ESSAY

Beyond a pedagogical tool: 30 years of *Molecular Biology of the Cell*

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Abstract | In 1983, a bulky and profusely illustrated textbook on molecular and cell biology began to inhabit the shelves of university libraries worldwide. The effect of capturing the eyes and souls of biologists was immediate as the book provided them with a new and invigorating outlook on what cells are and what they do.

The aim of *Molecular Biology of the Cell* (MBoC)[1], first published in 1983, was to rewrite cell biology and to create a new visual interpretation of the subject (FIG. 1). Looking for previous textbooks that might have had an equally important role in transforming the knowledge of cells, MBoC only compares to Wilson's classic *The Cell in Development and Inheritance*, which was first published in 1896 (REF. 2). *The Cell in Development and Inheritance* has been essential for cytology to become a self-contained discipline[3]. This year is the thirtieth anniversary of the publication of the first edition of MBoC, and to mark the occasion I invite readers to reflect on some of the features that made it, as one commentator once put it, "the most influential cell biology textbook of its time"[4]. I argue that the influence and success of MBoC relied on some key aspects of its production. The making of MBoC essentially defied the ongoing practices of textbook production at the time.

Two main reasons come to mind when thinking of why the first edition of MBoC, and the following editions in 1989, 1994, 2002 and 2007, have been so influential for the field of cell biology. The first one is related to textbooks being showcases for the state of knowledge in a particular subject. MBoC was one of the first books to capture the 'new' molecular knowledge of higher organisms that began to emerge in the early 1980s. By experimenting with prokaryotes between the 1940s and 1960s, molecular biology had developed several 'conceptual tools' that were transferred to eukaryotic cells from the mid 1970s onwards with the advent of genetic engineering[5]. Several experimental approaches to study specific aspects of eukaryotic cells, such as the mechanisms underlying genetic regulation and intracellular signalling, were relentlessly being undertaken in cell biology laboratories worldwide. No textbook, however, fully encapsulated such developments. The second reason for the influence of MBoC stems from its pedagogical qualities. Reaching such quality was a high priority for the authors and this was recognized by reviewers immediately after its first publication. The book was highly recommended for the classroom[6,7], and reviewers predicted it would be a great success as it simplified the teaching of a subject that, because of its rapid expansion, was becoming harder to teach[8]. In addition, some reviewers predicted that MBoC could be used as a pedagogical tool for more specialized audiences such as scientists[9,10].

> "The making of MBoC essentially defied the ongoing practices of textbook production at the time."

The pedagogical value of MBoC, as most reviewers agreed, was to be found in the design and quality of the illustrations, which condensed complex ideas into simple schematics, and in the clarity, consistency and emphasis on explanation achieved in its writing[8,11–14]. As later editions of MBoC were published, these values increased and remained unique despite mounting competition from other textbooks, such as *Molecular Cell Biology* by Lodish *et al.*[15], first published in 1986.

Although true, these reasons conceal other key aspects that have made MBoC so influential and successful. Beyond being a pedagogical tool and a showcase of existing knowledge, MBoC actually added new knowledge. The book embodied and heralded the epistemic and visual ethos of the so-called 'molecular revolution' of the early to mid 1970s; the revolution that gave rise to our current view of the nature and the functioning of cells as diverse collections of timely and specifically expressed interacting 'protein machines'[16]. MBoC offered an image of cells beyond that seen through the microscope and set the tone on how to study cells for many years to come.

