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OBITUARY

(Madeline) Ruth Bellairs (1926-2021)

Chris Wylie[1] and Claudio D. Stern[2,*]

Ruth Bellairs passed away on 30 December 2021 at the age of 95. Ruth was a legendary figure in chick embryology; she pioneered many new techniques and made some important discoveries, and we were both extremely fortunate to benefit from her extraordinary mentorship, C.W. as final honours project undergraduate in her lab and then as her PhD student (1967-70), and C.D.S. as her postdoc (1978-1984).

Ruth Bellairs (1926-2021) at the microscope in her lab (early 1980s). Photograph courtesy of Vivien St Joseph.

Ruth was born on 10 March 1926 in Halifax, Yorkshire, as the youngest of three sisters, to journalist parents, Trevor and Muriel Morgan. Her father worked for the local *Halifax Courier* (a Conservative paper) and her mother wrote for the *Guardian* (a Labour-leaning broadsheet), which must have led to some quite interesting conversations at home. They also ran a small farm and kept goats, and her father was a serious amateur numismatist. Ruth was educated at a private school in Halifax. Her oldest sister Joan, 6 years her senior, went to university, later becoming an entomologist. But at age 15, Ruth was advised by the local vicar to take a job at the local bank until she could find a husband.

Incensed by this, Ruth redoubled her efforts at school and, in 1944, gained a place at the University of Birmingham (which she chose on the basis of its Chair of Zoology, Lancelot Hogben, whose popular book *Science for the Citizen* she had read as a schoolgirl). It was at Birmingham that she met Michael Abercrombie, who had himself worked with C.H. Waddington and later became a pioneer in the field of cell motility. Upon graduation in 1947, she took a position in his laboratory in the Department of Anatomy and Embryology at University College London (UCL) to do a PhD, co-supervised by Sir Gavin de Beer who then held the Chair of Embryology (for an interesting account of her early years at UCL just after the war, see https://www.ucl.ac.uk/biosciences/sites/biosciences/files/cdb-about-short-history.pdf). In 1949 she was appointed to a Junior Lectureship (Assistant Professor) in the same department, where Ruth spent most of the rest of her working life (apart from a short stint at St Bartholomew's Medical School). She was promoted to a full Professorship in 1980 and retired to an emeritus position in 1991. Ruth was a pioneering female faculty member, coming into the field at a time when women were discouraged from applying for academic positions in science.

Ruth spent most of her career studying the chicken embryo, with occasional sorties into other model organisms. One of her first publications, in a 1951 issue of *Nature*, was on the culture of early reptile embryos (Bellairs, 1951). In her PhD work with Abercrombie, she used embryo culture methods devised by Dame Honor Fell and further developed by C.H. Waddington (Waddington, 1932, 1975). Ruth showed, by exchanging fragments of the primitive streak, that Hensen's node, the amniote organizer, is at least partly defined by influences from neighbouring cells in the area pellucida (Bellairs, 2018). Abercrombie's interest in the study of cell motility had a strong influence on Ruth. Her subsequent work, using carbon particles to follow the movements of cells, led to her demonstration that the definitive (future gut) endoderm, until then thought to arise from the initial lower layer of the embryo (hypoblast), was in fact derived from cells ingressing through the anterior primitive streak (Bellairs, 1953a,b, 1955, 1957) (the first two of these papers were published in the very first issue of Development's forerunner, the Journal of Embryology and Experimental Morphology). It took more than 40 years for both of these findings to become established as a general, conserved feature of vertebrate development, but have now become part of our common knowledge.

