The Essentials are an international, best-selling series of textbooks, all of which are designed to support lecture series or themes on core topics within the health sciences. They all include the Wiley E-Text, Powered by VitalSource as standard upon purchase of the book. This provides an interactive digital version of the book featuring downloadable text and images, highlighting and note taking facilities, book marking, cross-referencing, in-text searching, and linking to references and glossary terms. See www.wiley.com/go/essentials for further details.

Providing essential reading for medical, veterinary and biological science students, and students of physiology and trainees in obstetrics and gynaecology, the seventh edition of Essential Reproduction offers an up-to-date account of the fundamentals of reproduction within the context of cutting-edge knowledge and examples of its application. It provides a multidisciplinary approach integrating physiology, genetics, behaviour, anatomy and clinical science, to give thorough coverage of the study of mammalian reproduction.

- The latest on conceptual, informational and applied aspects of reproduction
- A new structure offering a more logical approach to study and revision
- Expanded further reading suggestions to support research

REVIEWS OF THE PREVIOUS EDITION

"...this is an excellent book which can be recommended highly as a standard undergraduate text, but which will also prove a pleasurable read to many more senior endocrinologists." The Endocrinologist

"I have rarely enjoyed reading a book so much and would strongly recommend it to all trainee obstetricians and gynaecologists and to all undergraduate medical and science students requiring a thorough introduction to human reproduction and to all requiring insight into the miracle of reproduction in man." South African Medical Journal

"All the major areas of reproduction are covered from sexual differentiation, regulation of gonadal function, action of steroids, implantation and establishment of placentation, maternal recognition and support of pregnancy, fetal physiology, events associated with parturition, lactation and maternal behaviour." British Journal of Obstetrics & Gynaecology

OF RELATED INTEREST


For more information on the complete range of Wiley-Blackwell medical student and junior doctor publishing, please visit: www.wileymedicaleducation.com

To receive automatic updates on Wiley-Blackwell books and journals, join our email list. Sign up today at www.wiley.com/email

All content reviewed by students for students
Wiley-Blackwell Medical Education books are designed exactly for their intended audience. All of our books are developed in collaboration with students. This means that our books are always published with you, the student, in mind. If you would like to be one of our student reviewers, go to www.reviewmedicalbooks.com to find out more.
Essential Reproduction
To Professor Sir Bob Edwards
Nobel Laureate in Physiology or Medicine 2010
who first stimulated my interest
in the science of reproduction
Essential Reproduction

Martin H. Johnson
MA, PhD, FRCOG, FSB, FMedSci
Professor of Reproductive Sciences
Department of Physiology, Development and Neuroscience
University of Cambridge
Fellow of Christ’s College, Cambridge
Cambridge, UK;
Honorary Academic Fellow of St Paul’s College
Sydney, NSW, Australia

Seventh edition
## Contents

Preface vii  
How to use this book viii  
Acknowledgements ix  
Features of your textbook x  

**PART 1: Introduction**  
1 What is reproduction? 3  

**PART 2: Making men and women** 33  
2 Sex 35  
3 Sexual maturation 50  
4 Gender 69  
5 Sexual selection 85  

**PART 3: Preparing for pregnancy** 103  
6 Making sperm 105  
7 Men 122  
8 Making eggs 133  
9 Women 151  

**PART 4: Making an embryo** 173  
10 Sperm and eggs 175  
11 Fertilization 189  
12 Initiating pregnancy 206  

**PART 5: Maintaining a pregnancy** 225  
13 Supporting the embryo and fetus 227  
14 Growing the fetus 245  
15 Fetal challenges 258  

**PART 6: A new individual** 271  
16 Preparing for birth 273  
17 Giving birth 283  
18 Lactation 297  
19 Postnatal care 309  

**PART 7: Manipulating reproduction** 323  
20 Regulating fertility 325  
21 Restoring fertility 340  
22 Society and reproduction 356  

Index 365  

---

**A companion website**

Your textbook is also accompanied by a FREE companion website that contains:  
- Figures from the book in PowerPoint format  
Log on to [www.essentialreproduction.com](http://www.essentialreproduction.com) to find out more.
Preface

There have been many advances in our understanding of the reproductive processes in humans since the sixth edition. Much of this progress has been due to the continuing application to reproductive studies of the expanding range and sensitivity of the techniques of molecular biology, which now allow much more sophisticated descriptions and manipulations of reproductive activities. Advances have also come from the development of live imaging techniques of greater utility. These include imaging of reproductive organs and also of brain function in situ, as well as less invasive long-term imaging of the behaviours of cells and embryos in culture. The advances in medical research on reproduction have been truly spectacular – which, in many parts of this edition, renders potentially dangerous extrapolations from other mammals to humans less necessary.

