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Colin Russell Austin 1914–2004

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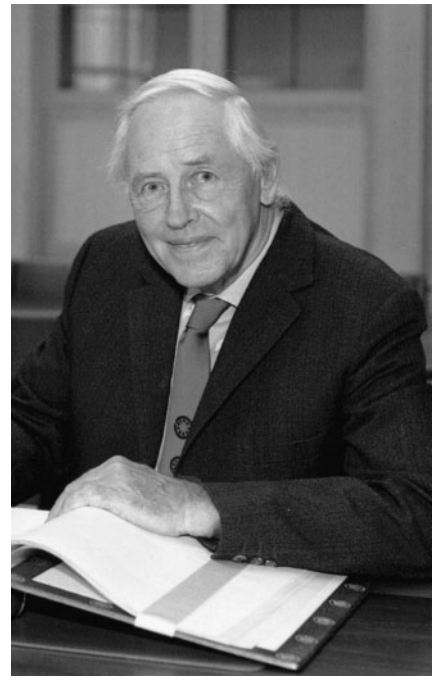
Colin Russell Austin, English by birth, initially graduated in Veterinary Science from the University of Sydney in 1936. The Second World War limited his career options, but he was fortunate to be employed by the CSIR Division of Animal Health in Sydney. In 1954 he was invited to join the staff of the Medical Research Council's laboratory in Mill Hill, London to study fertilization and early embryonic development in rats and rabbits. As a result, in 1962 he was asked to teach Fertilization and Gamete Physiology at the Marine Biological Laboratory, Woods Hole, Massachusetts, and subsequently became Professor of Embryology in the Medical School at Tulane University, New Orleans. This alerted the University of Cambridge to his potential and they created a special Charles Darwin Chair for him in 1967. This enabled him to support the work of his young student Robert Edwards on human *in vitro* fertilization and embryonic development that culminated in the award of the Nobel Prize to Edwards and Patrick Steptoe in 2010. Austin also devoted a great deal of his time to editing the 13-volume Cambridge University Press series of textbooks, *Reproduction in Mammals*, completing the series from his retirement home in Buderim, Queensland in 1986.

Colin Russell Austin, known from childhood as 'Bunny', was born in Sydney on 12 September 1914 and spent his early days in India where his father, a Lieutenant Colonel in the British Army, was stationed during the First World War. At the end of the war, the family returned to England and then emigrated to Australia when Bunny was 15. After finishing his secondary education he enrolled at the University of Sydney, where he obtained a Bachelor of Veterinary Science degree in 1936. Since veterinary practice did not appeal, he continued at University, completing a Bachelor of Science degree in 1938 and then working towards a Master of Science degree in Biochemistry that he was awarded in 1940. In that year, he became a member of the research staff of the Division of Animal Health of Australia's Council for Scientific and Industrial Research (CSIR, later CSIRO), where he stayed on the payroll until 1954 except for a couple of years, 1941–3, during the Second World War when he was seconded to the Dried Fruits Section of the Council's Division of Food Preservation and Transport, working on Army diets and nutrition. It was there that he met Patricia, a CSIR librarian, and they married in 1941. They had two sons, Mark and Richard.



In 1947, CSIR sent Bunny to work at the Medical Research Council laboratory in Mill Hill, London, where he spent a year before returning to Australia. He clearly made a very favourable

impression, because in 1954 he was appointed to a permanent post in the newly created National Institute for Medical Research at Mill Hill. In the same year, he was awarded a Doctor of Science degree by the University of Sydney for work on fertilization and associated phenomena in mammals.

At Mill Hill, Bunny eventually became Head of the Laboratory Animals Division from 1958 to 1961. The Austin family lived in Hadley Wood, North London, for ten years, and it was during this period that his scientific career took off, building on the study of fertilization and early embryonic development in rats and rabbits that he had started in Australia in collaboration with Dr A. W. H. Braden. Between 1948 and 1956, Bunny published ten papers in *Nature* (8, 10, 15, 16, 21, 22, 28, 30, 39, 42), and there were more to follow. Perhaps he will be best remembered for his 1952 paper in *Nature* (21). He showed that neither rabbit nor rat spermatozoa can fertilize their respective ova without a period of maturation in the female reproductive tract, a process he described as capacitation. He also found the time to write a landmark book, *The Mammalian Egg*, summarizing all these early findings. This was published by Blackwell, Oxford in 1961.

