (2000)
Structural Comparison of Dimeric Eg5, Nkin and Ncd Head-Nkin Neck Chimaera with Conventional Kinesin
EMBO J. **19** 5308-5314

Cross R.A. (2000)
Directing Direction (*News & Views*)
Nature **406** 839-840

Drummond, D.R. & Cross R.A. (2000)
Dynamics of interphase microtubules in *Schizosacharomyces pombe*
Current Biology **10** 766-775

Cross, R.A. & Carter,N.J. (2000)
Molecular Motors: a primer
Current Biology **10** R177-179

Anderson K. & Cross R.A. (2000)
Contact dynamics in keratocyte motility
Current Biology **10** 253-260

Cross R.A. (2000)
Molecular Motors: Kinesin's dynamically dockable neck
Current Biology **10** R124-R126

Carter N. & Cross R.A. (2000)
An improved microscope for bead and surface based motility assays
Methods in Molecular Biology **164** 73-89

Cross R.A., Crevel I., Carter,N..J., Alonso, M.C., Hirose, K., and Amos, L.A. (2000)
The conformational cycle of kinesin
Proc. Roy. Soc. Ser. B **355** 459-464

Cross R.A. (2000)
The mechano-biochemistry of molecular motors
Introductory article to *Molecular Motors* Essays in Biochemistry **35**

1999

Cross, R.A. (1999)
Walking Talking heads (dispatch)
Current Biology **9** R854-R856

Crevel, I., Carter, N., Schliwa, M. and Cross, R.A. (1999)
Coupled chemical and mechanical steps in a processive *Neurospora* kinesin
EMBO J **18** 5863-5872

Cross R.A. and Scholey, J. (1999)
Kinesin: the tail unfolds (*minireview*)
Nature Cell Biology **1** E119-121

Hirose K., Lowe,J., Alonso,M., Cross, R.A. and Amos,L.A. (1999)
Conguent docking of dimeric kinesin and ncd into 3D Cryo-electron microscopy maps of microtubule.motor.ADP complexes
Mol Biol Cell **10** 2063-2074

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1998

Mazumdar M. and Cross, R.A. (1998)
Engineering a lever into the kinesin neck
J Biol. Chem. **273** 29352-29359
Hirose K., Cross R.A., and Amos L. A. (1998)
Nucleotide-dependent Structural Changes in Dimeric NCD Molecules complexed to microtubules
J.Mol.Biol. **278** 389-400

Alonso M.C., van Damme, J., Vandekerckhove,J. and Cross R.A. (1998)
Proteolytic mapping of kinesin/ncd- microtubule interface: Nucleotide-dependent conformational changes in the loops L8 and L12
EMBO J **17** 945-951

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Crevel I-M T C., Lockhart, A. Cross, R.A. (1997)
Kinetic evidence for low processivity in Ncd and Eg5
J Mol Biol **273** 160-170

Cross R.A. (1997)
The Natural Economy of Kinesin
Current Biology **7** R631-633

Cross, R.A.(1997)
Kinesin's ratchet reversed: a diverting tail (*News and Views*)
Nature **389** 15-16

Amos L.A. and Cross, R.A. (1997)
Structural dynamics of molecular motors
Current Opinion in Structural Biology **7** 239-246

Hirose, K., Amos, W.B., Lockhart, A. Cross, R.A. and Amos,L.A. (1997)
Three dimensional cryoelectron microscopy of 16-protofilament microtubules: structure, polarity and interaction with motor proteins
J. Struc. Biol. **118** 140-148

Cross, R.A. (1997)
A protein-making motor protein (News and Views)
Nature **385** 18-19

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Hirose, K., Lockhart, A. Cross, R.A. and Amos,L.A. (1996)
Three dimensional cryoelectron microscopy of dimeric kinesin and ncd motor domains on microtubules
PNAS **93** 9539-9544

Fan,J. Griffiths, A., Lockhart, A., Cross, R.A. and Amos, L.A. (1996)
Microtubule minus ends can be labelled with a phage display antibody specific to alpha tubulin
J.Mol.Biol. **259** 325-330

Crevel M-T. C., Lockhart,A. and Cross, R.A. (1996)
Weak and strong states of kinesin and ncd
J.Mol. Biol **257** 66-76

Lockhart,A. and Cross, R.A. (1996)
Kinetics and Motility of the Eg5 Microtubule Motor
Biochemistry **35** 2365-2373