Major health and social issues continue to place reproduction at the centre of scientific, clinical, political and ethical discourse. The threat posed by the continuing growth in world population to the planet's resources and to our fragile climate presents a major challenge. The tragic and unnecessary high maternal mortality rates throughout much of the world are an indictment of our best efforts and intentions to ‘do better’ – as expressed in the WHO Millennium Aims. At least some progress is being made in managing the effects of infection with human immunodeficiency virus through the cheaper provision of generic drugs. However, it is unclear that transmission rates are coming down, a testament to the importance of understanding sexual behaviours and addressing the impact of gender inequalities. These issues are made more pressing by the rise in genitourinary infections that are resistant to antibiotics with their implications for individual fecundity. Continuing clinical developments in the field of assisted conception have expanded opportunities for the alleviation or circumvention of subfertility, genetic disability and, through stem cells, degenerative disease, but have also ignited new (and old) controversies. The explosion of obesity and the realization that both child and adult health and well-being are affected enduringly by life in utero have focused work on pregnancy, the placenta and the neonatal period of care. Finally, we are at last beginning to understand more fully how genetic expression during development interacts with environmental factors to influence complex behavioural phenotypes that include psychiatric disease and antisocial behaviour. It is clear from all these examples that reproduction reaches into all parts of our lives! Science thus forms just part of this book – albeit at its core. One might have hoped that the advances in scientific knowledge and understanding would helpfully inform prevailing socio-legal discussions, attitudes and values. Sadly, since the last edition, for much of the world, the enlightenment viewpoint based on a cool appraisal of evidence has been crushed in a miasma of antiscience rhetoric: whether against climate change, evolution, women's progress, or rights for sexual minorities.

On a more positive note, I am very happy to formally record here my delight that the Nobel Foundation at last decided to award the 2010 Nobel Prize for Physiology or Medicine to the dedicatee of this book, Professor Sir Bob Edwards. This belated award, followed by a Knighthood in 2011, recognized Bob's unique role in the development of research on human reproduction. Although his award cited his work on IVF, it explicitly recognized the wider role Bob has played in reproductive science, medicine and ethics, together with his pioneering role in communicating science to the public. Sadly, Bob's ill-health prevented him from receiving the prize in person. I was honoured that Bob and his wife and long-term scientific collaborator, Ruth, who received the prize on Bob’s behalf, both invited me to open the Nobel Symposium dedicated to his work. A flavour of his achievements can be gained from the published paper based on that lecture, which is freely available at http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3171154/?tool=pubmed

Finally, for this edition, the book has been totally restructured as well as updated. This restructuring hopefully gives better balance to the contents and a stronger narrative thread to the text. To aid this, in many places, more detailed information on deeper, comparative or applied aspects of some topics has been transferred to boxes, tables and figures. In addition, requests for more specific references have hopefully been met with longer reading lists divided into general and specific references. As before, many helpful comments, corrections and letters of advice have been received from readers, students and teachers all over the world. As always, in this seventh edition, now in its 33rd year, I have tried to provide for students of reproduction a compact and comprehensive text that carves through the micro-detail of the subject to bring out its theoretical cores, but illustrates it with experiment, information and context.

M.H.J.
Cambridge
2012
How to use this book

This book represents an integrated approach to the study of reproduction. There can be few subjects that so obviously demand such an approach. During my teaching of reproduction at Cambridge University, the need for a book of this kind was clear to me and my colleagues. I know this volume goes some way towards filling this need because of the many appreciative comments I receive from colleagues at scientific meetings as well as from the Cambridge students.

I have written the book about human reproduction in a comparative context for medical, veterinary and science students at all professional levels. Throughout, I have attempted to draw out the general, fundamental points common to reproductive events in all or most species. However, a great range of variation in the details of reproduction is observed amongst different species and, in some respects, very fundamental differences are also observed. Where the details differ, I have attempted to indicate this in the numerous tables and figures, rather than clutter the general emphasis and narrative of the text. Where the fundamentals differ, an explicit discussion is given in the text. These fundamental differences should not be ignored. For example, preclinical medical students may consider the control of luteal life in the pig, of parturition in the sheep or of ovarian cyclicity in the rat to be irrelevant to their future interests. However, as a result of extrapolation between species, in the past the human has been treated as a pig, a sheep and a rat (with much discomfort and detriment). If, on finishing this book, the student appreciates the dangers of uncritical extrapolations between species, I will have achieved a major aim.