Bunny's research in due course brought him transatlantic recognition. In 1962, he was made a F. R. Lillie Memorial Fellow and a member of the teaching staff of the Fertilization and Gamete Physiology Training Program at the Marine Biological Laboratory, Woods Hole, Massachusetts, USA, an appointment that lasted until 1968. For the first three years, he and Pat spent the months of June, July and August in that inspiring academic environment. But he also inspired those around him and so it was that he became Head of the Genetic and Developmental Disorders Research Program at the Delta Regional Primate Research Center, Covington, Louisiana and also Professor of Embryology in the Medical School at Tulane University, New Orleans, 1964–7. The availability of primates enabled him to start working on spermatozoa in the epididymis of monkeys (104), the liquefaction of primate semen (106), the preservation of primate spermatozoa by freezing (107), the use of a rectal probe for electroejaculation of apes and monkeys (111, 114) and, most importantly, the use of human postmenopausal gonadotrophin to stimulate ovarian follicular and oocyte development in monkeys (115). So humans must be next on the list!

Thus it was that his most important career move came in 1967, when he returned to England to take up a Chair that had been specially created for him at the University of Cambridge, the Charles Darwin Professorship in Animal Embryology in the Department of Physiology, together with a Fellowship at Fitzwilliam College. Here he was able to provide the perfect research environment for an up-and-coming young zoologist, Robert Edwards, who Bunny took into his department to develop, with his clinician colleague Patrick Steptoe, the contentious subject of human *in vitro* fertilization and embryo transfer—work that would eventually earn Edwards the 2010 Nobel Prize in Physiology or Medicine. Edwards and Bunny published their first paper together in 1959, on the induction of oestrus and ovulation in rats (67), but their most significant joint publication was in 1972 (131) on 'Initiation of human development *in vitro* and transfer of early embryos', presented at a UNESCO conference in Paris. In 1986, Bob Edwards had this to say of Bunny: 'I would like to stress my own deep debt to him during the most difficult period of human in-vitro fertilization, when he was a clear thinking supporter of the work, prepared to defend it publicly when there were few others around'. This refers to the fact that several senior Cambridge academics, including a Nobel Laureate, were deeply opposed to human *in vitro* fertilization and would have torpedoed all the efforts of Edwards and Steptoe, had it not been for Bunny's unwavering support as Charles Darwin Professor. Darwin would have been proud of Bunny! Bunny retired in 1981 and afterwards he and Pat settled in Buderim, Queensland. In 1987 he was elected a Fellow of the Australian Academy of Science, a fitting recognition of a great scientific career.

Scientific Achievements

In 1986, Professor Ryuzo Yanagimachi, Professor of Anatomy and Reproductive Biology at the University of Hawaii and an extremely distinguished gamete biologist, summarized Bunny's scientific contributions in the following words: 'I, and I believe all reproductive biologists working on mammalian fertilization today, consider Dr Austin as the founder of the modern study

Figure 1. Bunny Austin's chapter 'The Egg' in *Reproduction in Mammals*, Second Edition, 1982, Volume 1, has on page 61 this beautiful drawing by John Fuller, taken from the frontispiece of William Harvey's classic book *De generatione animalium* (1651). It shows the hands of Jove holding apart the two halves of an egg, from which are emerging a plant, an insect, an amphibian, a reptile, a bird, a ruminant and even a human being, beautifully summarized in the words 'Ex ovo omnia' that might have been Bunny's motto.

of mammalian fertilization. Between 1948 and 1955, when he was in Australia, Dr Austin published 34 research papers on mammalian fertilization. His outstanding contributions to the field of mammalian reproduction are: the co-discovery of the phenomenon of sperm capacitation; the first description of the acrosome reaction of mammalian spermatozoa; the discovery of the zona reaction; and the first detailed description of normal and abnormal fertilization. Without the pioneering studies of Dr Austin we would be far behind where we are today in reproductive biology. If it were not for Dr Austin, the success of human *in vitro* fertilization, for example, would have been set back at least a decade, or perhaps never occurred.' That is praise indeed.

Reproduction in Mammals

There can be no doubt that one of Bunny's greatest achievements was as the Senior Editor and a major contributor to the Cambridge University Press series *Reproduction in Mammals* that he and I brought together. When planning this series, we decided first and foremost to make the books highly readable to undergraduates, to intersperse the text with excellent illustrations drawn by our Cambridge colleague John Fuller and, if possible, to avoid using tables since these break up the flow of the argument.

The first volume, Germ Cells and Fertilization, was published in 1972. The other volumes were: 2. Embryonic and Fetal Development, 3. Hormones in Reproduction, 4. Reproductive

Patterns, 5. Artificial Control of Reproduction, 6. The Evolution of Reproduction, 7. Mechanisms of Hormone Action, and 8. Human Sexuality. These were all published between 1972 and 1980. To write the chapters, we hand-picked scientists from around the world whom we knew personally and we never had a refusal! Either Bunny or I, and sometimes both of us, had a chapter in each volume, thereby giving us a sense of ownership of the series. It met with a very warm reception from both teachers and students.

