

SEVENTH EDITION

Nunn's Applied Respiratory Physiology



Andrew B Lumb

Foreword by: Ronald G Pearl

CHURCHILL
LIVINGSTONE
ELSEVIER

Nunn's
Applied Respiratory Physiology

Commissioning Editor: Timothy Horne
Development Editor: Carole McMurray
Project Manager: Frances Affleck
Designer/Design Direction: Charles Gray
Illustration Manager: Bruce Hogarth
Illustrator: Tim Loughhead/Robin Dean

Nunn's Applied Respiratory Physiology

SEVENTH EDITION

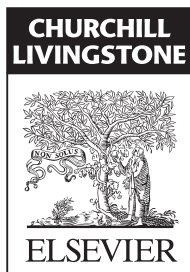
Andrew B Lumb MB BS FRCA

*Consultant Anaesthetist, St James's University Hospital; Senior Clinical Lecturer in Anaesthesia,
University of Leeds, Leeds, UK*

Foreword by

Ronald G Pearl MD PhD

*Dr Richard K and Erika N Richards Professor and Chairman, Department of Anesthesia, Stanford University School of
Medicine, Stanford, CA, USA*



EDINBURGH LONDON NEW YORK OXFORD PHILADELPHIA ST LOUIS SYDNEY TORONTO 2010

CHURCHILL
LIVINGSTONE
ELSEVIER

© 2010 Elsevier Ltd. All rights reserved

No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. Details on how to seek permission, further information about the Publisher's permissions policies and our arrangements with organizations such as the Copyright Clearance Center and the Copyright Licensing Agency, can be found at our website: www.elsevier.com/permissions.

This book and the individual contributions contained in it are protected under copyright by the Publisher (other than as may be noted herein).

First edition 1969
Second edition 1977
Third edition 1987
Fourth edition 1993
Fifth edition 1999
Sixth edition 2005
Seventh edition 2010

ISBN 978 0 7020 2996 7

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library

Library of Congress Cataloging-in-Publication Data

A catalog record for this book is available from the Library of Congress

Notices

Knowledge and best practice in this field are constantly changing. As new research and experience broaden our understanding, changes in research methods, professional practices, or medical treatment may become necessary.

Practitioners and researchers must always rely on their own experience and knowledge in evaluating and using any information, methods, compounds, or experiments described herein. In using such information or methods they should be mindful of their own safety and the safety of others, including parties for whom they have a professional responsibility.

With respect to any drug or pharmaceutical products identified, readers are advised to check the most current information provided (i) on procedures featured or (ii) by the manufacturer of each product to be administered, to verify the recommended dose or formula, the method and duration of administration, and contraindications. It is the responsibility of practitioners, relying on their own experience and knowledge of their patients, to make diagnoses, to determine dosages and the best treatment for each individual patient, and to take all appropriate safety precautions.

To the fullest extent of the law, neither the Publisher nor the authors, contributors, or editors, assume any liability for any injury and/or damage to persons or property as a matter of products liability, negligence or otherwise, or from any use or operation of any methods, products, instructions, or ideas contained in the material herein.

ELSEVIER

your source for books,
journals and multimedia
in the health sciences

www.elsevierhealth.com

Working together to grow
libraries in developing countries

www.elsevier.com | www.bookaid.org | www.sabre.org

ELSEVIER

BOOK AID
International

Sabre Foundation

The
Publisher's
policy is to use
paper manufactured
from sustainable forests

Contents

Foreword ix
Preface xi

PART 1 BASIC PRINCIPLES 1

1. **The atmosphere 3**
 - Evolution of the atmosphere 3
 - The greenhouse effect 9
 - Turnover rates of atmospheric gases 10
 - Oxygen, ozone and ultraviolet screening 11
 - Evolution and adaptation 11
2. **Functional anatomy of the respiratory tract 13**
 - Mouth, nose and pharynx 13
 - The larynx 15
 - The tracheobronchial tree 16
 - The alveoli 20
 - Alveolar cell types 22
 - The pulmonary vasculature 23
3. **Elastic forces and lung volumes 27**
 - Elastic recoil of the lungs 28
 - Elastic recoil of the thoracic cage 35
 - Pressure/volume relationships of the lung plus thoracic cage 36
 - Lung volumes 36
 - Principles of measurement of compliance 37
 - Principles of measurement of lung volumes 40
4. **Respiratory system resistance 43**
 - Physical principles of gas flow and resistance 43
 - Respiratory system resistance 46
 - Factors affecting respiratory resistance 47
 - Muscular control of airway diameter 49
 - Drug effects on airway smooth muscle 51
 - Compensation for increased resistance to breathing 54
 - Principles of measurement of respiratory resistance and closing capacity 55
5. **Control of breathing 61**
 - The origin of the respiratory rhythm 61
 - Central nervous system connections to the respiratory centre 65
 - Peripheral input to the respiratory centre and non-chemical reflexes 66
 - The influence of carbon dioxide on respiratory control 68
 - The influence of oxygen on respiratory control 71
 - Integration of the chemical control of breathing 75
 - Periodic breathing 76
 - Breath holding 76
 - Drug effects on the control of breathing 76
 - Methods for assessment of breathing control 78
6. **Pulmonary ventilation 83**
 - Upper airway muscles 83
 - Respiratory muscles of the trunk 84
 - Integration of respiratory muscle activity 86
 - Neuronal control of respiratory muscles 89
 - Respiratory muscle fatigue and disuse 91
 - The work of breathing 92
 - Measurement of ventilation 94
 - Measurement of ventilatory capacity 96
 - Assessment of the respiratory muscles 97
7. **The pulmonary circulation 99**
 - Pulmonary blood flow 99
 - Pulmonary blood volume 100
 - Pulmonary vascular pressures 101

