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OBITUARY

Obituary: Professor John Michael Squire

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John Michael Squire passed away on 31st January 2021, a victim of the Covid-19 pandemic. He is survived by his wife, Melanie, their four daughters and ten grandchildren. John had a distinguished career investigating the structural basis of muscle contraction, largely at Imperial College London over the period from 1973 until his retirement in 2006.

John was born on 27th June 1945 in Grapenhall, Cheshire, UK. His father, Vincent, was a chemist at Proctor and Gamble. As his mother Mary suffered from severe asthma, John and his elder sister Margaret had to attend boarding schools. Consequently, from the age of 13, John attended the famous Fettes College in Edinburgh, which followed the English education system. In his spare time he was an avid Meccano fan making challenging models.

John's alma mater was King's College, University of London, where he read Physics (BSc, 1966), following in the footsteps of his father, who was also a graduate of King's. John went on to undertake his PhD at King's College under the supervision of Dr Arthur Elliott in the Biophysics Department in Drury Lane. His project on the structure of synthetic polymers using X-ray fibre diffraction formed the basis of much of his future work. Here he was surrounded by enthusiastic muscle researchers, including Gerald Elliott, Barry Millman and Jack Lowy as well as the charismatic Jean Hanson. On the completion of his PhD in 1969, Jean's influence in particular led him to become a dedicated and lifelong muscle researcher.

Denmark years, 1970–1971

John and Melanie married in 1969 having originally met in Barnet Hospital where he was briefly a patient and where Melanie was working as a nurse. Subsequently, Melanie had

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to cease her nursing career because an archaic law forbade married nurses from practising. Later that year they left for Denmark where John joined a vibrant young group that Jack Lowy had established at the newly formed Biophysics Institute at Aarhus University near Copenhagen to study the structure of smooth muscle. The group included Vic Small, John Haselgrove and Peter Vibert. Although John and his colleagues found working under Jack Lowy somewhat problematic in personal terms, John's stay in Denmark was highly productive scientifically and it was to play an important part in his career. He collaborated with Vic Small to study the structure of smooth muscle and together they were able to show that the myosin filaments had a side-polar structure that would facilitate the large contraction observed in this muscle. They proposed a detailed model of the structure of smooth muscle describing how the muscle might contract (Small and Squire 1972). Insight from this study caused John to think about the geometry with which myosin molecules pack together and which might give rise to the observed variation in size and shape that characterises myosin filaments in different organisms and different classes of muscle. This led him to propose, rather boldly, a general packing model for all myosin filaments as defined by the interactions between constituent myosin molecules (Squire 1971).

The general model demonstrated John's ability to find an underlying pattern within disparate facts. The origin and influence of the model is discussed in detail in the accompanying review by Ken Taylor (Taylor 2023). Using cryo-electron microscopy, Ken and his team were the first to determine the molecular structure of a myosin filament backbone in insect flight muscle. He had high praise for John in his 2016 paper: "We find it remarkable that a myosin-packing scheme proposed 43 years ago based on a myosin assembly found in vertebrate smooth muscle could so accurately predict the myosin rod arrangement in insect flight muscle, a muscle about as different functionally from vertebrate smooth muscle as evolution could have produced" (Hu et al. 2016).

Melanie recalls that their stay in Denmark was a happy period in their lives. However, there were problems with the management of the institute. As Gerald Elliott remarked in his obituary of Jack Lowy, Jack was "abrasive… but also highly intelligent" (Elliott 2000) and this fed through to an authoritarian management style. The situation deteriorated further when new laws introduced in Denmark allowed staff to elect their own head of department. Jack took badly to being deposed and there was widespread discontent in the institute. This prompted John to take the decisive action to resign and return to the UK after only two years, in the process selling the house that he and Melanie had only recently bought. Several other staff left around the same time. However, career-wise, the Denmark years can be considered his first lucky break with his collaboration with Vic Small leading to the development of the myosin general model.