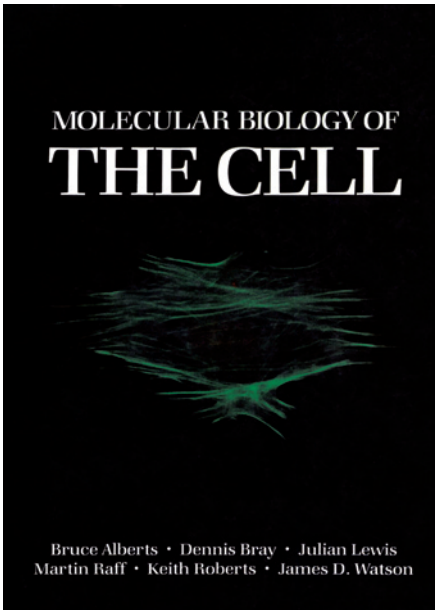

Figure 1 | **The front cover of *Molecular Biology of the Cell* first edition (1983).** "In a time when our biological landscape is dominated by immunofluorescence images and more recently by GFP labelled proteins it is hard to remember what a wow factor such images had early on. No other books at that time had a coloured image on the front, let alone an actual cell! This image used fluorescent phalloidin, rather than an antibody, for staining F-actin and T antigen for staining the nucleus, rather than DAPI, and was taken by Bob Pollack, one of the authors originally fingered by Jim for MBoC. The image also represented the then very active research area of the cytoskeleton. I also wanted to use the black background of the image to go all over, i.e. a black book, which was a controversial subject at the time, but turned out to be a good marketing tool to 'differen Science tiate' us from any other books." (Keith Roberts, personal communication). Image is reproduced, with permission, from REF. 1 © (1983) Garland Science.

The origins

The original idea of a book such as MBoC belonged exclusively to James Watson. In the early 1970s, he wisely spotted a latent hurdle for his long-time vision of transforming the whole biology field into a molecular science[17]. He recognized that the knowledge of cell biology at the time was almost entirely based on light and electron microscopy investigations, and for students this hardly integrated any new molecular biology. Therefore, Watson believed in the need for a new textbook that would combine these two fields. As Martin Raff recalls, for

Watson producing MBoC would be a "very important way of modernising the way cell biology was taught and perhaps even how cell biology was done"[18].

With that idea in mind, in July 1974, Watson wrote a letter to Keith Roberts, a plant cell biologist who worked at the John Innes Institute in Norwich and a long-term collaborator. Watson invited Roberts, who was also the illustrator of *Molecular Biology of the Gene* (MBoG)[19], to become an author of a new textbook that could 'sweep the field'[18]. In the beginning of 1976, as part of the process of gathering authors for the book, Watson asked a publisher (not the final publisher) to contact Raff from University College London and to invite him to become involved in the book project. The importance of incorporating Raff as an author did not escape Watson's attention. Raff was seen as a prominent immunologist after he published an important paper in *Nature* on a specific lymphocyte marker[20], and he was also known as an effective communicator via television programmes and an author of published scientific reviews. After some insistence from the publisher, Raff finally agreed to meet the incipient group.

The first formal meeting took place in London in 1977. Among the attendees were Watson, Roberts, Raff, Gavin Borden (the new publisher) and Joe Sambrook. After being briefed by Watson on the scientific importance of publishing such a textbook and after Borden presented preliminary reports that demonstrated the existence of a selling niche, Roberts confirmed his participation, and Raff decided to fully embark on the initiative. For over a year following that meeting, other scientists, including Sambrook, Bob Goldman and Bob Pollack, all cell biologists from the Cold Spring Harbor laboratory, and Keith Porter, a distinguished cell biologist from the University of Colorado, participated in the initiative, although they were not authors of the textbook. In early 1978, following Raff's suggestion, Bruce Alberts, a professor at the Department of Biophysics and Biochemistry at the University of California, San Francisco (UCSF), joined the team of authors. Originally, he joined for a short summer session, but then stayed because of his good working relationship with Raff. In late 1979, two more authors joined the team: Julian Lewis, a lecturer at the anatomy department at Kings College London; and Dennis Bray, a cell biologist from the Medical Research Council (MRC) Cell Biophysics Unit at Kings College London, who replaced Keith Porter[21].