- Pulmonary vascular resistance 102
 - Passive changes in pulmonary vascular resistance 103
 - Active control of pulmonary vascular resistance 106
 - Drug effects on the pulmonary circulation 111
 - Principles of measurement of the pulmonary circulation 112
 - 8. Distribution of pulmonary ventilation and perfusion 119**
 - Distribution of ventilation 119
 - Distribution of perfusion 123
 - Ventilation in relation to perfusion 125
 - Dead space 128
 - Venous admixture or shunt 132
 - The effect of scatter of \dot{V}/\dot{Q} ratios on arterial P_{O_2} 136
 - Principles of assessment of distribution of ventilation and pulmonary blood flow 137
 - 9. Diffusion of respiratory gases 145**
 - Fundamentals of the diffusion process 145
 - Diffusion of oxygen in the lungs 147
 - Diffusion of carbon dioxide in the lungs 151
 - Diffusion of carbon monoxide in the lungs 151
 - Factors affecting 'diffusing capacity' 153
 - Diffusion of gases in the tissues 155
 - Principles of measurement of carbon monoxide diffusing capacity 156
 - 10. Carbon dioxide 159**
 - Carriage of carbon dioxide in blood 159
 - Carbamino carriage 162
 - Factors influencing the carbon dioxide tension in the steady state 166
 - Carbon dioxide stores and the unsteady state 170
 - Apnoea 171
 - Carbon dioxide carriage during hypothermia 172
 - Outline of methods of measurement of carbon dioxide 173
 - 11. Oxygen 179**
 - The oxygen cascade 179
 - The carriage of oxygen in the blood 187
 - The role of oxygen in the cell 197
 - Transport of oxygen from the lungs to the cell 202
 - Oxygen stores 205
 - Control of the inspired oxygen concentration 206
 - Cyanosis 207
 - Principles of measurement of oxygen levels 208
 - Measurement of oxygen consumption and delivery 211
 - 12. Non-respiratory functions of the lung 217**
 - Filtration 217
 - Defence against inhaled substances 218
 - Processing of endogenous compounds by the pulmonary vasculature 222
 - Pharmacokinetics and the lung 225
 - The endocrine lung 226
 - 13. The history of respiratory physiology 229**
 - Ancient civilizations 229
 - The Renaissance 232
 - Experimental physiology in the 17th century 235
 - Chemistry and respiration 238
 - Early development of current ideas of respiratory physiology 240
- PART 2 APPLIED PHYSIOLOGY 247**
- 14. Pregnancy, neonates and children 249**
 - Respiratory function in pregnancy 249
 - The lungs before birth 250
 - Events at birth 251
 - Neonatal lung function 253
 - Premature birth and the lungs 255
 - Sudden infant death syndrome (SIDS) 256
 - Development of lung function during childhood 257
 - 15. Exercise 261**
 - Oxygen consumption during exercise 261
 - Anaerobic metabolism 264
 - The ventilatory response to exercise 265
 - Fitness and training 266
 - 16. Sleep 269**
 - Normal sleep 269
 - Sleep-disordered breathing 271
 - 17. High altitude and flying 279**
 - Respiratory system responses to altitude 280
 - Altitude illness 286
 - Flying 287
 - The respiratory system of birds 289
 - 18. High pressure and diving 293**
 - Exchange of oxygen and carbon dioxide 293

- Effects attributable to the composition of the inspired gas 296
 Types of diving activity and their respiratory effects 297
 Respiratory aspects of decompression illness 299
19. Respiration in closed environments and space 303
 Closed-system anaesthesia 303
 Submarines 304
 Space 305
 Microgravity 308
 Biospheres 309
20. Drowning 313
 Physiology of immersion 313
 Physiological mechanisms of drowning 314
 The role of hypothermia 315
 Principles of therapy for near-drowning 315
21. Smoking and air pollution 317
 Tobacco smoke 317
 Mechanisms of smoking related lung damage 320
 Air pollution 321
22. Anaesthesia 327
 Control of breathing 327
 Pattern of contraction of respiratory muscles 331
 Change in functional residual capacity 333
 Atelectasis during anaesthesia 334
 Respiratory mechanics 337
 Gas exchange 340
 Other effects of general anaesthesia on the respiratory system 345
 Special conditions arising during anaesthesia 346
 Regional anaesthesia 347
 Respiratory function in the postoperative period 348
23. Changes in the carbon dioxide partial pressure 355
 Causes of hypocapnia 355
 Causes of hypercapnia 356
 Effects of carbon dioxide on the nervous system 356
 Effects on other physiological systems 358
 Hypercapnia in clinical practice 360
24. Hypoxia 363
 Biochemical changes in hypoxia 363
 Mechanisms of hypoxic cell damage 365
 P_{O_2} levels at which hypoxia occurs 367
 Effects of hypoxia 368
25. Anaemia 371
 Pulmonary function 371
 Oxygen delivery 372
 Anaemia and exercise 374
 What is the optimal haemoglobin concentration in the clinical setting? 375
26. Hyperoxia and oxygen toxicity 377
 Hyperoxia at normal atmospheric pressure 378
 Hyperbaric oxygenation 379
 Oxygen toxicity 380
 Defences against reactive oxygen species 385

PART 3 PHYSIOLOGY OF PULMONARY DISEASE 391

27. Ventilatory failure 393
 Pattern of changes in arterial blood gas tensions 393
 Causes of ventilatory failure 394
 Relationship between ventilatory capacity and ventilatory failure 397
 Breathlessness 398
 Principles of therapy for ventilatory failure 399
28. Airways disease 403
 Asthma 403
 Chronic obstructive pulmonary disease 409
 Cystic fibrosis 412
 Assessment of airway disease by exhaled breath analysis 414
29. Pulmonary vascular disease 419
 Pulmonary oedema 419
 Pulmonary embolism 425
 Pulmonary hypertension 428
 Hepatopulmonary syndrome (HPS) 429
30. Diseases of the lung parenchyma and pleura 431
 Pulmonary collapse 431
 Pulmonary consolidation (pneumonia) 434
 Interstitial lung disease and pulmonary fibrosis 435
 Lung cancer 438
 Pleural disease 444
31. Acute lung injury 451
 Clinical aspects of acute lung injury 451
 Mechanisms of acute lung injury 454
 Principles of therapy 456

32. Respiratory support and artificial ventilation	463
Non-invasive ventilation	463
Intermittent positive pressure ventilation (IPPV)	465
Clinical use of IPPV	470
Positive end-expiratory pressure	475
Physiological effects of positive pressure ventilation	477
Ventilator-associated lung injury	481
Artificial ventilation for resuscitation	483
Extrapulmonary gas exchange	484
33. Pulmonary surgery	491
Physiological aspects of common interventions	491
One-lung ventilation	497
Lung transplantation	502
Appendix A Physical quantities and units of measurement	511
Appendix B The gas laws	515
Appendix C Conversion factors for gas volumes	517
Appendix D Symbols and abbreviations	519
Appendix E Mathematical functions relevant to respiratory physiology	521
Index	529

Foreword

It is a great honor to write the foreword for the seventh edition of *Nunn's Applied Respiratory Physiology*. Since publication of the first edition in 1969, *Nunn's Applied Respiratory Physiology* has been the classic textbook on this critical subject. The challenge for any textbook on respiratory physiology has been to present the information in a manner which provides for the changing needs of the reader throughout his or her career. The beginning student often learns respiratory physiology from the mathematical analysis of gas exchange; the more advanced student may be interested in the underlying cellular and molecular mechanisms; and the clinician needs to understand the impact of altered respiratory physiology on specific disease states. The ideal textbook therefore has the daunting challenge of providing a comprehensive but easily understood approach for all three readers. Despite the rapid evolution of knowledge in this field, *Nunn's Applied Respiratory Physiology* has accomplished this task throughout the past four decades. In this age of multi-authored contributions, it is a tribute to Andrew Lumb that he has been the sole author for the past three editions (with the exception of the first chapter on the atmosphere which continues to be written by Dr. Nunn). The cohesion inherent in a single-authored textbook allows for internal consistency so that interrelated concepts can be readily appreciated by the reader. In addition, a single-authored textbook avoids duplication of material, so that a vast topic is comprehensively covered in just over 500 pages.