Scientifically, however, things were changing fast, and so we decided to produce a completely new edition of Volumes 1–5 between 1982 and 1986, in response to requests from our readers for a more up-to-date and detailed treatment of the subjects. As a result, the volumes doubled in size and a few tables crept in, but John Fuller's beautiful drawings continued to enlighten the text (Fig. 1). There were a few title changes, with Volume 3 becoming Hormonal Control of Reproduction, Volume 4, Reproductive Fitness, and Volume 5, Manipulating Reproduction. Much of the work for the new edition was done in Australia, with Bunny now living in Buderim while I had moved from Cambridge via the University of Edinburgh to Monash University in Melbourne, meaning that we were still able to keep in touch. Appropriately, Bunny had the last word because he wrote the final chapter in the new Volume 5, which he entitled 'Barriers to Population Control'—a prescient theme in a world in which human population growth is one of the major problems facing mankind.

Bibliography

Books (written)

The Mammalian Egg. Blackwell Scientific Publications, Oxford. (1961).

Fertilization. Prentice-Hall Inc., Englewood Cliffs, NJ. (1965).

Ultrastructure of Fertilization. Holt, Rinehart and Winston, New York. (1968).

Books (edited)

Sex Differentiation and Development. Memoirs of the Society for Endocrinology No 7. Cambridge, at the University Press. (1960).

Cell Mechanisms in Hormone Production and Action. Memoirs of the Society for Endocrinology No 8. Cambridge, at the University Press. (1961). With P. C. Williams.

A Symposium on Agents Affecting Fertility. L. & A. Churchill, London. (1965). With J. S. Perry.

Reproduction in Mammals. Cambridge University Press. With R. V. Short.

Book 1. *Germ Cells and Fertilization*. (1972).

Book 2. *Embryonic and Fetal Development*. (1972).

Book 3. *Hormones in Reproduction*. (1972).

Book 4. *Reproductive Patterns*. (1972).

Book 5. *Artificial Control of Reproduction*. (1972).

Book 6. *The Evolution of Reproduction*. (1976).

Book 7. *Mechanisms of Hormone Action*. (1979).

Book 8. *Human Sexuality*. (1980).

The Mammalian Fetus in Vitro. Chapman and Hall, London. (1973).

Mechanisms of Sex Differentiation in Animals and Man. Academic Press, London and New York. (1981). With R. G. Edwards.

Reproduction in Mammals, 2nd Edition. Cambridge University Press. With R. V. Short.

Book 1. *Germ Cells and Fertilization*. (1982).

Book 2. *Embryonic and Fetal Development*. (1982).

Book 3. *Hormonal Control of Reproduction*. (1984).

Book 4. *Reproductive Fitness*. (1985).

Book 5. *Manipulating Reproduction*. (1986).

Research Reports, Abstracts, Reviews, Chapters, etc

1. The clinical examination of urine. *Lab. J. Australasia*, June, pp. 1–14. (1941). With J. H. Rofe.
2. The thiamine (vitamin B_1) content of the urine of *Trichosurus vulpecular*. *J. Proc. R. Soc. NSW.*, **75**, 118–121. (1941). With A. Bolliger.
3. The reproductive hormones: a review of chemical and physical aspects. *Aust. Vet. J.*, **17**, 222–228. (1941).
4. The determination of carotene: a critical evaluation. *J. CSIR*, **17**, 115–126. (1944). With J. Shipton.
5. Endocrinology and animal production. *Aust. Vet. J.*, **22**, 48–54. (1946).
6. The metabolism of thiamine in the sheep. *Aust. J. Exp. Biol. Med. Sci.*, **25**, 147–155. (1947).
7. The effect of hexoestrol on the food intake of sheep. *Aust. J. Exp. Biol. Med. Sci.*, **25**, 343–346. (1947). With W. K. Whitten, M. C. Franklin and R. L. Reid.
8. Function of hyaluronidase in fertilization. *Nature*, **162**, 534. (1948).
9. Phase-contrast microscopy in the study of fertilization and early development of the rat