When Lewis joined, having already spent two years on the project, the team morale was at its lowest. As Raff recalls, most of the first drafts of the chapters were not usable, especially the chapters written by external authors as they did not fit the writing style of those written by Roberts, Alberts and himself[18]. At that point, Lewis, who had been invited by Alberts to write one chapter on the basis of his work in developmental biology, was at a meeting in the United States and dropped by at Fort Hill on Long Island to deliver his work[18]. The chapter Lewis presented (which he co-wrote with his colleague Cheryl Tickle) impressed Alberts, Raff, Roberts and Watson. In Raff's view, it became their best written chapter and gave them the boost they really needed[18]. From that moment on, a definitive and solid authorial alliance was formed (FIG. 2).

The role of Watson in cementing the unity of that authorial alliance was essential. Early in 1978, when trying to persuade Alberts to become an author, he told him:

> *Bruce the point is that no matter what you or Martin or Keith or me or anybody else does in science somebody else is going to do it in weeks, in months at worse in a couple of years, but this book, if you don't do this book, no one is going to do the book this way and a whole generation of cell biologists will be deprived, so this will be, if you take it on and do it well, the most important thing you probably do in your career.*[18]

The team spirit and its dynamics

More important than the continuous encouragement from Watson was the way the authors built a unity. The role of MBoC in marking a new era of cell biology would not have been possible without the strong connections at the personal and professional level that the final authorial line-up achieved. The production of the book, despite being well-planned, took many unexpected turns. In addition to authorial reshuffling, the subject content also changed. The second half of the book was originally planned to contain a molecular description of different kinds of organisms (such as *Escherichia coli* and ciliates). However, as Roberts explained, after the first draft of the commissioned chapters began to arrive in the summer of 1979, it was soon realized by the authors that what was envisioned for the first half of the book would be enough to fill its full capacity. Thus MBoC resulted in a book giving a molecular explanation to classical cellular themes such as cell movement, secretion, or cytoskeleton structure[18].

Moreover, the publication of the book took almost 8 years rather than the 2 years that were originally planned. As observed by Alberts:

> *What was advertised as an effort requiring only two summers turned out to involve an exhausting series of meetings that required more than 365 12-hour days from each author.*[22]

Figure 2 | **The authorial team and the editor of *Molecular Biology of the Cell* first edition (1983).** The picture was taken soon after the book was published. From left to right: Bruce Alberts, Keith Roberts, Martin Raff, Gavin Borden, James Watson, Dennis Bray and Julian Lewis. Image courtesy of Keith Roberts.

Raff, Roberts and Lewis all remember the strain that this situation put on their relationships with their partners, families, close friends and laboratory members. Building trustworthy relationships among the authors was essential not only for easing those strains but also for the short-, mid- and long-term objectives that such an immense task required. The special bond among the team members, which grew stronger as they worked together, included trust in each other's moral values and professional capacities and an understanding of each other's strengths and weaknesses. Essential for that bond was a deep sense of belonging to a new scientific culture that valued openness, innovation, risk taking and individual entrepreneurship[23].

Another key factor for achieving this unity was the early layout of the working conditions. First, it was decided that they should all work together in the same location for long periods of time (for 6 weeks during the summer). The first meeting took place in 1978 in a property that Watson owned in Martha's Vineyard. The next meeting was held in 1979 in Fort Hill, an estate on the headland of Cold Spring Harbor. Second, a simple division of labour was decided with each author writing a chapter or two on their respective areas of expertise: Raff was going to write a chapter on immunology and another one on cell membranes; Alberts was writing one chapter on cell chemistry and thermodynamics and another chapter on molecular genetics; Lewis was writing one chapter on development; Bray was writing one chapter on the cytoskeleton; and Roberts was writing one chapter on plants. The agreement was that everything else that the authors did not dare or did not want to write about would be written by other experts[18]. However, in the summer of 1979, as the pieces from outside experts were not written in the style they hoped to achieve, they decided to write most of the chapters themselves with the outside experts only providing advice and feedback[18,21].