This seventh edition maintains the tradition of presenting respiratory physiology in a manner which can be readily understood by students, clinicians and investigators. The book continues the three part approach which was first adopted in the fifth edition. The first section on basic principles covers anatomy, mechanics, control of breathing, ventilation, circulation, ventilation-perfusion matching, diffusion, carbon dioxide, oxygen, and non-respiratory functions of the lung. Although the basic concepts have not changed, the content has been updated with recent advances such as alternative models to explain lung recoil and expanded sections on tissue oxygen and on airway lining fluid and ciliary activity. The second section on applied physiology discusses the effects of pregnancy, exercise, sleep, altitude, pressure, drowning, smoking, anesthesia, hypocapnia, hypercarbia, hypoxia, hyperoxia, and anemia. The third part on physiology of pulmonary disease discusses specific clinical disorders (ventilatory failure, airways disease, pulmonary vascular disease, parenchymal lung disease, acute lung injury), ventilatory support, and pulmonary surgery. These chapters have been extensively updated as new information has entered the literature in areas such as pulmonary hypertension and management of patients with acute respiratory failure. Valuable changes which were made in the last edition have been continued, including double column pages, color figures, and the key points section of each chapter.

For more than four decades, *Nunn's Applied Respiratory Physiology* has been the standard text for understanding this challenging but critical subject. I congratulate Dr. Lumb on continuing this tradition with a superb seventh edition which deserves

its place on the bookshelves of students, researchers, and clinicians interested in understanding normal respiratory physiology and in treating patients with respiratory disorders.

Ronald G Pearl
Stanford
2010

Preface to the seventh edition

Over the past 41 years *Nunn's Applied Respiratory Physiology* has developed into a renowned textbook on respiration, providing both physiologists and clinicians with a unique fusion of underlying principles and their applications. With Dr John Nunn's retirement in 1991 a new author was required, and, as Dr Nunn's final research fellow in the Clinical Research Centre in Harrow, I was honoured to be chosen as his successor. As a practising clinician with a fascination for physiology and an interest in medical education, the seventh edition has again focussed on combining a clear, logical and comprehensive account of basic respiratory physiology with a wide range of applications, both physiological and clinical. This approach acknowledges the popularity of the book among doctors from many medical specialties and will hopefully provide readers with a scientific background with an even greater insight into the applications of respiratory physiology. Clinical chapters in Part 3 of the book are not intended to be comprehensive reviews of the pulmonary diseases considered, but in each case they provide a detailed description of the physiological changes that occur, accompanied by a brief account of the clinical features and treatment of the disease.

Key references are identified by an asterisk in the reference list following each chapter. These references are highlighted because they either provide outstanding recent reviews of their subject or describe research that has had a major impact on the topic under consideration.

Advances in respiratory physiology since the last edition are too numerous to mention individually. Clarification of some fundamental concepts has been provided, e.g. the definitions of oxygen saturation

and haemoglobin oxygen carrying capacity (Hufners constant). Other new topics include the contribution of airway lining fluid to lung defence mechanisms, the biphasic nature of hypoxic pulmonary vasoconstriction, and a new look at tissue oxygen diffusion patterns based on work done by Krogh more than 100 years ago that identifies tissue regions where hypoxia is most likely to occur, referred to as the 'lethal corner'.

New topics for Part 3 of the seventh edition include pleural diseases and lung cancer. Pneumothorax and pleural effusions occur in many different clinical specialties, and the physiology and pathophysiology of the pleural space is now included in Chapter 30. Whilst many, sometimes rare, lung diseases have been covered in Part 3 for years, lung cancer has been a significant omission. Lung cancer remains common, is mostly preventable by avoiding tobacco smoke and environmental radon, and, relative to many other cancers, remains difficult to treat due to its usually late presentation. A detailed description of how lung cancer develops from a molecular level to its clinical presentation is now included in Chapter 30, along with a brief account of its treatment.

Pulmonary surgery (Chapter 33) is new for the seventh edition. Although surgery of the lungs and pleura is only performed in specialised hospitals, the prevalence of smoking worldwide means that these operations, a majority of which are for cancer treatment, will remain common for some decades yet. Thoracic surgery procedures are also evolving, with less invasive techniques for accessing the lungs and pleura slowly replacing the trauma of a thoracotomy. Safe and successful use of these techniques

relies on all staff involved having a thorough understanding of the physiological changes that occur.

I wish to personally thank the many people who have helped with the preparation of the book, including the numerous colleagues who have encouraged and assisted my acquisition of knowledge in subjects not so close to my own areas of expertise. I am indebted to Professor Pearl for his kind words in the Foreword, and would like to thank Professor Hedenstierna for providing the excellent CT scans in Figure 33.3. I remain especially indebted to Dr Nunn for his continued support of the book and its author, and would like to thank him for once again providing an excellent Chapter 1 on the origins of Earth's atmosphere. His

statement that 'Fossil fuels were buried over the course of 350 million years, and probably all that is recoverable will be burned in 300' is thought provoking. Last, but by no means least, I would like to thank Lorraine, Emma and Jenny for again tolerating a preoccupied and reclusive husband/father for so long. Jenny, when aged 5, often enquired about my activities in the study, until one evening she nicely summarised my years of work by confidently informing me that 'if you don't breathe, you die'. So what were the other 527 pages about?

Andrew Lumb
Leeds 2010

PART 1

Basic principles

This page intentionally left blank

Chapter 1

The atmosphere

John F Nunn

KEY POINTS

- The mass of the Earth and its distance from the sun provide optimal conditions of gravity and temperature for long-term liquid surface water and the retention in its atmosphere of oxygen, nitrogen and carbon dioxide.
- Primitive life-forms generated energy by photosynthetic reactions, producing oxygen, and so facilitating the development of an oxygen-containing atmosphere and aerobic organisms.
- Carbon dioxide was initially the main component of the Earth's atmosphere, but by 300 million years ago rock weathering and photosynthesis had reduced its concentration to current low levels.
- There is now an acceptance that human activity is causing an increase in atmospheric carbon dioxide, unprecedented in the last 40 million years.

The atmosphere of Earth is radically different from that of any other planet in the solar system (Table 1.1) and may well be rare on planets of other stars in the universe as a whole. The unique character of our atmosphere is because of two main reasons. First, temperature has permitted the existence of liquid surface water for at least 3800 million years (Ma), and this has resulted in weathering of silicate rocks, reducing the concentration of carbon dioxide far below the levels still pertaining in the rocky planets Venus and Mars. Secondly, the existence of liquid surface water enabled living organisms to appear at a very early stage: life forms then evolved to undertake oxygenic photosynthesis. When oxygen sinks were saturated, oxygen appeared in the atmosphere and some organisms

began to utilise highly efficient oxidative metabolic pathways. An atmosphere containing oxygen is in inorganic chemical disequilibrium, and is an indication of the existence of life.