egg. *J. R. Micr. Soc.*, **68**, 13–19. (1948). With J. Smiles.
10. Number of sperms required for fertilization. *Nature*, **162**, 534. (1948).
11. Fertilization and the transport of gametes in the pseudo-pregnant rabbit. *J. Endocr*., **6**, 63–70. (1949).
12. The fragmentation of eggs following induced ovulation in immature rats. *J. Endocr*., **6**, 104–110. (1949).
13. The functions of the endocrine system in pregnancy. *Aust. Vet. J.*, August, pp. 190–193. (1949).
14. The fecundity of the immature rat following induced super-ovulation. *J. Endocr*., **6**, 293–301. (1950).
15. Fertilization of the rat egg. *Nature*, **166**, 407. (1950).
16. Activation and the correlation between male and female elements in fertilization. *Nature*, **168**, 558. (1951).
17. Observations on the penetration of the sperm into the mammalian egg. *Aust. J. Sci. Res., Ser. B*, **4**, 581–596. (1951).
18. The formation, growth and conjugation of the pronuclei in the rat egg. *J. R. Micr. Soc*., **71**, 295–306. (1951).
19. The development of pronuclei in the rat egg, with particular reference to quantitative rela- tions. *Aust. J. Sci. Res., Ser. B*, **5**, 354–365. (1952).
20. The development of the rat spermatid. *J. R. Micr. Soc*., **71**, 397–406. (1952). With C. Sapsford.
21. The 'capacitation' of mammalian sperm. *Nature*, **170**, 326. (1952).
22. Passage of the sperm and the penetration of the egg in mammals. *Nature*, **170**, 919. (1952). With A. W. H. Braden.
23. Nucleic acids associated with the nucleoli of living segmented rat eggs. *Exp. Cell Res.*, **4**, 249–251. (1953).
24. The distribution of nucleic acids in rats eggs in fertilization and early segmentation. I. Studies on living eggs by ultraviolet microscopy. *Aust. J. Biol. Sci.*, **6**, 324–333. (1953). With A. W. H. Braden.
25. The distribution of nucleic acids in rats eggs in fertilization and early segmentation. II. Histochemical studies. *Aust. J. Biol. Sci.*, **6**, 665–673. (1953). With A. W. H. Braden.
26. Fertilization and fertility in mammals. *Aust. J. Vet.*, May, pp. 129–132. (1953). With A. W. H. Braden.
27. The growth of knowledge on mammalian fertilization. *Aust. J. Vet.*, July, pp. 191–198. (1953).
28. Polyspermy in mammals. *Nature*, **172**, 82. (1953). With A. W. H. Braden.
29. An investigation of polyspermy in the rat and rabbit. *Aust. J. Biol. Sci*., **6**, 674–692. (1953). With A. W. H. Braden.
30. Nucleus formation and cleavage induced in unfertilized rat eggs. *Nature*, **173**, 999. (1954). With A. W. H. Braden.
31. Reactions of unfertilized mouse eggs to some experimental stimuli. *Exp. Cell Res.*, **7**, 277–280. (1954). With A. W. H. Braden.
32. Time relations and their significance in the ovulation and penetration of eggs in rats and rabbits. *Aust. J. Biol. Sci.*, **7**, 179–194. (1954). With A. W. H. Braden.
33. Induction and inhibition of the second polar division in the rat egg and subsequent fertilization. *Aust. J. Biol. Sci.*, **7**, 195–210. (1954).
34. The reaction of the zona pellucid to sperm penetration. *Aust. J. Biol. Sci.*, **7**, 391–409. (1954). With A. W. H. Braden and H. A. David.
35. Anomalies in rat, mouse and rabbit eggs. *Aust. J. Biol. Sci.*, **7**, 537–542. (1954). With A. W. H. Braden.
36. The number of sperms about the eggs in mammals and its significance for normal fertilization. *Aust. J. Biol. Sci.*, **7**, 543–551. (1954). With A. W. H. Braden.
37. Fertilization of the mouse egg and the effect of delayed coitus and of hot-shock treatment. *Aust. J. Biol. Sci.*, **7**, 552–565. (1954). With A. W. H. Braden.
38. The fertile life of mouse and rat eggs. *Science*, **120**, no. 3120. (1954). With A. W. H. Braden.
39. Polyspermy after induced hyperthermia in rats. *Nature*, **175**, 1038. (1955).
40. Acquisition de la capacite fertilisatrice des spermatozoids ("capacitation") dans les voies genitales femelles. In: *La Fonction Tubaire*, pp. 22–27. Masson et Cie, Paris. (1955).
41. Observations on nuclear size and form in living rat and mouse eggs. *Exp. Cell Res*., **8**, 163–172. (1955). With A. W. H. Braden.
42. Study of fertility. *Nature*, **178**, 185–187. (1956).
43. An attempt to produce the Hertwig effect by X-irradiation of male mice. *Studies in Fertility*, **8**, 121–131. (1956). With H. M. Bruce.
44. Cortical granules in hamster eggs. *Exp. Cell Res.*, **10**, 533–540. (1956).
45. Ovultation, fertilization and early cleavage in the hamster (*Mesocricetus auratus*). *J. R. Micr. Soc.*, **75**, 141–154. (1956).
46. Effect of continuous oestrogen administration on oestrus, ovulation and fertilization in rats and mice. *J. Endocr.*, **13**, 376–383. (1956). With H. M. Bruce.
47. Activation of eggs by hypothermia in rats and hamsters. *J. Exp. Biol*., **33**, 338–347. (1956).