Zoology Department, Oxford University, 1971 to 1973

John now needed to find a job at short notice and was immensely grateful to Professor John Pringle in the Zoology Department in Oxford, who offered him a Higher Scientific Officer position in late 1971. The position itself, though not a step forward in status, had the great benefit of essentially allowing him to be a free agent. John was introduced to asynchronous insect flight muscle on which Pringle had made the discovery of its unique stretch activation and which had also proved highly informative in structural analysis (Reedy et al. 1965). John's general packing model for thick filaments had explained the occurrence of different forms of the thick filament characterised by different numbers of myosin molecules within each of their crowns of crossbridges. Building on this insight John set about determining experimentally the number of molecules in a crown of crossbridges in four different muscles - rabbit psoas, guinea pig smooth muscle, Lethocerus (insect) flight and leg muscles. John collaborated with Richard Tregear for this study, and it was probably the only time he ran SDS gels. The results were compatible with the predictions of his model but were insufficiently precise to be conclusive (Tregear and Squire 1973).

The highlight of John's time in Oxford was his collaboration with David Parry, who was working at the same time in the lab of Andrew Miller, in which they discovered one of the fundamental mechanistic concepts of muscle function, the steric blocking model of thin filament regulation (Parry and Squire, 1973). The details of this collaboration are in the accompanying paper by David Parry, part of the collection celebrating John Squire's career (Parry 2022). Suffice to say here that the Oxford stint turned out to be the second lucky break for John. The paper resulting from John's collaboration with David put forward the steric blocking model of thin filament regulation which, to this day, remains central to our current understanding of muscle contraction and which was one of the most important scientific contributions of John's career.

Imperial College London, 1973–2006

In 1973 John joined Imperial College as lecturer in the Department of Metallurgy and Materials Science. This transition from biological sciences to a physical sciences environment, although on the face of it an unconventional move, proved again an important and beneficial development in John's career. John's own undergraduate training in physics and his PhD work on synthetic polymers formed the basis of his teaching. To support his research, he set up the Biopolymer Group and proceeded to recruit a series of excellent PhD students, many of whom were attracted from the ranks of Imperial College undergraduates by the quality of his lectures. For John, a major attraction of the department was its state-of-the-art electron microscopy centre including an impressive 1-million-volt electron microscope with its ability to view thick ~ 1 µm samples. He subsequently moved to the newly formed Biophysics Section in the Department of Physics in 1984 becoming a Reader and then Professor in 1995. In 1999 he moved to the newly established Division of Biomedical Sciences in the Faculty of Medicine and became head of the Biological Structure and Function Section (Fig. 1).

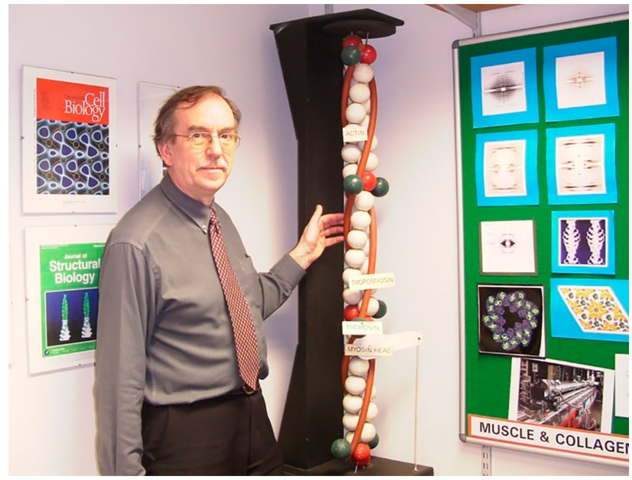

Fig. 1 John in his office at Imperial College showing the actual model that he built to illustrate thin filament regulation

After joining Imperial College John embarked on a new line of research directed towards understanding the structural basis of the contractile mechanism in muscle: this was to form the central theme of his subsequent research work. The starting point was a series of electron microscope studies of the arrangement of thick filaments in the A-band. Working with Pradeep Luther, John's first PhD student, John and Pradeep investigated the A-bands from frog skeletal muscle which was commonly used at the time in X-ray fibre diffraction and muscle mechanics studies. With meticulous sample preparation they were able to obtain almost precise transverse sections, which allowed them to identify a disordered superlattice of thick filaments characterised by 180° rotations about their long axes (Luther and Squire 1980); this is reviewed in the accompanying paper by Rick Millane and Pradeep Luther (Millane and Luther 2023). John and Pradeep went on to extend these studies to the A-bands from muscles in a wide range of other vertebrates, showing that in most cases they are also characterised by the disordered superlattice (Luther et al. 1996). Interestingly, bony fish muscle proved to be the exception, in which the thick filaments were found to be in the same rotational alignment, thereby giving rise to a simple lattice (Luther et al. 1995).