Once sketches of figures or pieces of text were finished by one of the authors or by an invited expert, they circulated this material to the rest of the team members for suggestions and corrections for as many rounds as necessary until everyone was pleased with the result. These work dynamics, which were quite novel at the time, improved the quality of the writing and was enormously educational for the authors. Raff recalls that Alberts, who knew little about immunology, would ask fundamental questions that changed the way he would write and think about the subject. He acknowledged that reading Alberts' chapter on thermodynamics, and the chapters that were written by the other authors, was equally educational for him[18].

MBoC and novelty

The team's work relied on trustworthy relationships, with its members learning from and posing fundamental questions to each other. Moreover, the authors' entrepreneurial and non-hierarchical culture was a crucial and an unprecedented approach to writing a biosciences textbook. More importantly, this novel work culture resulted in a multi-authored textbook with a single voice, a key achievement that was immediately noticed by many reviewers and later recognized by scientists worldwide as a key hallmark of its success.

MBoC was not only easy to read, it was in fact transforming the writing of biosciences. Importantly, it prioritized the telling of a well-nuanced story over one based on a mere description of facts. 'Concept headings' were extensively used to this aim. Such type of headings, which use boldface sentences that summarize the main ideas covered in following paragraphs, had previously been used by Watson in MBoG and became more refined and further exploited in MBoC[24]. They were designed to help the reader to retain complex ideas on cell functioning by organizing the text into 'bite-sized' and 'digestible' sections[25].

Striking a balance between describing facts and writing a well-nuanced story was not always easy. Watson and Raff, for example, sometimes disagreed over that balance. Watson, despite insisting on concept headings, thought that "the more facts the better" because they provided students with a better sense of how much they knew[18]. Overall, however, the telling of a straightforward story about a molecular mechanism prevailed even if it risked excessive speculations. The following comment by Raff succinctly encapsulates how the team members saw themselves working:

> *Everything we would write should have a story, it should be interesting, it should have a reason, don't learn a fact unless there is something about the fact that helps advance the story.*[18]

Raff's comment unveils yet another key aspect that set MBoC apart from previously published cell biology textbooks. Although they were extremely cautious about making claims on cell functioning that had not been fully confirmed experimentally, MBoC contained more speculation than any other textbook at the time. As acknowledged by Roberts, some of the data the authors came across while discussing experimental findings with other scientists became "as gospel in the book" before these data were published[18]. This was noticed by a reviewer who wrote:

> *[MBoC] is more adventurous than many previous textbooks in cell biology, in that it does not hesitate to make generalizations and to suggest possible mechanisms (where neither may be totally documented).*[13]

Nevertheless, because speculating never meant jumping to conclusions, there is no apology from the authors for that[18]. The early 1980s were times when, as Raff put it, "for many things there was no story and hence the most sensible thing to do was to tell one, one that of course made biological sense"[18].

Another way in which MBoC was novel was that it catalysed research in its making. Because of the decisive role of Alberts and Raff in the making of MBoC, the book promoted new experimental research avenues and thus proved fundamental to the establishment of new networks among laboratories. Alberts and Raff had good connections with scientists working in related fields and spent a considerable amount of time reviewing their work, and they consequently suggested key experiments to do. As Raff vividly expressed:

> *We were shocked at how little was known. I mean fundamental things that would be easy to find out have never been asked, never been done, so we would call up the experts and say, do you know what is the half-life of this protein (I don't know), you don't know, why is it that you don't know, could you do it, could you find out. It would be very useful to know when we are telling the story.*[18]

The creation of a solid imagery was as important as writing sound stories about molecular mechanisms underlying cell functioning. It was immediately noticeable that MBoC contained more images than any other existing cell biology textbook. It has an average of 68 images per chapter, whereas a chapter from a book such as *Cell and Molecular Biology* by De Robertis and De Robertis (1980)[26] would contain