EVOLUTION OF THE ATMOSPHERE

FORMATION OF THE EARTH AND THE PRE-BIOTIC ATMOSPHERE

The earth was formed by a relatively short lived, but intense, gravitational accretion of rather large planetesimals, orbiting the newly formed sun some 4560 Ma ago. The kinetic energy of the impacting bodies was sufficient to raise the temperature to a few thousand degrees Celsius. This would have melted the entire Earth, resulting in loss of the primary atmosphere.

Earth cooled rapidly by radiation when the initial bombardment abated, and the very high temperature (Hadean) phase is not thought to have lasted longer than a few hundred Ma. The crust solidified, but massive outgassing continued, resulting in an atmosphere mainly comprising carbon dioxide and steam (Table 1.2) as probably occurred on Venus and Mars.^{1,2} In the case of Earth, the water vapour condensed to surface water, and there is good evidence that oceans existed about 3800 Ma ago and perhaps even earlier.³ Once Earth's crust was cool, and surface water was in existence, it was possible for comets and meteorites to leave a secondary veneer of their contents, including water and a wide range of organic compounds.⁴

Important physico-chemical changes occurred in the early secondary atmosphere. Helium and

PLANET	ATMOSPHERE		
Mercury	Extremely tenuous		
Venus	Carbon dioxide	96.5%	+ Traces: Argon, Helium, Neon,
	Nitrogen	3.5%	Krypton (all < 20 ppmv)
Earth	Nitrogen	78.08%	Water vapour – variable
	Oxygen	20.95%	Neon 18.2 ppmv
	Argon	0.93%	Helium 5.2 ppmv
	Carbon dioxide	0.039%	Methane 1.8 ppmv
Mars	Carbon dioxide	95.3%	Oxygen 0.13 %
	Nitrogen	2.7%	Carbon monoxide 0.27 %
	Argon	1.6%	+ traces: Neon, Krypton, Xenon
Jupiter	Hydrogen	89%	Methane 1750 ppmv
	Helium	11%	+ Traces: Ammonia, Water vapour etc.
Saturn	Hydrogen	94%	Methane 4500 ppmv
	Helium	6%	+ Traces: Ethylene, Phosphine

ppmv, parts per million volume.
 Earth's data for carbon dioxide has been updated (see text).
 (Planetary data are from Taylor,¹ reproduced from Nunn² by permission of the Geologists' Association.)

Table 1.2 Average composition of gas evolved from Hawaiian volcanoes

CONSTITUENT	PERCENT
Water vapour	70.75
Carbon dioxide	14.07
Sulphur dioxide	6.40
Nitrogen	5.45
Sulphur trioxide	1.92
Carbon monoxide	0.40
Hydrogen	0.33
Argon	0.18
Sulphur	0.10
Chlorine	0.05

(Data are from reference 5, reproduced from reference 2 by permission of the Geologists' Association.)

hydrogen tended to be lost from the Earth's gravitational field. Ammonia dissociated to nitrogen and hydrogen, the former retained and the latter lost from the atmosphere. Some carbon dioxide might have been reduced by hydrogen to form traces of methane, but very large quantities slowly reacted with surface silicates to become trapped as carbonates, while forming silica (weathering). Traces of water vapour underwent photodissociation to

hydrogen and oxygen. However, oxygen from this source was present in only minimal quantities, and the early atmosphere is no longer thought to have been as strongly reducing as was formerly believed.⁶

The initial very high partial pressure of carbon dioxide, and probably some methane, would have provided a powerful greenhouse effect to offset the early minimal weak solar radiation, which was some 30% less than today (Figure 1.1). However, the Sun commenced its main sequence of thermonuclear fusion of hydrogen to helium about 3000 Ma ago. Since then solar radiation has been increasing steadily as the Sun proceeds remorselessly towards becoming a red giant, which will ultimately envelop the inner planets. It is fortunate that increasing solar radiation has been approximately offset by a diminishing greenhouse effect, due mainly to decreasing levels of carbon dioxide (see below). As a result, Earth's temperature has remained relatively stable, permitting the existence of surface water for the last 3800 Ma.

SIGNIFICANCE OF MASS OF EARTH AND DISTANCE FROM SUN

Small bodies, such as Mercury and most of the planets' satellites, have a gravitational field which is too weak for the retention of any significant

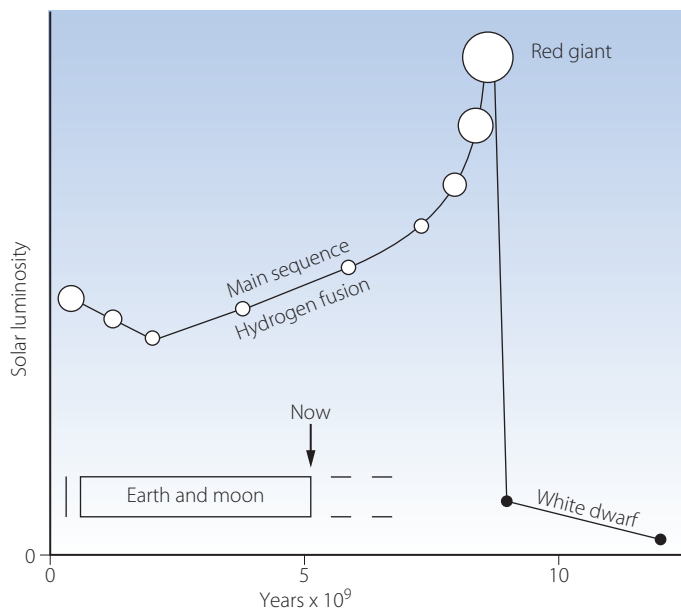


Fig. 1.1 Solar luminosity plotted against the age of the Sun, with the open circles giving a qualitative impression of the diameter of the Sun. Superimposed is an indication of the life of the Earth and Moon, which is now about half way through the main sequence of the Sun deriving its energy from hydrogen fusion to helium. The times can only be very approximate. (After reference 7 with kind permission of Springer Link and Business Media.)

atmosphere (Figure 1.2). The gas-giants (Jupiter, Saturn, Uranus and Neptune) have a gravitational field which is sufficiently strong to retain all gases, including helium and hydrogen, thereby ensuring the retention of a reducing atmosphere. The gravitational field of the Earth is intermediate, resulting in a differential retention of the heavier gases (oxygen, carbon dioxide and nitrogen), while permitting the escape of hydrogen and helium. This is essential for the development of an oxidising atmosphere and life as we know it. Water vapour (molecular weight only 18) would be lost from the atmosphere were it not for the cold trap at the tropopause.

Surface temperature of a planetary body is crucial for the existence of liquid water, which is essential for life and therefore the composition of our atmosphere. To a first approximation, temperature is dependent on the distance of a planet from the Sun, and the intensity of solar radiation (Figure 1.2). The major secondary factor is the greenhouse effect of any atmosphere which the planet may possess. Mercury and Venus have surface temperatures far above the boiling point of water. All planets (and their satellites) which are further away from the Sun than Earth have a surface temperature too cold for

liquid water to exist today. However, there is now evidence that Mars had liquid surface water in the past,⁸ now present only as ice.⁹

Earth is the only planet in the solar system which has both a mass permitting retention of an oxidising atmosphere, and a distance from the Sun at which the temperature permits liquid water to exist on its surface. It is difficult to see how there could be life as we know it anywhere in the solar system outside the small parallelogram in Figure 1.2. However, an environment similar to that of the earth may well exist on some planets of the 10^{22} other sun-like stars in the universe.