Taken together these electron microscope observations had important implications for the quality of the data that might be obtained in X-ray fibre diffraction experiments. While the disordered superlattice characteristic of most vertebrate muscles gives rise to complex sampling effects in diffraction patterns, the regular simple A-band lattice seen in bony fish, being essentially crystalline, was expected to lead to significantly more detailed diffraction patterns. Along with Jeff Harford, another of John's PhD students, John showed that this was indeed the case (Harford and Squire 1986). The diffraction patterns from plaice muscle (a bony fish), initially obtained using lab X-ray sources and subsequently the Daresbury Synchrotron Radiation Source, were characterised by a series of discrete reflections on the thick filament layer-lines consistent with a crystalline lattice (Harford and Squire 1986). In contrast, the corresponding layer-lines observed in X-ray diffraction patterns from other vertebrates had a complex sampling pattern, as expected from their intrinsic statistical disorder (Luther and Squire 2014). It was immediately apparent to John that bony fish muscle was a superior system for fibre diffraction analysis with its potential to reveal important details in the mechanism of muscle contraction, taking advantage of high intensity synchrotron radiation sources to provide time-resolved data.

At this stage John set out to use fibre diffraction to solve the structure of the thick filament within the fish muscle A-band, focusing on the myosin heads and their behaviour during contraction. For this the rich and detailed diffraction patterns he and Jeff were obtaining from fish muscle needed to be converted into a set of indexed diffraction peaks with measured intensities which would then be used to model the structure. It became clear, however, that the software available at the time to do this in a rigorous fashion was lacking. John set out to address this by setting up a new collaborative computing project, CCP13, for which he obtained research council funding. CCP13 came into being in 1992. It was modelled on CCP4, an existing related collaborative computing project which provided and supported software for macromolecular crystallography to the scientific community. John went on to chair CCP13 from its inception in 1992 until its research council funding ceased in 2005. A number of scientists, including Richard Denny, Ganeshalingam Rajkumar and Andrew He, were employed within the project and were responsible for developing the CCP13 suite of programs for processing fibre diffraction data (Rajkumar et al. 2007). Alongside software development, John organised a series of CCP13 meetings which brought together many of the UK-based and international research groups working on fibre diffraction. Communication within the field was also fostered by the CCP13 annual newsletter which, in later years, became the Fibre Diffraction Review. Both were edited by John.

Having established a solution for the software to process the diffraction data, the next step was to model the data. For this John recruited a new PhD student, Liam Hudson. Together they developed the software to systematically search for positions and orientations of myosin heads on the thick filaments within the A-band using the recently published crystal structure of the myosin head (Rayment et al. 1993). At this time, the resulting model for the resting state of fish muscle (Hudson et al. 1997) was probably the most detailed description of the myosin head arrangement in the vertebrate A-band then available. John envisioned this as the starting point for a programme of work which he named "Muscle the Movie" which would use time-resolved fibre diffraction to describe the structural changes of the myosin heads during the process of contraction. He went on to pursue this approach in subsequent years and, some 14 years after his retirement, this culminated in work published in 2019 with Felicity Eakins, a PhD student of his from the early 2000s (Eakins et al. 2019).

John's fibre diffraction-derived model of the vertebrate thick filament was not universally accepted. In particular, subsequent cryo-EM studies of relaxed tarantula thick filaments (Woodhead et al., 2005) revealed an interacting head structure which was significantly different from John's model. The interacting head conformation had been previously identified in cryo-EM studies of smooth muscle myosin (Wendt et al. 2001) and was also subsequently identified in negatively-stained EM studies of vertebrate cardiac muscle (Al-Khayat et al. 2013; Zoghbi et al. 2008). John fully accepted the validity of the EM-derived interacting head arrangement but considered that this might represent an additional ordered state of resting muscle co-existing with the arrangement identified in his original model (Knupp et al. 2019). Furthermore, calculations by Carlo Knupp and John (Knupp et al. 2019) showed that the interacting myosin head models as described in (Zoghbi et al. 2008) and (Al-Khayat et al. 2013) gave a significantly less good fit to fibre diffraction data from plaice muscle than John's original model. On the other hand, a recent investigation from Roger Craig's lab into the interpretation of fibre diffraction patterns from plaice muscle indicated that if the radius of interacting head motif was increased to compensate for shrinkage in the negatively-stained images good agreement with the fibre diffraction data was obtained (Koubassova et al. 2022). Most recently, the interacting head arrangement has been clearly demonstrated in both cryo-electron tomography studies of native cardiac sarcomeres from Stefan Raunser's lab (Tamborrini et al. 2023) and cryo-EM studies of isolated cardiac thick filaments in Roger Craig's lab (Dutta et al. 2023). Thus, there is a discrepancy between John's fibre diffraction-derived model and the recently established interacting head motif in human cardiac muscle as well as, most likely, in other vertebrate skeletal and cardiac muscle. A possible explanation for this was provided by (Koubassova