Science is uncertain and provisional, and this provisionality has been illustrated in several places in this book. I have not tried to give a simple story where a simple story does not exist. Uncertainty can be hard to handle, especially in medicine, but it is a reality that is as important as those informational facts that we think we have certain knowledge of – indeed, knowing the boundary between the certain and the uncertain is perhaps the most important knowledge of all. For you students, this uncertainty also provides future research opportunities!

Confinelements of space have unfortunately necessitated the omission of the subject of embryonic development from the text. To give only passing reference to this fascinating subject would be an injustice; to treat it fully would require a text of similar length to the present one. I recommend that the interested student seeks this information elsewhere.

I suggest that you first read through each chapter with only passing reference to tables, boxes and figures. In this way, I hope that you will grasp the essential fundamentals of the subject under discussion. Then re-read the chapter, referring extensively to the tables and figures and their legends, in which much detailed or comparative information is located. Finally, because my approach to reproduction is an integrated one, the book needs to be taken as a whole, as it is more than the sum of its constituent chapters.
Acknowledgements

I owe particular thanks to many people for help at many stages of the preparation of this edition: to present and former students for their interest, stimulation and responsiveness; to my colleagues at Wiley-Blackwell for their help and advice; to the AudioVisual Media team in the Anatomy School at Cambridge for advice and help with photographic illustrations; to the Histology section of the Department of Physiology, Development and Neuroscience, Cambridge for making available slides for photography; to Professor Peter Braude, Professor Graham Burton, Professor Tomas Hökfelt, J. Moeselaar, Dr Tony Plant, Dr J.M. Tanner and Dr Pauline Yahr for allowing me to use their original photographs and data; and to my many colleagues who read and criticized my drafts and encouraged me in the preparation of this edition.
Features of your textbook

Welcome to the new edition of *Essential Reproduction*. Over the next few pages you will be shown how to make the most of the learning features included in the textbook.

The Anytime, Anywhere Textbook

For the first time, your textbook comes with free access to a **Wiley E-Text: Powered by VitalSource** – a digital, interactive version of this textbook which you own as soon as you download it.

Your **Wiley E-Text: Powered by VitalSource** allows you to:

**Search:** Save time by finding terms and topics instantly in your book, your notes, even your whole library (once you’ve downloaded more textbooks)

**Note and Highlight:** Colour code, highlight and make digital notes right in the text so you can find them quickly and easily

**Organize:** Keep books, notes and class materials organized in folders inside the application

**Share:** Exchange notes and highlights with friends, classmates and study groups

**Upgrade:** Your textbook can be transferred when you need to change or upgrade computers

**Link:** Link directly from the page of your interactive textbook to all of the material contained on the companion website

To access your **Wiley E-Text: Powered by VitalSource**:

- Find the redemption code on the inside front cover of this book and carefully scratch away the top coating of the label.
- Visit [www.vitalsource.com/software/bookshelf/downloads](http://www.vitalsource.com/software/bookshelf/downloads) to download the Bookshelf application.
- If you have purchased this title as an e-book, access to your **Wiley E-Text: Powered by VitalSource** is available with proof of purchase within 90 days. Visit [http://support.wiley.com](http://support.wiley.com) to request a redemption code via the ‘Live Chat’ or ‘Ask A Question’ tabs.
- Open the Bookshelf application on your computer and register for an account.
- Follow the registration process and enter your redemption code to download your digital book.
- For full access instructions, visit: [www.essentialreproduction.com](http://www.essentialreproduction.com).
CourseSmart gives you instant access (via computer or mobile device) to this Wiley-Blackwell eTextbook and its extra electronic functionality, at 40% off the recommended retail print price. See all the benefits at www.coursesmart.com/students.

Instructors . . . receive your own digital desk copies! It also offers instructors an immediate, efficient, and environmentally-friendly way to review this textbook for your course.

For more information visit www.coursesmart.com/instructors. With CourseSmart, you can create lecture notes quickly with copy and paste, and share pages and notes with your students. Access your Wiley CourseSmart digital textbook from your computer or mobile device instantly for evaluation, class preparation, and as a teaching tool in the classroom.

Simply sign in at http://instructors.coursesmart.com/bookshelf to download your Bookshelf and get started. To request your desk copy, hit ‘Request Online Copy’ on your search results or book product page.

A companion website

Your textbook is also accompanied by a FREE companion website that contains:
- Figures from the book in PowerPoint format
Log on to www.essentialreproduction.com to find out more.

Features contained within your textbook

Every chapter ends with a Key learning points box which can be used for both study and revision purposes.

We hope you enjoy using your new textbook. Good luck with your studies!
Part 1
Introduction