ORIGIN OF LIFE AND THE DEVELOPMENT OF PHOTOSYNTHESIS

Amino acids and a wide range of organic compounds are found in a type of meteorite known as carbonaceous chondrites.⁴ Therefore, whether or not such compounds were actually synthesised on the early Earth, as Stanley Miller had proposed,⁶ it is highly likely that a wide range of organic compounds were available on the pre-biotic Earth when liquid oceans were formed.

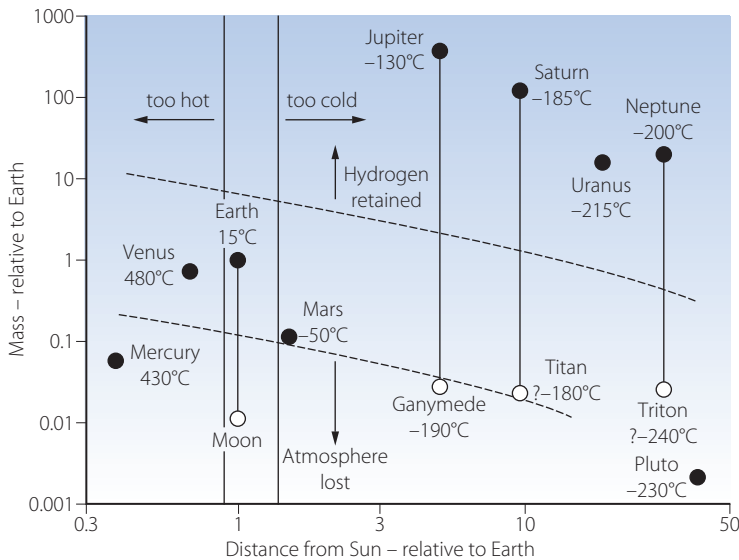


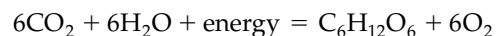
Fig. 1.2 The planets and some of their larger satellites, plotted according to distance from the Sun (abscissa), and mass (ordinate), both scales being logarithmic and relative to Earth. Mean surface temperatures are shown. Potential for life as we know it exists only within the parallelogram surrounding the Earth.

It is less easy to explain the next stage in the evolution of life. An essential feature of all life is the synthesis of proteins using a ribonucleic acid (RNA) template, usually transcribed from the genetic code carried on deoxyribonucleic acid (DNA). There would appear to have been a classical 'chicken and egg' situation. Useful proteins could not be formed without the appropriate sequences in RNA or DNA: RNA and DNA could not be polymerised without appropriate enzymes which are normally proteins. Nevertheless, life did appear, perhaps in the first instance with the genetic code carried only on RNA, or even the much simpler peptide nucleic acid (PNA).¹⁰

An essential requirement for life is the availability of bio-usable forms of energy. The forms of available energy and their location at the dawn of life remain a mystery. However, one cannot ignore the possibility of hydrothermal vents, such as the black smokers along the mid-ocean ridges at great depths, which still support very simple life forms on the basis of chemoautotrophy. They are totally independent of sunlight, and exploit the profound chemical disequilibrium between the emerging hot, reducing and acid water, containing hydrogen sulphide, methane, ammonia, phosphorus and a range of metals, and the surrounding sea water.¹¹ It is likely that there have been hydrothermal vents

on Earth for as long as surface water has coexisted with volcanic activity. Chemoautotrophs might, therefore, have appeared as early as 3800 Ma ago.

Hydrothermal vents provide an extremely constrained and hazardous environment for life, dependent on the continued existence of the energy supply. A much more attractive alternative was to utilise the limitless availability of energy in the form of solar visible light. The most familiar of such reactions is the oxygenic photosynthesis of glucose summarised as follows:



The biochemical adaptation from thermal detection in hydrothermal vents to photosynthesis does not seem to have been insuperable,¹² and it was thought that photosynthesising cyanobacteria (blue-green algae) may have existed 2700 Ma ago.¹³ However, it has recently been suggested that this crucial development may have occurred later, closer to 2400 Ma ago when oxygen first appeared in the atmosphere.¹⁴ At a later date, cyanobacteria underwent symbiotic incorporation into the cells of certain eukaryotes to become chloroplasts, which then conferred the biochemical benefits of photosynthesis on their hosts, which include all plants.

THE APPEARANCE OF OXYGEN IN THE ATMOSPHERE

Oxygenic photosynthesis releases oxygen, apparently as a waste product. Initially it accumulated in the surface waters of the oceans, where it oxidised soluble ferrous iron (Fe^{2+}), leached from basalt, which was then deposited as insoluble ferric iron oxide (Fe^{3+}) in the vast so-called banded iron formations. This process prevented concentrations of oxygen in the atmosphere reaching 10^{-5} bar until about 2320 Ma ago.¹⁵ After the atmosphere attained a higher but critical level of oxygen about 1800 Ma ago, banded iron formations seldom appeared, and iron was thereafter deposited in red (ferric) beds.²

Oxygen continued to accumulate in the oceans and atmosphere, probably reaching a peak of 25–35% of an atmosphere 300 Ma ago¹⁶ (Figure 1.3). It then decreased to about 14%, contributing to the end-Permian mass extinction at the end of the Palaeozoic Era, about 250 Ma ago.² Thereafter it rose slightly above the present atmospheric level for about 100 Ma.

BIOLOGICAL CONSEQUENCES OF AN OXIDISING ENVIRONMENT

It seems likely that the appearance of molecular oxygen in their environment would have been unwelcome to anaerobic organisms. Chapter 26 describes the toxicity of oxygen and its derived free radicals, against which primitive anaerobes would probably have had no defences. Three lines of response can be identified. Some anaerobes sought an anaerobic micro-environment in which to remain and survive. Others developed defences in depth against oxygen and its derived reactive species (page 385). The best response was the development of aerobic metabolism, which gave enormous energetic advantages over organisms relying on anaerobic metabolism (page 200). This required the symbiotic incorporation of purple bacteria which became mitochondria, and the increased availability of biological energy was essential for the evolution of all forms of life more complex than micro-organisms.