Fig. 2 John with Mike Reedy (left), Tom Irving (facing away from camera) and Carlo Knupp (right) at Advanced Photon Source, Argonne National Laboratory, USA, in 2008, during a session on the synchrotron looking at insect flight muscle

et al. 2022), who pointed out that the relatively low resolution of the useable diffraction data obtained with current technology made it rather insensitive to the conformation of the myosin heads. So, it may be that John's vision of providing a detailed kinetic description of myosin head conformation during muscle contraction directly from fibre diffraction from fish muscle was hampered by instrumental limitations in the quality of the diffraction data. If this is the case, it is to be hoped that future improvements in synchrotron beamline and detector technology may result in sufficient enhancements in the resolution to realise his vision (Fig. 2).

In parallel with his fibre diffraction work John pursued structural biology of striated muscle by electron microscopy. In the late 70s, he teamed up with Michael Sjostrom who had just produced spectacular negatively stained electron micrographs of cryosections of striated muscle. This led to a detailed description of the fine structure in skeletal muscle A-band (Sjostrom and Squire 1977). The use of cryosections was continued by the authors culminating in the cryo-EM study of cardiac muscle (Huang et al. 2023), part of the collection celebrating John's life and career. Together with Ed Morris, he developed the technique of structure determination by single particle analysis of electron micrographs of isolated actin and myosin filaments. This led to insightful papers on thick and thin filament structure(Al-Khayat et al. 2006; Paul et al. 2009; Paul et al. 2010). The highlight was the paper on the determination of human cardiac muscle thick filament structure (Al-Khayat et al. 2013). John is a co-author in the accompanying paper on the novel use of zebrafish to study cardiac diseases resulting from mutations in thin filaments proteins (Bradshaw et al. 2023).

By the end of his first decade at Imperial John had embarked on and completed his 700-page monograph, "The Structural Basis of Muscular Contraction" (Squire 1981). This was a great success and even now well-thumbed copies can be seen in laboratories all over the world. He also wrote or edited several books on muscle and fibrous proteins. Furthermore, he contributed numerous reviews in both books and journals, notably his 1997 review with Ed Morris on thin filament regulation (Squire and Morris, 1998). John's memoir of his scientific career would have been interesting reading but, unfortunately, he was taken away too quickly. Maybe that is a reminder to senior researchers to pen their memoirs for the sake of the community and future generations. Fortunately, we have one historical memoir from John with a personal commentary: "Muscle contraction: Sliding filament history, sarcomere dynamics and the two Huxleys" (Squire 2016).

Since his PhD days, he retained a passion for coiled-coil proteins. Together with David Parry he organised four-yearly workshops in the scenic village of Alpbach located in the Austrian Alps region starting from 1993 up to 2009. The workshops were on "Coiled-coils, Collagen and Co-proteins". David Parry discusses these conferences in his accompanying paper (Parry 2022).

John's research group at Imperial College was consistently drawn from a diverse range of nationalities and cultures. The supportive environment he inspired frequently led to long-standing friendships. The group, family members and occasional academic visitors were typically invited round to an annual summer party at John and Melanie's house in Egham (Fig. 3). These took place in their beautiful garden, where despite the vicissitudes of the London weather, somehow the sun always seemed to shine. John was an excellent mentor assisting former group members in their further careers: many continued to interact and work with him on collaborative projects.