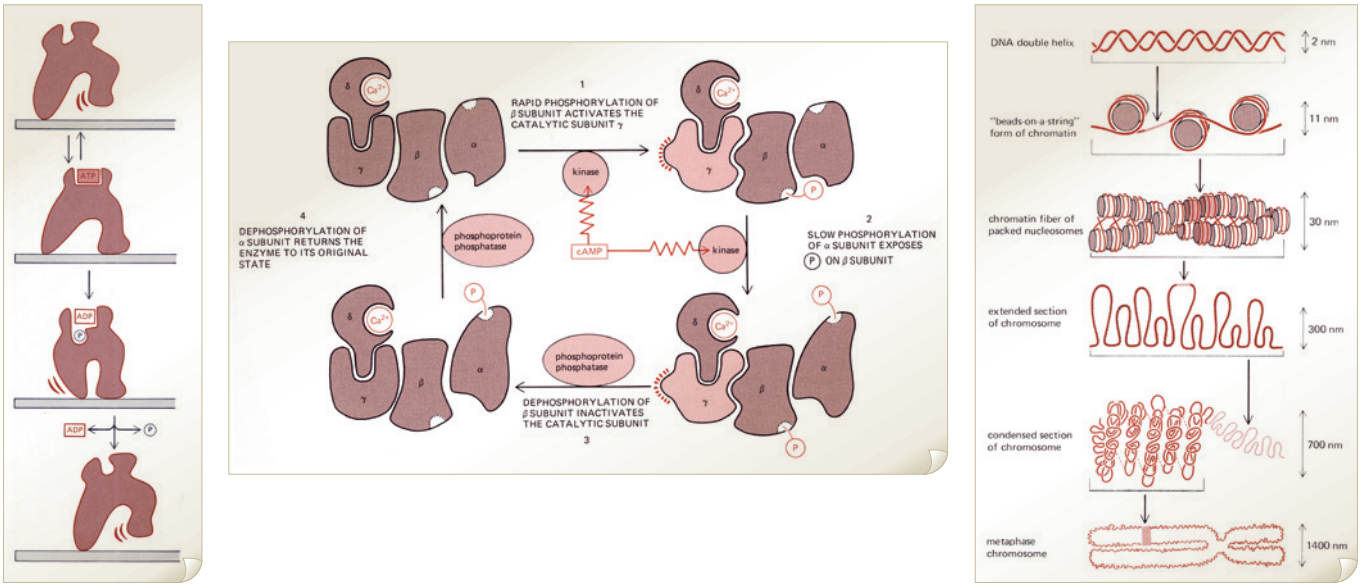

Figure 3 | **Examples of figures from the first edition of *Molecular Biology of the Cell* (MBoC).** The images shown in MBoC were key for transforming the complex picture of cellular mechanisms that was emerging from experimental data into simple 'visual concepts' to explain the functioning of cells by showing, for example, molecular movement (left) and molecular interactions (middle). Many of the images enabled readers to integrate one single molecular event into different levels of cellular organization (right). Three conformations of a so called walking protein (left). The transition between these conformations is dependent on the hydrolysis of a bound ATP. The activation and inactivation of phosphorylase kinase in response to cyclic AMP (middle). Different stages of chromatin compaction (right). Images are reproduced, with permission, from REF. 1 © (1983) Garland Science.

only 15 (REF. 18). Almost every page in the main body of MBoC contains an image. Of even more relevance is the fact that all the images were not only expanding how molecular biology was displayed visually, but they were also able to tell a complementary story to that in the related text and could even be read almost independently. The images in MBoC were so to the point that, as Lewis recalls, he came across people who had read the book by solely looking at the pictures[18]. Most of the images were, as concept headings in writing, very helpful tools to understand the complex picture of the molecular biology of a cell that was unravelled by experiments (FIG. 3).

The images shown in MBoC were pivotal for the pedagogical relevance of the book. More crucially, they helped to promote the modelling of molecular processes, which is an essential tool in the present work of cell biologists, developmental biologists and other specialists. For those who saw the book for the first time back in 1983, the images would have been simply unforgettable, and they would have immediately realised that a textbook with such visual quality would never languish in obscurity. Although all authors contributed in one way or another to the production of the images, Roberts took on the main responsibility of producing and organizing them. Having an 'artist' in the team who was, in Raff's opinion, "a genius at taking complex concepts and putting them into an aesthetic and simple diagrammatic form" was essential for the success of MBoC[18].