Later, using the method of embryo culture developed by Dennis New (New, 1955), which allowed the normal expansion of the blastula over the vitelline membrane, she made important contributions to both the mechanism and significance of these movements. Using time-lapse microcinematography on 16 mm black and white celluloid rolls, Ruth followed the movements of cells in the embryo during various developmental processes from gastrulation to early organogenesis. Later, she became particularly interested in exploring how isolated embryonic cells and tissues move and interact *in vitro*, for which she also used time-lapse, no doubt influenced by the work of Abercrombie. Ruth was a very early pioneer in the use of the electron microscope (EM) for studying

[1]Emeritus Professor, Division of Developmental Biology, Cincinnati Children's Hospital Medical Center, Burnet Ave, Cincinnati, OH 45229, USA. [2]Department of Cell and Developmental Biology, University College London, Gower Street, London WC1E 6BT, UK.

*Author for correspondence (c.stern@ucl.ac.uk)

C.D.S., 0000-0002-9907-889X

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Early bonding with the chick? A photograph taken in 1927/28 on the family farm, showing the three sisters (from left to right) Gwenda, Ruth and Joan. Gwenda died of diphtheria aged 4, probably soon after this photograph was taken. Courtesy of Vivien St Joseph.

chick embryogenesis, taking advantage of the fact that her department at UCL had purchased the first transmission EM in the UK in the early 1950s. Over a period of many years, she gathered massive amounts of detailed information about many embryonic processes, including formation of the primitive streak (gastrulation), somite formation, neural tube and placode development, mesoderm and gut development, the tail bud, the Wolffian duct, rotation of the heart tube and much more. She also developed a keen interest in cell adhesion, the extracellular matrix, the influences of cell-cell and cell-substrate interactions, and the cell behaviours guiding morphogenesis, areas that have now become very fashionable again. When monoclonal antibodies appeared in the 1970s, along with improved methods to visualise the distribution of antigens both in whole embryos and in sections, Ruth jumped at the opportunity and exploited the technology to the full for studying the extracellular matrix, the cytoskeleton and other components, with great care and precision.

London was a centre for the study of embryogenesis in the 1940s and 50s, and UCL had the only Department of Anatomy and Embryology in the country. On 19th February 1948, just one year after arriving at UCL as a PhD student, she (as Miss M.R. Morgan) took part in a gathering of 13 colleagues at King's College London that resolved to found the Embryologists' Club (with Elisabeth Fraser in the Chair and J.P. Hill as President), which later became the Society for Developmental Biology, and later still, the British Society for Developmental Biology (Slack, 2000; Bellairs, 2018) (the archives of early papers of the society, including minutes of that first meeting, are held at https://figshare.com/articles/dataset/Embryologists_Club_Notes/5899636). One of the other 13 people present at that inaugural meeting was Dr Angus d'Albini Bellairs, who later became her husband. Angus Bellairs became a world-famous herpetologist – his two-volume book *The Life of Reptiles* (Bellairs, 1969) is still considered the bible in the field.

On first meeting, Ruth Bellairs seemed to be almost a contradiction in terms; she had a stature reminiscent of more formal times, in action and achievement a first-class scientist, and a pioneer for women in science. She somehow carried off all of these without any obvious contradiction or effort. She was also the perfect mentor. In the lab, where she spent most of her time (an object lesson for all the office-bound PIs of today), she combined unflappable *joie de vivre* with a serious and competent precision. She had endless stamina, often spending the whole day at the microscope undertaking complicated surgery without getting up more than a couple of times to make herself a cup of tea. While performing the surgery, she would chat away about what we were doing, what she was doing, and intersperse little nuggets of practical help with more philosophical insights into how each of our experiments fitted into the greater scheme of the research project. Ruth mentored by example, not by command. The lab was a happy and productive place. Even the few months it took to carry out an undergraduate honours project in her lab were enough to convert one of us (C.W.) from aspiring medic to lifelong laboratory scientist.

Ruth's knowledge of embryology (human as well as chick) was immense – not only the descriptive aspects, but also her deep knowledge of the underlying history and of the people who made the discoveries. A fraction of this knowledge was distilled into her excellent *Atlas of Chick Development* (Bellairs, 1998; Bellairs and Osmond, 2005, 2014, with a fourth edition in preparation).