1995

Hirose, K., Lockhart, A., Cross, R.A. & Amos, L.A. (1995)
Nucleotide-dependent angular change in kinesin motor domain bound to tubulin
Nature **376** 277-279

Cross R.A. (1995)
On the hand over hand footsteps of kinesin heads
J Mus Res Cell Mot **16** 91-94

Lockhart, A., Cross, R.A. McKillop,D.F.A. (1995)
ADP release is the rate limiting step of the MT activated ATPase of non-claret disjunctional and kinesin
FEBS Lett. **368** 531-535

Lockhart, A., Crevel, M-T. C. & Cross, R.A. (1995)
Kinesin and ncd bind through a single head to microtubules and compete for shared MT binding site
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1994

Lockhart,A. and Cross, R.A. (1994)
Origins of reversed directionality in the ncd molecular motor
EMBO J. **13** 751-757

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Hodge, T.P., Cross, R.A. and Kendrick-Jones, J. (1992)
Role of a COOH-terminal nonhelical domain in the self-assembly of a vertebrate myosin rod
J. Cell Biol. **118** 1085-1095

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MgATP binding changes neither the shape nor the flexibility of the heads of single myosin molecules
J Struct. Biol. **109** 208-213

Way, M., Pope, B., Cross, R.A., Kendrick-Jones, J. and Weeds, A.G. (1992)
Expression of the N-terminal domain of dystrophin in E. Coli and demonstration of binding to F-actin.
FEBS letters **301** 243-245

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Molecular Motors
J. Cell Sci supplement **14**, The Company of Biologists, Cambridge UK.

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STEM mass determination of in vitro self-assembled smooth muscle myosin filaments
J. Mol. Biol. **222** 455-458

Cross, R.A., Geeves, M.A. and Kendrick-Jones, J. (1991)
A nucleation-elongation mechanism for the self-assembly of side polar sheets of smooth muscle myosin
EMBO J. **10** 747-756

Faruqi, A.R., Cross, R.A. and Kendrick-Jones, J. (1991)
Solution small-angle X-ray scattering studies on myosin with a multiwire area detector
J Appl Cryst **24** 852-856

Ankrett, R.J., Rowe, A.J., Cross, R.A., Kendrick-Jones, J., and Bagshaw, C.R. (1991)
A folded 10S conformer of myosin from a striated muscle and its implications for regulation of ATPase activity
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Functional properties of a full length and a mutant chicken gizzard caldesmon expressed in E. Coli.
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J.Cell Biol. **109** 549-556

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Active site trapping of nucleotide by smooth and nonmuscle myosins
J.Mol. Biol. **203** 173-181

Bennett, J.P., Cross, R.A., Kendrick-Jones, J. and Weeds, A.G. (1988)
Spatial pattern of myosin phosphorylation in contracting smooth muscle cells: Evidence for contractile zones
J Cell Biol. **107** 2623-2629

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How phosphorylation controls the self-assembly of vertebrate smooth and non-muscle myosins
Biochem Soc Trans **16** 501-503

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Salt dependent dimerisation of caldesmon
FEBS Letters **219** 306-310

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Solubility-determining domain of smooth muscle myosin rod
FEBS Lett. **200** 355-360

Cross, R.A., Cross, K.E. and Sobieszek,A. (1986)
ATP-linked monomer-polymer equilibrium of smooth muscle myosin: the free folded monomer traps ADP.Pi
EMBO J **5** 2637-2641

Furst,D.O., Cross, R.A. DeMey,J. and Small, J.V. (1986)
Caldesmon is an elongated, flexible molecule localised in the actomyosin domains of smooth muscle
EMBO J **5** 251-257

1985

Cross,R.A. and Sobieszek, A. (1985)
Influence of smooth muscle myosin conformation on myosin light chain kinase binding and on phosphorylation
FEBS Lett. **188** 367-374

1984

Cross,R.A. (1984)
Bending of smooth muscle myosin rod
FEBS Lett. **176** 197-201

Cross,R.A., Bardsley,R.G, Ledward,D.A. Small, J.V. and Sobieszek,A. (1984)
Conformational stability of the myosin rod
Eur.J. Biochem. **145** 305-310

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Reversible helix-coil transition of pig stomach myosin rod
FEBS lett. **162** 189-192