Roberts was already a very experienced illustrator when he embarked on the MBoC project. Among the books he had illustrated, apart from Watson's MBoG, were John Kendrew's *The Thread of Life* (1968)[27] and Albert L. Lehninger's *Short Course in Biochemistry* (1973)[28]. He was influenced by the imagery of the classic biochemistry textbooks by Lehninger and Lubert Stryer[29]. According to Roberts', Stryer's *Biochemistry* (published in 1981) set the standards for molecular design by possessing a crystal clear illustration programme[18]. Moreover, in his opinion, having such a type of illustrations is what separates a properly authored textbook from one that just uses images from other people. Roberts created an illustration programme for MBoC on the basis of five 'pragmatic' rules of depiction[18,25]. Because of their quality, these rules, although originally developed for Roberts' personal guidance, were later incorporated in the Garland Publishing editorial depiction rules acting as a guide for the production of images in other biology textbooks.

Like for many creators, Roberts' pictorial style has been influenced by the work of others. A primary inspiration for him was the two ribbons depiction of DNA, created by Odile Crick (the wife of Francis Crick) for the original article on the DNA structure in 1953. Roberts was amazed by the capacity of that tiny line drawing to capture all the conceptual points of the proposed structure in its simplicity[25]. More importantly, however, was the influence of the multi-authored book *The New Landscape in Art and Science* (published in 1956), which was edited by Gyorgy Kepes[30], a hungarian-born painter, art theorist and professor at the college of visual arts at Harvard University. *The New Landscape in Art and Science* was a multifaceted book aimed at exploring the commonalities and the productive crosstalk between art and science. The essays it contained reflected on a time (between the 1940s and 1960s) when previously unseen phenomena such as a milk drop or a bullet hitting an apple became visible owing to the emergence of a panoply of new scientific and photographic techniques. Although they did not represent molecular processes, the importance of such images for the creation of a conceptual and highly pedagogical imagery of the invisible that MBoC attempted to portray was undeniable. This was very relevant for Roberts. It helped him to fully exploit the emergent imagery of molecular biology and its power to infer models for cell biological processes. As Roberts succinctly put it:

> *I think that the whole idea of being able to see the unseeable is certainly what made me and my science.*[18]

The backstage protagonists

The input from the publisher Borden on the production of MBoC proved essential. Borden was a former linguist and classicist from Harvard who ran, together with his wife Libby, a small publishing company called Garland Publishing. Producing MBoC was a big risk for them, as they had no experience in the field of scientific publishing. Until then, they had only been involved in 'small jobs', such as reprinting theses for universities. Their most important productions before MBoC were a small art book and a facsimile of the holograph manuscripts for Ulysses by James Joyce. Furthermore, their company was on the verge of bankruptcy when they embarked on the production of MBoC. Roberts recalls, that although the MBoC venture was risky, Borden had been persuaded by Watson as he thought that Borden was perfectly suited to embark in such a "manic thing"[18].

Encouraged by Watson, Borden managed to borrow 1 million US dollars to pay for the initiative to materialize. The money was sensibly administered as it was used to pay for skilful market research, which was performed to warrant reasonable sales for the book, but also to cover personal expenses. This included paying for the accommodation of the authors when they gathered together to write and for their travel expenses to reach the different venues where those gatherings took place (London, New York, San Francisco and Norwich)[18,21]. Of special note was the investment in a small house in St John's Wood near the Abbey Road studios in London, which was originally rented and later purchased by Borden. This location provided inspiration for the back cover of the 1994 and 2002 editions, which were similar to album covers from The Beatles[21].