48. Effects of hypothermia and hyperthermia on fertilization in rat eggs. *J. Exp. Biol*., **33**, 348–357. (1956).
49. Early reactions of the rodent egg to spermatozoon penetration. *J. Exp. Biol*., **33**, 358–365. (1956). With A. W. H. Braden.
50. Environmental modification of oestrus in the vole. *Nature*, **179**, 592–593. (1957). With H. Chitty.
51. Preliminaries to fertilization in mammals. In: *The Beginnings of Embryonic Development*, pp. 71–107. Am. Assoc. Adv. Sci., Washington, DC. (1957). With M. W. H. Bishop.
52. Sec chromatin in early cat embryos. *Exp. Cell Res.*, **13**, 419–421. (1957). With E. C. Amoroso.
53. Fertilization in mammals. *Biol. Rev*., **32**, 296–349. (1957).
54. Fertilization, early cleavage and associated phenomena in the field vole (*Microtus agrestis*). *J. Anat.*, **91**, 1–11. (1957).
55. Fate of spermatozoa in the uterus if the mouse and rat. *J. Endocr.*, **14**, 335–342. (1957).
56. Oestrus and ovulation in the field vole (*Microtus agrestis*). *J. Endocr.*, **15**, iv. (1957).
57. Mammalian spermatozoa. *Endeavour*, **16**, 137–150. (1957).
58. Capacitation of mammalian spermatozoa. *Nature*, **181**, 851. (1958). With M. W. H. Bishop.
59. Research within the laboratory-animal division. In: *Symposium*. Organized by the Laboratory Animals Centre of MRC. Royal Society of Medicine, 5 May. (1958).
60. Permeability of rabbit, rat and hamster egg membranes. *Exp. Cell Res.*, **15**, 260–261. (1958). With J. E. Lovelock.
61. Some features of the acrosome and perforatorium in mammalian spermatozoa. *Proc. R. Soc., B*, **149**, 234–240. (1958). With M. W. H. Bishop.
62. Role of the rodent acrosome and perforatorium in fertilization. *Proc. R. Soc., B*, **149**, 241–248. (1958). With M. W. H. Bishop.
63. Entry of spermatozoa into the Fallopian-tube mucosa. *Nature*, **183**, 908–909. (1959).
64. Differential fluorescence in living rat eggs treated with acridine orange. *Exp. Cell Res.*, **17**, 35–43. (1959). With M. W. H. Bishop.
65. The role of fertilization. *Perspectives Biol. Med*., **3**, 44–54. (1959).
66. Presence of spermatozoa in the uterine-tube mucosa of bats. *J. Endocr.*, **18**, viii–ix. (1959). With M. W. H. Bishop.
67. Induction of oestrus and ovulation in adult rats. *J. Endocr.*, **18**, vii–viii. (1959). With R. G. Edwards.
68. Prospective experimental animals for medical research. *J. Anim. Tech. Assoc.*, **10**, 1–6. (1959).
69. The mammalian egg. *Endeavour*, **18**, 130–143. (1959). With E. C. Amoroso.
70. Fertilization and development of the egg. In: *Reproduction in Domestic Animals*, eds. H. H. Cole and P. T. Cupps. Academic Press; New York and London. 1st Ed. Chap. 12; 2nd Ed. Chap. 13.
71. Syngamy in a mammalian egg. Study by phase-contrast microscopy. *Med. Biol. Illustr.*, **10**, 62–63. (1960).
72. Fate of spermatozoa in the female genital tract. *J. Reprod. Fert.*, **1**, 151–156. (1960).
73. Capactitation and the release of hyaluronidase from spermatozoa. *J. Reprod. Fert*., **3**, 310–311. (1960).
74. Fertilization. In: *Marshall's Physiology of Reproduction*, 3rd edition, ed. A. S. Parkes, vol. 1, pt. 2, chap.10. Longmans, Green; London. (1960). With A. Walton.
75. Anomalies of fertilization leading to triploidy. *J. Cell Comp. Physiol*., **56**, suppl. 1, 1–15. (1960).
76. Egg. In: *Encyclopedia of Biological Sciences*, ed. P. Gray, pp. 327–328. Reinhold; New York. (1961).
77. Significance of sperm capacitation. In: *Proc. IV Int. Congr. Anim. Reprod., Hague*. (1961).
78. Fertilization of mammalian eggs *in vitro*. *Int. Rev. Cytol*., **12**, 337–359. (1961).
79. Sex chromatin in embryonic and fetal tissue. *Acta Cytol*., **6**, 61–68. (1962).
80. Evidence against participation of a jelly-spitting agent in sperm penetration of *Arbacia* eggs. *Biol. Bull*., **123**, 470. (1962). With J. Piatigorsky.
81. Action of neuraminidase on *Arbacia* spermatozoa. *Biol. Bull*., **123**, 471–472. (1962). With R. L. Brinster.
82. Relationship of fertilizin to the acrosome reaction in *Arbacia*. *Biol. Bull*., **123**, 473. (1962). With J. Piatigorsky.
83. Passage of spermatozoa through the chorion of *Ciona* eggs. *Biol. Bull*., **123**, 472. (1962). With S. D. Ezell, jr.
84. Axial body and filament formation in oyster sperms. *Biol. Bull*., **123**, 474–475. (1962). With D. H. Spoon and A. Forer.
85. Introducing new animals to the laboratory. *New Scientist*, **17**, 117–120. (1962).
86. Fertilization in *Pectinaria* (=*Cistenides*) *gouldii*. *Biol. Bull*., **124**, 115–124. (1963).
87. Acrosome loss from the rabbit spermatozoon in relation to entry into the egg. *J. Reprod. Fert*., **6**, 313–314. (1963).
88. Sperm morphology of *Emerita talpoida*. *Biol. Bull*., **125**, 361–362. (1963). With K. R. Barker.
89. Ultrastructure of *Pectinaria gouldii* gametes. *Biol. Bull*., **125**, 364. (1963). With R. Lambson.
90. Fine structure of *Nereis limbata* spermatozoa. *Biol. Bull*., **125**, 362. (1963). With J. F. Fallon.