Despite being able to switch on a look that could turn the unwary medical student to stone, Ruth was exceptionally warm and friendly. She was an excellent teacher of human embryology to medical and life sciences students. Her lectures on human embryology (a difficult four-dimensional subject) to medical students were exceptional; clear and entertaining. Well before the days of PowerPoint, when the main visual aids were a blackboard and chalk, and the projection of transparencies (which Ruth referred to as 'lantern slides'), she often constructed large models to illustrate developmental processes. For example, to demonstrate the rotation of the gut, Ruth made a 'cloth model' consisting of a wooden board, a sheet of fabric, wool stuffing and some rubber tubing, using hooks to pin the various structures to the board to illustrate the complex folding movements. Another example was a model of the folding and septation of the early heart tube to generate the adult pattern, using two pairs of stockings stuffed with old scraps of material. After the laughter had subsided, the students were very happy to acknowledge that they would not have been able to understand these events without this approach. Indeed, one of us (C.D.S.) inherited the original 'cloth model' of the gut and continued to use it for a decade for teaching embryology to Oxford medical students.

Ruth's practical classes for medical students (mainly embryology) were legendary, and provided the same rigour as Ruth applied to her research. She would provide to each medical student a set of serially sectioned pig embryos, taken during the period of organogenesis, and plasticine (modelling clay) of different colours. Students were then expected to work through the serial sections, and then to use these to construct a 3D model of each major organ of the embryo. Once the shock of this requirement had worn off, it turned out to be great fun and more instructive than any formal lecture on the subject. Both of us were taught how to interpret these serial sections and then enlisted to help teach embryological anatomy in the classroom. The ability to do these 3D reconstructions, as well as how to recognise different tissues and organs in histological sections, remained with us for the rest of our careers and played a hugely important part in both our research and our teaching.

Ruth was a role model for her trainees, not only as a scientist but as a person. She was always interested, always ready to help, and always ready to discuss whatever was on our minds, personal as well as professional problems. She was endlessly polite and cheerful in the lab. Problems were always solvable with a little thought and effort. Mistakes were always corrected with a minimum of fuss, and never any acrimony. Both of us remember her philosophy of 'be

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kind to your juniors – some day they will be your boss'. This turned out to be an uncanny prediction as, some years later, one of us (C.D.S.) became head of the same department in 2001, where she was still Professor Emerita.

When one of us (C.W.) expressed an interest in working with her for a PhD to study the molecular aspects of early chicken development (mRNA had only been 'discovered' two years previously), Ruth volunteered the information that she did not know all that much about molecular biology, but that it might be wise to do a postgraduate course of some kind before starting the Ph.D. She then identified such a course at St. Bartholomew's (Barts) Hospital, contacted Eric Crook (Chair of Biochemistry at Barts) to arrange an introduction, and C.W. then went to study Biochemistry for a second B.Sc. before starting in her lab. Despite her proclaimed 'ignorance', she then carefully read, and provided insights into, the resulting research project, as well as C.W.'s first papers, which she then refused to co-author: 'it's your work Chris, you should be the author'; an unimaginable response nowadays.

Ruth had many interests apart from science. She loved travel. This may have started early in her career when, in 1955, she was awarded a fellowship to travel to the USA to carry out some experiments on fish (*Fundulus*) embryos with J.P. Trinkaus, another pioneer in cell biology and cell motility. Later, she particularly enjoyed her frequent trips to India, where she also undertook other pieces of research, including studies on an Indian millipede. Ruth also loved to read, including poetry, had a deep appreciation of Oriental rugs and she was very skilled at knitting and needlework. She also collected rare 'Stanhopes' – very small objects made of wood, bone or ivory with a tiny lens, to which was glued an almost microscopic photograph: looking through the lens would allow the photograph to be appreciated without a microscope.

Ruth had an attitude to life and science that will be sorely missed – chick embryology, as well as the whole of British developmental biology, owe an enormous amount to her work, her teachings and her never-ending kindness.

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