The contribution of Borden, however, went far beyond the money he invested and the market research he designed and supervised. Borden had an essential role in creating the team spirit he believed the authors needed to write as freely and as creatively as possible. During the long writing sessions, Borden never put pressure on the authors to speed up the publication of the book, rather the opposite, despite the many delays. As Raff recalls:

> *When we were in these group meetings he would drag us away to play tennis, he would drag us away to go swimming or boating, or something … he made it like a summer camp to make it fun.*[18]

Moreover, Raff remembers working with Borden:

> *You always had the feeling that whatever you needed you could have … if we needed another expert to write something he would never say no, it would be too costly.*[18]

The work atmosphere created by Borden is remembered with special fondness by Roberts who recognizes that his approach was crucial for turning a diverse mixture of inexperienced authors, none of whom was a proper cell biologist, into a solid team, in which everyone was friendly but at the same time also critical of each other's work[18].

The work of Miranda Robertson was also important for the production of MBoC. Before working as the developmental editor of MBoC she worked for *Nature*. Joining the project in 1976, her role as a text editor was crucial, and her work was key for the organization of the day-to-day agenda of 'have to do' activities. Moreover, she knew better than the authors how to write for a broad audience. Robertson made sure that the writing was, as the authors recognized in the preface of the first edition, lucid and coherent[1].

More importantly, Robertson, together with Borden, organized a massive network composed of university undergraduate students and university teachers to provide feedback, opinions and suggestions on the drafted chapters. Because of its consistency and extent, the market research and feedback that Borden and Robertson provided, although being common practice among textbook publishers owing to an increasingly competitive market[31,32], took an unprecedented dimension. The reports gathered by Robertson helped the authors enormously to improve the quality of the content of each chapter. Such comments were particularly important as they reflected the academic interests of the potential readership of the book. In other words, the work of Borden and Robertson was essential for making MBoC a consumer-tailored product, a key attribute for increasing the sales of the book and to warrant its success.

The other group of backstage protagonists that proved essential for the production of MBoC was the huge number of hidden, although acknowledged, collaborators. Estimated by a reviewer to be 75 well-known cell biologists[33] and dubbed by another as "an army of international helpers"[14], the collaborators had a central role not only in generating pictures and pieces of writing and in editing and reviewing chapters, but also in informing the authors of the latest experimental outputs from their laboratories. The end result was a framework of consent for the different proposals for cell functioning that the authors of MBoC put forward. Such consent proved crucial for the broad acceptance of the explanations of molecular mechanisms that the book proposed.

Conclusion

The success of MBoC at rewriting the subject of cell biology cannot be separated from the way it was produced. MBoC was far more than a showcase of knowledge and a pedagogical tool. It helped to put in place the first pieces of the highly intricate 'jigsaw' of molecular knowledge on eukaryotes that is the basis for current research in the biosciences.

Thirty years on from its first edition, it is clear that MBoC has indeed swept the field, as Watson had anticipated in a letter to Roberts in 1974 (REF. 18). The quality of the book has remained intact despite the core team of authors changing in later editions. Key authors embracing the working paradigm set by the original authors were Alexander Johnson and Peter Walter who both worked on the third edition of the book (1994) and became full authors of the fourth edition (2002).

> *Their contribution was vital for the updating of the book. Also important for the success of MBoC was the first and subsequent editions of* Molecular Biology of the Cell: The problems book, *co-authored by Tim Hunt and John Wilson. Another important contributor was Nigel Orme who converted all of Roberts' hand drawn images into computer images when the book ventured into full colour in 1984. Many other people contributed to the production of MBoC over the years, all of whom were acknowledged by the authors in the prefaces of the first and subsequent editions. (K. Roberts, personal communication)*

More importantly, MBoC has been translated into ten languages and is read by millions worldwide. The several editions passed the million mark in sales in 2002 (REF. 34). The clarity of its text and visuals and the originality of its production made it, as one reviewer states, "an inspiring, almost awe-inspiring" textbook[14], one that perhaps, as the back covers of the fourth edition and the fifth edition of MBoC suggest, changed the landscape of cell biology in the same way that The Beatles changed music.

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Competing interests statement
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