91. Fertilization and transport of the ovum. In: *Conference on Physiological Mechanisms Concerned with Conception*, New York, chap. 6, pp. 285–320. Pergamon Press; New York. (1963). Ed. C. G. Hartman.
92. Spermatozoon of *Pseudobranchus striatus axanthus*. *J. Reprod. Fert.*, **7**, 123–125. (1964). With C. L. Baker.
93. Spermatophores and spermatozoa of the squid *Loligo pealii*. *Proc. R. Soc., B,* **161**, 143–152. (1964). With C. Lutwak-Mann and T. Mann.
94. Gametogenesis and fertilization in the Mesozoan *Dicyema aegira*. *Parisitology*, **54**, 597–600. (1964).
95. Behaviour of spermatozoa in the female genital tract and in fertilization. In: *Proc. V Congr. Int. Reprod. Anim. Fecond. Artif.*, Trento. September. (1964).
96. A fine-structure study of the activation reactions of *Nereis limbata* gametes. *Biol. Bull.*, **127**, 369. (1964). With J. F. Fallon.
97. Sperm centrioles and their role in fertilization. In: *Proc. V Congr. Int. Reprod. Anim. Fecond. Artif.*, Trento. September. (1964).
98. Fine structure of the snake sperm tail. *J. Ultrastr. Res.*, **12**, 452–462. (1965).
99. Ultrastructural changes in the egg during fertilization and the initiation of cleavage. In: *Ciba Foundation Symposium on Preimplantation Stages of Pregnancy*, eds. G. E. W. Wolstenholme and M. O'Connor, pp. 3–22. Churchill; London. (1965).
100. Single-handed artificial insemination of rabbits. *J. Inst. Anim. Tech.*, **17**, 103–105. (1966). With E. N. Fussell and J. D. Rousel.
101. Sex chromatin in embryonic and fetal tissues. In: *The Sex Chromatin*, ed. K. L. Moore, chap. 15, pp. 241–254. (1966).
102. Capacitation of spermatozoa. *Proc. V World Congr. Fertil. Steril.*, Stockholm, June, pp. 685–689. (1966).
103. Fine structure of gametes of *Nereis limbata* (Annelida) before and after interaction. *J. Exp. Zool.*, **166**, 225–242. (1967).
104. Selective phagocytosis of spermatozoa in the epididymis of bulls, rabbits and monkeys. *Fertil. Steril.*, **18**, 509–516. (1967). With J. D. Roussel and O. T. Stallcup.
105. Entry of *Cerebratulus* spermatozoa into *Echinarachnius* eggs. *Biol. Bull.*, **133**, 477–478. (1967). With P. J. Olds.
106. Enzymic liquefaction of primate semen. *Int. J. Fertil.*, **12**, 288–290. (1967). With J. D. Roussel.
107. Preservation of primate spermatozoa by freezing. *J. Reprod. Fert.*, **13**, 333–335. (1967). With J. D. Roussel.
108. Capacitation of spermatozoa. *Int. J. Fertil.*, **12**, 25–31. (1967).
109. *In vitro* fertilization and the sperm acrosome reaction in the hamster. *J. Exp. Zool.*, **166**, 317–324. (1967). With C. Barros.
110. Membrane vesiculation as a feature of the mammalian acrosome reaction. J. Cell Biol., **34**, C1–C5. (1967). With C. Barros, J. M. Bedford and L. E. Franklin.
111. Use of the rectal probe method for electrical ejaculation of apes, monkeys and a prosimian. *Lab. Anim. Care*, **17**, 528–530. (1967). With E. N. Fussel and J. D. Roussel.
112. Chromosome deterioration in aging eggs of the rabbit. *Nature*, **213**, 1018–1019. (1967).
113. Prevention of coagulation in monkey semen by surgery. *J. Reprod. Fert.*, **15**, 153–155. (1968). With W. E. Greer and J. D. Roussel.
114. Improved electro-ejaculation of primates. *J. Inst. Anim. Tech.*, **19**, 22–32. (1968). With J. D. Roussel.
115. Use of human postmenopausal gonadotropin (Pergonal) for promoting ovarian follicular and oocyte development in monkeys. In: *Use of Nonhuman Primates in Drug Evaluation. A Symposium*, ed. H. Vagtborg, pp. 162–171. University of Texas Press; Austin and London. (1968). With J. D. Roussel and T. H. Clewe.
116. Inhibition of ovulation by systemically administered actinomycin D in the hamster. *Endocrinology*, **83**, 177–179. (1968). With C. Barros.
117. Bibliography of sperm-egg interactions in mammals. *Bibl. Reprod.*, **13**, 133–279. (1968).
118. Capacitation of sperm. *New Scientist*, 31 July, pp. 232–234. (1968).
119. Variations and anomalies in fertilization. In: *Fertilization*, eds. C. B. Metz and A. Monroy, vol. 2, chap. 10. Academic Press; New York. (1969).
120. Sperm capacitation – biological significance in various species. In: *Advances in the Biosciences*, **4**, pp. 5–11. Schering Symp. on Mechanisms Involved in Conception, Berlin, ed. G. Raspe. Pergamon Press; Vieveg, London. (1970).
121. Ageing and reproduction: post-ovulatory deterioration of the egg. *J. Reprod. Fert.*, Suppl. 12, pp. 39–53. (1970).
122. Bibliography on sperm capacitation. *Bibliogr. Reprod.*, **16**, 1–8; 141–148. (1970).
123. The egg and fertilization. *Sci. J.*, June, pp. 37–42. (1970).
124. Interpretation of the phenomenon of sperm capacitation. In: *Animal Reproduction and Artificial Insemination*. Published in honour of Telesforo Bonadonna. Societa Italiana per il Progresso della Zootechnica, pp. 11–15. (1972).