Fig. 3 One of the regular garden parties that we enjoyed at John's house in Egham (2003). Seated/kneeling, from left: Raghu Govada, Amy Nneji, John Squire, Melanie Squire, Lata Govada, Pradeep Luther. Standing, from left: Paula da Fonseca, Ed Morris, Hind AL-Khayat, Samia Nneji, Gwen Nneji, Cathy Timson, Adetoun Baruwa, Andrew He, Sahir Khurshid, Carsten Peters, Florian Schoiber, Ganeshaligam Rajkumar, Neerja Luther, Ashwini Oswal, Pretty Sagoo, Vishal Luther, Carlo Knupp

Post-retirement years, 2006 on

John retired from Imperial in 2006. This was an opportunity to spend more time with his family and grandchildren, but the decision may have been influenced by complex upheavals in organisation imposed by Imperial's hierarchy, a phenomenon not uncommon in other academic institutions. John and Melanie moved to Salisbury to be closer to some of their grown-up children and families. One of the upsides of his retirement that he cherished was that, freed from university admin, he had more time to do research. As well as continuing his affiliation with Imperial college as a Visiting Professor, he accepted a place as an Honorary Research Fellow at the University of Bristol, joining the Muscle Contraction Group in the School of Physiology. Here he worked with Gerald Offer and K.W. Ranatunga on modelling and understanding the cross-bridge cycle (Knupp et al. 2009). Carlo Knupp based at nearby Cardiff University established a strong and productive collaboration with John. John also worked with Charles Michel and Kenton Arkill on defining the molecular mechanisms underlying endothelial glycocalyx filtration (Squire et al, 2001; Arkill et al. 2011) and with Danielle Paul on high-resolution 3D cryo-electron microscopy of thin filaments (Paul et al. 2020) (see accompanying papers, (Arkill et al. 2022; Bradshaw et al. 2023)). He also found the time to share his vast knowledge of the muscle field to write some excellent reviews on muscle structure and function (Squire 2010, 2011, 2016, 2019; Squire et al. 2017) and on fibrous proteins (Parry et al. 2008).

Summary

Over his career of more than 50 years, John touched the lives of all those he associated with, be they colleagues, collaborators, students, and friends. He maintained a substantial network of collaborations with scientists all over the world. That so many were happy to continue to do science with John in this way serves as a testament both to the esteem which he was held scientifically and to the fact that he was a pleasure to work with. He was a loyal friend and a mentor always willing to give wise advice and insight. He had boundless energy organising conferences at home and abroad, writing and editing books. He will be much remembered for all his contributions to science and society.

Some memories from Melanie Squire

John had so many interests and hobbies throughout his life although science was a constant and shaped family life from the beginning. When our four daughters were growing up, they learned to expect their father to be working in his study either writing research papers or working on his books. However, somehow, he found the time to use his woodworking skills to convert our attic and made them all magical bedrooms to enjoy.

Fig. 4 John and Melanie on holiday in Wellington, New Zealand in 2007. John also spent part of the time with Rick Millane and attended a conference organised by David Parry

He also loved music, especially classical and church music and belonged to numerous Church choirs throughout his life. As children they were able to share this passion and have many memories of playing duets and singing along with him.

As they grew and left home, I was able to join him on some of his travels. In later life we discovered the joys of cruising (Fig. 4). I remember John finding it almost impossible to fit in all the interests he had on these holidays and each day was filled with lectures, crosswords, classical concerts, fine dining and spectacular shows.

The arrival of our ten grandchildren brought him immense joy and he was often moved to tears by the love they shared with him. He was fortunate to be able to pursue his interests to the very end and his last few days were peaceful and many of his family and close friends were able to share precious moments with him.

An anecdote from Danielle Paul, PhD student and collaborator

At the European Muscle conference in Kent, UK in 2019 I was excited to show John some new data. It was tomographic data that I had been working on with a collaborator from

Bristol (Mark Dodding). The tomograms were of cellular protrusions that contained a large number of microtubules and, more surprisingly, it seemed that the microtubules were filled with actin filaments. We wanted to show definitively that the helical filaments were actin and to do that I had started to examine the layer line (LL) patterns. As the LL patterns didn't exactly agree with canonical actin's helical parameters, I was eager to discuss this with John. After taking one look at it he quickly said, "if that isn't actin Danielle you are measuring it wrong". With that I calibrated it and remeasured everything, and John took these measurements and modelled two novel conformers of actin. John's contribution to that analysis was huge and timely, and he brought his wealth of experience of actin structure that really aided the interpretation of the data. This work revealed the existence of microtubule luminal actin for the first time, and this has and is continuing to make a big impact in the cytoskeletal field (Paul et al. 2020).

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Declarations

Competing interests The authors declare no competing interests.

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