Photosynthesis and aerobic metabolism eventually established a cycle of energy exchange between plants and animals, with its ultimate energy input in the form of solar visible light, which was interrupted only under exceptional circumstances. Such circumstances included major meteor strikes and exceptional volcanic activity, both of which can throw vast

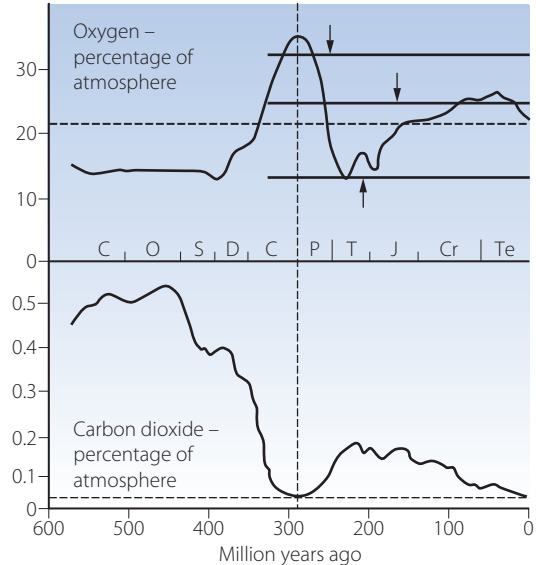


Fig. 1.3 Long-term changes in oxygen and carbon dioxide concentrations during the last 600 Ma. Broken horizontal lines show present atmospheric levels. The vertical broken line shows the Carboniferous/Permian boundary. The continuous horizontal lines with arrows show some oxygen limits suggested by the geological record of forest fires.² Geological periods shown by their capital letters are: Cambrian, Ordovician, Silurian, Devonian, Carboniferous and Permian (Palaeozoic Era), and Triassic, Jurassic, Cretaceous (Mesozoic Era) and Tertiary. Recent research suggests levels of carbon dioxide may be slightly less than shown, but the nature of the changes is not in doubt. (From Nunn,² reproduced by permission of the Geologists' Association).

quantities of persistent dust into the atmosphere and cause extinctions by blocking photosynthesis.

CHANGES IN CARBON DIOXIDE LEVELS

After the major outgassing phase of the newly formed earth, the concentration of carbon dioxide in the atmosphere probably exceeded 90% of an atmosphere.¹⁷ It declined rapidly, due to weathering ($\text{CO}_2 + \text{CaSiO}_3 \rightarrow \text{SiO}_2 + \text{CaCO}_3$) and photosynthesis, reaching about 0.5% at the time of the beginning of the overt fossil record, the Palaeozoic Era, from 570 Ma ago (Figure 1.3). A secondary major decline to near the present atmospheric level occurred during the Carboniferous Period, when the coal-forming forests involved photosynthesis and carbon burial on a massive scale. A sharp increase occurred at the end of the Permian Period (the last Period of the Palaeozoic Era) about 250 Ma

ago, and carbon dioxide may have contributed to the end-Permian mass extinction. This coincided with the decrease in oxygen concentration mentioned above. Carbon dioxide concentrations rose to about 0.2% of an atmosphere just before 200 Ma ago, and then declined until about 20 Ma ago, when it entered a range of the order of 180–300 parts per million, volume (ppmv), which was not seriously exceeded until the last few decades.¹⁸

CARBON DIOXIDE AND THE ICE AGES

Carbon dioxide is a greenhouse gas, with a doubling of atmospheric concentration causing an increase in global average surface temperature '... likely to be in the range 2 to 4.5°C ... values substantially higher than 4.5°C cannot be excluded.'¹⁹ DeConto cites the carbon dioxide threshold for Antarctic glaciation as 750 ppmv and for the northern hemisphere as 280 ppmv.¹⁸ However, there is also a periodicity in solar insolation (Milankovitch cycles) which initiates glacial and interglacial cycles. For the last 500 ka, the dominant cycle has been the degree of ellipticity of the Earth's orbit, with a periodicity of about 100 ka,

and its effect is very clear in the mean global temperature record for the last 420 ka derived from Antarctic ice cores (Figure 1.4).²⁰

Figure 1.4 also shows a remarkably close correlation between temperature and the atmospheric concentration of carbon dioxide. Detailed analysis of time relations shows that the start of end-glacial warming usually preceded the start of the increase in carbon dioxide by a few thousand years. The initial warming released carbon dioxide from stores and then the increased carbon dioxide concentration provided powerful positive feed-back to temperature. The resultant warming is far greater than can be accounted for simply by the change in insolation.

Casual inspection of Figure 1.4 suggests that the next glacial period is overdue. However, it appears that the rhythmic changes in global mean temperature shown for the last 420 ka will not continue, as we now enter a long phase when the Earth's orbit will remain almost circular. The 100 ka cycle will be in virtual abeyance for about 50 ka, during which there will be a prolonged interglacial.²² However, it is highly unlikely that mean global temperature will

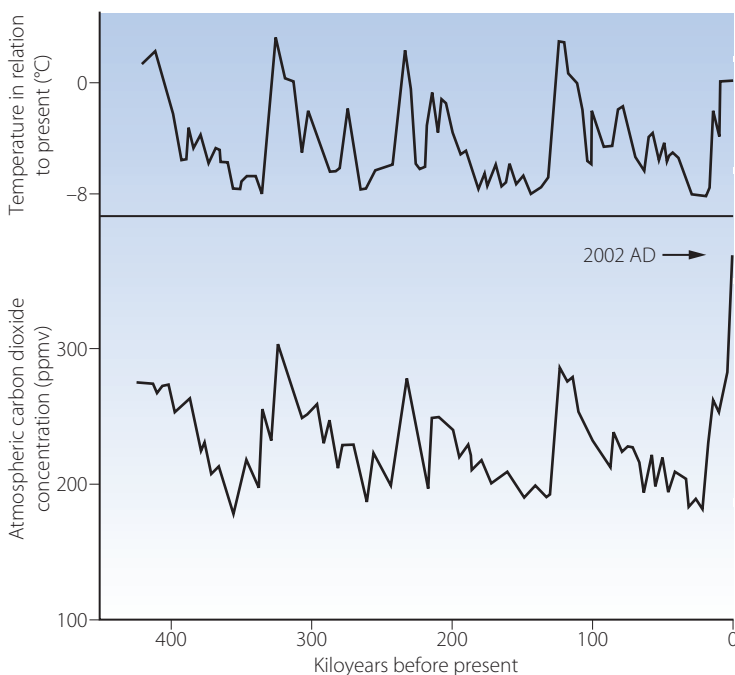


Fig. 1.4 General trends for temperature and atmospheric carbon dioxide concentration, obtained from ice cores from Vostok, Antarctica, for the last 420 000 years. In 2009 the atmospheric carbon dioxide concentration is expected to reach 387 ppmv (see Table 1.3). (Data from Petit et al.²⁰ and reproduced in part from reference 21, with the permission of the Editor of the Optimum Population Trust Journal.)

remain constant, due to the current increase in the atmospheric carbon dioxide concentration, unprecedented in the last 20 Ma.

RECENT CHANGES IN CARBON DIOXIDE LEVELS

Atmospheric carbon dioxide remained close to 280 ppmv from the beginning of the current interglacial until the start of the industrial revolution (AD 1750). In the next 200 years it increased to 310 ppmv which averaged 0.155 ppmv/yr (Table 1.3). The annual rate of increase rose progressively and, from AD 2000 to 2009, reached 1.89 ppmv/yr, which is nearly 200 times the rate during the rapid rewarming after the last glacial period (Figure 1.4).