125. Aspects of spermatogenesis. In: *The Use of Non-human Primates Research on Human Reproduction*, pp. 42–44. Proc. Symp. WHO and the Ministry of Health of the USSR, Sukhumi, Georgia, eds. E. Diczfalusi and C. C. Standley. (1972).
126. Experimental control of reproduction in primates. In: *Breeding Primates*, ed. W. I. B. Beveridge, pp. 184–197. Karger; Basel. (1972).
127. Fertilization. In: *Reproduction in Mammals*, eds. C. R. Austin and R. V. Short, Book 1, Chap. 5. Cambridge University Press. (1972).
128. Pregnancy losses and birth defects. In: *Reproduction in Mammals*, eds. C. R. Austin and R. V. Short, Book 2, Chap. 5. Cambridge University Press. (1972).
129. The ethics of manipulating human reproduction. In: *Reproduction in Mammals*, eds. C. R. Austin and R. V. Short, Book 5, Chap. 6. Cambridge University Press. (1972).
130. Components of capacitation. In: *The Regulation of Mammalian Reproduction*, eds. S. J. Segal, R. Crozier, P. A. Corfman and P. G. Condliffe, pp. 247–256. Thomas; Springfield. (1972). With B. D. Bavister and R. G. Edwards.
131. Initiation of human development *in vitro* and transfer of early embryos. In: *VII CIOMS Round Table Conference*, ed. S. Btash, pp. 178–187. Maison de l'UNESCO; Paris. (1972). With R. G. Edwards.
132. Bibliography on mammalian sperm acrosomal enzymes. *Bibliog. Reprod.*, **22**, 927–928; 1109–1111. (1973).
133. Embryo transfer and sensitivity to teratogenesis. *Nature*, **244**, 333–334. (1973).
134. Ovulation and embryo development in mouse, rat and man. In: *International Research Communications System*, March. (1973). With D. L. Cockroft, R. G. Edwards, R. L. Gardner, R. Gosden, C. W. S. Howe, M. H. Johnson, M. H. Kaufman, D. A. T. New, V. E. Papaiouannou, C. E. Steele, A. E. Szulman and D. G. Whittingham.
135. Implications of viviparity. In: *The Mammalian Fetus In Vitro*, ed. C. R. Austin, pp. 1–13. (1973).
136. Principles of fertilization. *Proc. R. Soc. Med.*, **67**, 925–927. (1974).
137. Recent progress in the study of eggs and spermatozoa: insemination and ovulation to implantation. In: *MTP International Review of Science. Reproductive Physiology. Physiology Series One*, vol. 8, ed. R. O. Greep, chap. 4. Butterworth's University Park Press; London and Baltimore. (1974).
138. Fertilization. In: *Concepts of Development*, eds. J. Lash and J. R. Whittaker, Chap. II. Sinauer Associates Inc, Connecticut. (1974).
139. Preliminaries to the acrosome reaction in mammalian spermatozoa. In: *The Functional Anatomy of the Spermatozoon*, ed. B. A. Afzelius, pp. 83–87. Pergamon Press; Oxford. (1974).
140. Sperm fertility, viability and persistence in the female tract. *J. Reprod. Fert.*, Suppl. 22, 75–89. (1975).
141. Preparation of the mammalian spermatozoon for fertilization. *J. Sci. Soc. Thailand*, **1**, 23–29. (1975).
142. Membrane fusion events in fertilization. *J. Reprod. Fert.*, **44**, 155–166. (1975).