On this basis, extrapolation of trends from AD 1750 to the present suggests that the concentration might reach 1000 ppmv by the year AD 2100. This prediction is similar to computed predictions based on analysis of the many primary factors governing atmospheric CO₂ concentrations.²³ Thus we may expect to reach the highest concentration since 24 Ma ago, and above the threshold for Antarctic glaciations.¹⁸ Whether the rate of change continues its present exponential course is critically dependent on the continued efficiency of the global carbon sinks, and attempts to control emissions with all its current political uncertainty. The only certain limitation on emissions would seem to be exhaustion of the world's fossil fuels. Global warming may have disturbing short term effects on ocean currents, particularly a weakening of the north Atlantic conveyor (including the Gulf Stream).²⁴ This could result in a substantial cooling of north-western Europe.

Table 1.3 Recent changes in atmospheric carbon dioxide concentrations

DATE	ATMOSPHERIC CO ₂		RATE OF CHANGE
	MASS IN Gt	ppmv	ppmv PER YEAR
18 ka ago	420	200	
10 ka ago	588	280	0.01
1750 AD	588	280	0
1950 AD	651	310	0.15
2000 AD	777	370	1.20
2009 AD	813	387	1.89

Gt, gigatonne; ka, thousand years; ppmv, parts per million, volume. Data are from various sources. (Reproduced from Nunn² by permission of the Geologists' Association) and most recently from Mauna Loa directly.

THE GREENHOUSE EFFECT

The balance of heat gain from solar radiation is the difference between incoming radiation, mainly in the visible wave lengths, and outgoing radiation which is largely infra-red. The latter is partially trapped in the troposphere, mainly by water vapour (60%) and carbon dioxide (25%). Atmospheric water vapour concentration increases with rising global temperature and therefore provides positive feed-back to global warming. It is estimated that the present greenhouse effect raises the mean surface temperature of the Earth by some 30°C. Carbon dioxide makes a major contribution to the very high surface temperature of Venus (480°C), hotter than Mercury but further from the Sun.

OTHER GREENHOUSE GASES

There are no infra-red absorption bands for water vapour and carbon dioxide between 7 and 13 μm wavelength, and heat loss in this band is considerable. It follows that any gas or vapour with strong infra-red absorption in this range will have a disproportionate greenhouse effect. Such a gas could be considered not so much as thickening the panes in the greenhouse as replacing a missing pane.

After water and carbon dioxide, the most important greenhouse gases are ozone (8% of total effect) and methane (3% of total effect) which is present in the atmosphere at a concentration of only 2 ppmv, but rapidly increasing: it absorbs infra-red some 25 times as effectively as carbon dioxide. Dissolved methane is currently escaping from lakes in the melting tundra, but of greater concern is the vast quantity of buried methane held at high pressure and low temperature in cages of water molecules, known as hydrates or clathrates. Massive escape from hydrates is thought to have been a major factor in the Palaeocene/Eocene Thermal Maximum, 55 Ma before present, with temperature rises of 5–6°C.²⁵ Fortunately the half-life of methane in the atmosphere is only about six years. The chlorofluorocarbons (2% of total effect) absorb infra-red some 10000 times as effectively as carbon dioxide, but present atmospheric concentrations are only of the order of 0.003 ppmv. However, with their long half life, they cannot be ignored. Nitrous oxide, mainly of biological origin, also makes a small contribution.

With Earth in an approximately circular orbit for the next 50 ka and solar gain likely to remain reasonably constant,²² greenhouse gases are now the

major factors governing global temperature. Carbon dioxide is rising rapidly towards the highest levels in the last 24Ma and water vapour will increase with rising temperature. The mean global temperature is predicted to increase to within 90% confidence limits of 1.5–4.5°C by AD 2100. Temperature has already increased by 0.6°C in the last century, mostly since 1950.²⁶ Not the least serious consequence will be melting of polar ice which has the ultimate potential to raise sea level by 67m. Sea level has been rising at about 1.8mm/year since AD 1850 but, since 2004, there have been several reports of increased sea level rise up to 3.0mm/year and predictions for 2100 indicate a total sea level rise for this century of 0.35–0.5m.²⁷

TURNOVER RATES OF ATMOSPHERIC GASES

Biological and geological turnover rates of carbon dioxide are quantitatively totally different.² Living organisms, the atmosphere and surface waters of the

oceans contain about 2200Gt (gigatonnes) of carbon. The annual exchange between photosynthesis and aerobic metabolism is approximately 100Gt annually, with anthropogenic burning of fossil fuels and deforestation currently releasing about 8Gt/year in 2002 as shown in Figure 1.5. The total release of carbon from burning and flaring of fossil fuels has now risen from 5Gt/yr in 1983 to 7.7Gt/yr in 2005, most of the increase since AD 2002 being attributable to China.

In stark contrast, geological stores (ocean depths, organic biomass and limestone) have a carbon content in excess of 30000000Gt, but with an annual turnover (volcanoes, weathering, etc.) of less than 0.1Gt per year. Thus, long term changes are governed by the geological stores, while very rapid atmospheric changes can occur as a result of anthropogenic activity. Fossil fuels were buried over the course of 350Ma, and probably all that is recoverable will be burned in 300 years.

Atmospheric stores of oxygen are almost 600 times greater than those for carbon dioxide. If oxygen decreases at the same rate as the current increase in carbon dioxide, it would take 40000

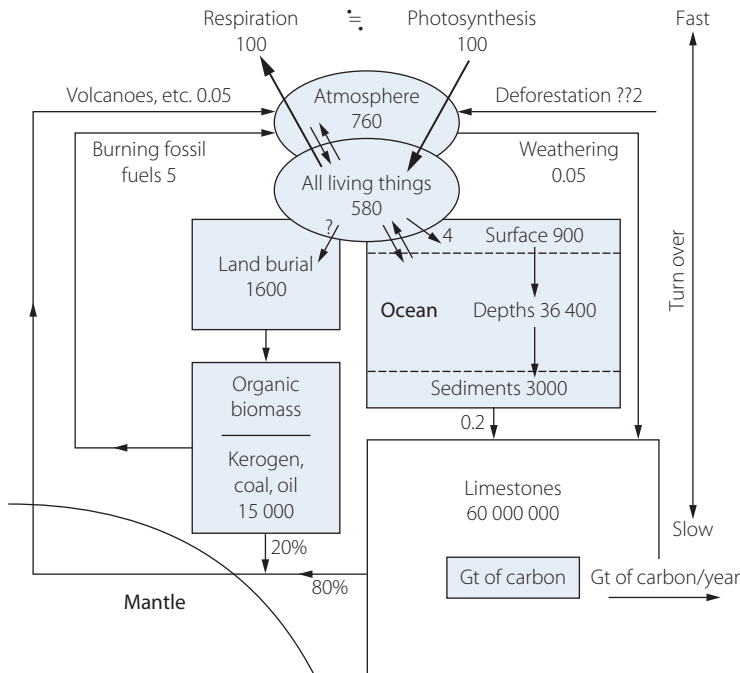
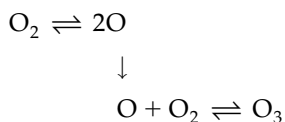


Fig. 1.5 Stores and turnover of carbon dioxide. Stores are in Gt (gigatonnes) and turnover in Gt per year. For recent increases in the burning of fossil fuels see text. (After reference 2, where sources are cited. Reproduced by permission of the Geologists' Association.)

years for sea level P_{O_2} to fall to the level which pertains in Denver today.

OXYGEN, OZONE AND ULTRAVIOLET SCREENING

In addition to its toxicity and potential for more efficient metabolism, oxygen had a profound effect on evolution by ultraviolet screening. Oxygen itself absorbs ultraviolet radiation to a certain extent, but ozone (O_3) is far more effective. It is formed in the stratosphere from oxygen which undergoes photodissociation producing free oxygen atoms. The oxygen atoms then rapidly combine with oxygen molecules to form ozone thus:

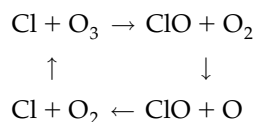


The absolute quantity is very small, being the equivalent of a layer of pure ozone only a few millimetres thick. A Dobson unit of ozone is defined as the equivalent of a layer of pure ozone 0.01 mm thick. About 10% of the total atmospheric ozone is in the troposphere, mainly as a pollutant. This also acts as an ultraviolet screen and may become relatively more important in the years to come.

Life evolved in water which provided adequate screening from ultraviolet radiation. The first colonisation of dry land by plants and animals was in the late Silurian Period about 400 Ma years ago, and it has been suggested that this coincided with oxygen and ozone reaching concentrations at which the degree of ultraviolet shielding first permitted organisms to leave the shelter of an aqueous environment.

Ozone is in a state of dynamic equilibrium in the stratosphere and its concentration varies markedly from year to year, in addition to displaying a pronounced annual cycle. Ozone can be removed by

the action of many free radicals including chlorine and nitric oxide. Highly reactive chlorine radicals cannot normally pass through the troposphere to reach the stratosphere, but the situation was disturbed by the manufacture of chlorofluorocarbons (e.g. CF_2Cl_2) for use as propellants and refrigerants. These compounds are highly stable in the troposphere with a half-life of the order of 100 years. This permits their diffusion through the troposphere to reach the stratosphere, where they undergo photodissociation to release chlorine radicals, which then react with ozone as follows:



Chlorine is recycled and it has been estimated that a single chlorine radical will destroy 10000 molecules of ozone before it combines with hydrogen to form the relatively harmless hydrochloric acid. The Antarctic 'hole' in the ozone layer forms in October of each year, when spring sunlight initiates photochemical reactions. Minimal levels fell from 300 Dobson Units in 1960 to a lowest point (88) in 1995.²⁸ Slight recovery to reach 100 had occurred by 2004.

EVOLUTION AND ADAPTATION

This chapter has outlined the environmental conditions and biological factors under which the atmosphere has evolved to its present composition. In the past, nothing has been permanent, and we can expect a continuation of the interaction between organisms and their environment. What is new is that one species now has the power to cause major changes in the environment, and the atmosphere in particular. These changes will affect a wide range of organisms, and result in the extinction of certain species.

References

1. Taylor SR. *Solar system evolution*. Cambridge: Cambridge University Press; 1992.
- *2. Nunn JF. Evolution of the atmosphere. *Proc Geol Assoc*. 1998;109:1–13.
3. Nisbet EG, Sleep NH. The habitat and nature of early life. *Nature*. 2001;409:1083–1091.
4. Oró J. Early chemical stages in the origin of life. In: Bengtson S, ed. *Early Life on Earth*. Nobel Symposium No. 84. New York: Columbia University Press; 1994:48–59.
5. MacDonald GA, Hubbard DH. *Volcanoes of the National Parks in Hawaii*. 6th ed. Honolulu: Hawaii Natural History Association; 1972.

6. Miller SL. A production of amino acids under possible primitive earth conditions. *Science*. 1953;117:528–529.
7. Chapman CR, Morrison D. *Cosmic catastrophes*. London: Plenum Press; 1989;97.
8. Malin MC, Edgett KS. Evidence of persistent flow and aqueous sedimentation on early Mars. *Science*. 2003;302:1931–1934.
9. Schorghofer N. Dynamics of ice ages on Mars. *Nature*. 2007;449:192–194.
10. Böhler C, Nielsen PE, Orgel LE. Template switching between PNA and RNA oligonucleotides. *Nature*. 1995;376:578–581.
11. Nisbet EG. Archaean ecology. In: Coward MP, Reis AC, eds. *Early Precambrian Processes*. London: Geological Society; 1995:27–51.
12. Nisbet EG. Origins of photosynthesis. *Nature*. 1995;373:479–480.
13. Kasting JF. The rise of atmospheric oxygen. *Science*. 2001;293:819–820.
- *14. Rasmussen B, Fletcher IR, Brocks JJ, Kilburn MR. Reassessing the first appearance of eukaryotes and cyanobacteria. *Nature*. 2008;455:1101–1104.
15. Bekker A, Holland HD, Wang PL, et al. Dating the rise of atmospheric oxygen. *Nature*. 2004;427:117–120.
- *16. Berner RA, Van den Brooks JM, Ward PD. Oxygen and evolution. *Science*. 2007;316:557–558.
17. Kaufman AJ, Xiao S. High CO₂ levels in the Proterozoic atmosphere estimated from analyses of individual microfossils. *Nature*. 2003;425:279–282.
18. DeConto RM, Pollard D, Wilson PA, Pälike H, Lear CH, Pagani M. Thresholds for Cenozoic bipolar glaciation. *Nature*. 2008;455:652–656.
19. Christensen JH, Hewitson B, Busuioic A, et al. Regional climate projections, *Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 2007.
20. Petit JR, Jouzel J, Raynaud D, et al. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*. 1999;399:429–436.
21. Nunn JF. Climate change and sea level in relation to overpopulation. *J Optimal Population Trust*. 2004;4:3–9.
22. Loutre MF, Berger A. Future climatic changes: are we entering an exceptionally long interglacial? *Climatic Change*. 2000;46:61–90.
23. Jones CD. Meteorological Office, personal communication. 2005.
24. Broecker WS. Thermohaline circulation, the Achilles heel of our climate system: will man-made CO₂ upset the current balance? *Science*. 1997;278:1582–1588.
25. Story M, Duncan RA, Swisher CC. Paleocene-Eocene thermal maximum and opening of the northeast Atlantic. *Science*. 2007;316:587–589.
26. Karl TR, Trenberth KE. Modern global climate change. *Science*. 2003;302:1719–1723.
27. Nunn JF. Climate change and rising sea level. *Optimum Population Trust Journal*. 2006;6:14–19.
28. Jones AE, Shanklin JD. Continued decline of total ozone over Halley, Antarctica, since 1985. *Nature*. 1995;376:409–411.