143. Report on a visit to Chulalongkorn University, Bangkok, Thailand, November 1974–March 1975. In: *Royal Society Leverhulme Visiting Professor to Chulalongkorn University, Bangkok, Thailand*. RSLVP/2(74/75). (1975).
144. Ovulation induction in primates. *Lab. Anim. Handb.*, **6**, 121–126. (1975).
145. Fate of spermatozoa in the female genital tract and the problem of induction of local antisperm immunity in women. In: *Development of Vac- cines for Fertility Regulation*. WHO Session in III International Symposium on Immunology of Reproduction, Varna, Bulgaria, pp. 63–80. (1975).
146. Development anomalies arising from errors of fertilization and cleavage. In: *Current Topics in Pathology*, eds. E. Grundmann and W. H. Kirsten. Vol. 62, *Developmental Biology and Pathology*, eds. A. Gropp and K. Benirschke, pp. 3–6. (1976).
147. Specialization of gamets. In: *Reproduction in Mammals*, eds. C. R. Austin and R. V. Short, Book 6, Chap. 5. Cambridge University Press. (1976).
148. Spermatozoa and ova: the role of membranes in the fertilization process. In: *Mammalian Cell Membranes. Vol. 3, Surface Membranes of Spe- cific Cell Types*, eds. G. A. Jamieson and D. M. Robinson, chap. 8. Butterworth; London. (1977).
149. Patterns in metazoan fertilization. In *Current Topics in Developmental Biology. Vol. 12, Fertilization*, eds. A. A. Moscona and A. Monroy, pp. 1–9. Academic Press; New York, San Francisco, London. (1978).
150. Sperm surface changes leading to sperm-egg fusion. In: *Spermatozoa, Antibodies and Infertility*, eds. J. Cohen and W. F. Hendry, pp. 31–36. Blackwell Scientific Publications; Oxford. (1978).
151. Advantages, difficulties and dilemmas of artificial breeding. (Introduction). In: *Symposia of the Zoological Society of London, Number 43: 'Artificial Breeding of Non-domestic Animals'*, ed. P. F. Watson, pp. 1–6. Academic Press; London. (1978).

152. Bisexuality and the problem of its social acceptance. *J. Med. Ethics*, **4**, 132–137. (1978).
153. The use of non-human primates as models for research in human problems. In: *Recent Advances in Primatology. Vol. 4, Medicine*, eds. D. J. Chivers and E. H. R. Ford, pp. 223–227. Academic Press; London. (1978).
154. Introduction. In: *Mechanisms of Sex Differentiation in Animals and Man*, eds. C. R. Austin and R. G. Edwards, pp. 1–54. Academic Press; London. (1981). With R. G. Edwards and U. Mittwoch.
155. The egg. In: *Reproduction in Mammals*, 2nd edit., eds. C. R. Austin and R. V. Short, pp. 46–62. (Book 1, Germ Cells and Fertilizaion.) Cambridge University Press. (1982).
156. Evolution of the copulatory apparatus. *Bolletino Zoologica*, (1984).
157. Sperm maturation in the male and female genital tracts. In: *Biology of Fertilization*, eds. C. B. Metz and A. Monroy. Academic Press; New York. (1986).
158. Barriers to population control. In: *Reproduction in Mammals*, 2nd edit. Book 5, *Manipulating Reproduction*, eds. C. R. Austin and R. V. Short. Cambridge University Press. (1986).