Understanding Reproduction

Our understanding of reproduction and reproductive processes is often biased towards the behaviour of organisms most familiar to us. As a consequence, the amazing diversity in the phenomena of reproduction and sex is often overlooked.

Understanding Reproduction addresses all the main facets of this large chapter of the life sciences, including discussions of asexual reproduction, parthenogenesis, sex determination, reproductive effort and much more. The book features an abundance of examples from across the tree of life, including animals, plants, fungi, protists and bacteria.

Written in an accessible and easy-to-digest style, overcoming the intimidating diversity of the technical terminology, this book will appeal to interested general readers, biologists, science educators, philosophers and medical doctors.

Giuseppe Fusco is Associate Professor of Zoology in the Department of Biology of the University of Padova. His research is in the area of evolutionary biology, with a focus on the variation produced in each generation through reproduction and development, the 'raw material' on which natural selection and other mechanisms of evolutionary change operate. He is editor of the volumes *Evolving Pathways: Key Themes in Evolutionary Developmental Biology* (2008), *From Polyphenism to Complex Metazoan Life Cycles* (2010), *Arthropod Biology and Evolution: Molecules, Development, Morphology* (2013), *Perspectives on Evolutionary and Developmental Biology* (2019) and author, with Alessandro Minelli, of *The Biology of Reproduction* (2019).

Alessandro Minelli was Professor of Zoology at the University of Padova until his retirement in 2011. He previously served as the Speciality Chief Editor for evolutionary developmental biology for the journal *Frontiers in Ecology and Evolutionary Biology*. He was previously Vice-President of the European Society for Evolutionary Biology. Having studied animals for the majority of his career, on retirement he decided to study plant evolutionary development.

He is the author of *Biological Systematics* (1993), *The Development of Animal Form* (2003), *Forms of Becoming* (2009), *Perspectives in Animal Phylogeny and Evolution* (2009), *Plant Evolutionary Developmental Biology* (2018), *The Biology of Reproduction* (2019, with Giuseppe Fusco) and *Understanding Development* (2021).

The ***Understanding Life*** series is for anyone wanting an engaging and concise way into a key biological topic. Offering a multidisciplinary perspective, these accessible guides address common misconceptions and misunderstandings in a thoughtful way to help stimulate debate and encourage a more in-depth understanding. Written by leading thinkers in each field, these books are for anyone wanting an expert overview that will enable clearer thinking on each topic.

Series Editor: Kostas Kampourakis http://kampourakis.com

Published titles:

Understanding Evolution	Kostas Kampourakis	9781108746083
Understanding Coronavirus	Raul Rabadan	9781108826716
Understanding Development	Alessandro Minelli	9781108799232
Understanding Evo-Devo	Wallace Arthur	9781108819466
Understanding Genes	Kostas Kampourakis	9781108812825
Understanding DNA Ancestry	Sheldon Krimsky	9781108816038
Understanding Intelligence	Ken Richardson	9781108940368
Understanding Metaphors in the Life Sciences	Andrew S. Reynolds	9781108940498
Understanding Cancer	Robin Hesketh	9781009005999
Understanding How Science Explains the World	Kevin McCain	9781108995504
Understanding Race	Rob DeSalle and Ian Tattersall	9781009055581
Understanding Human Evolution	Ian Tattersall	9781009101998
Understanding Human Metabolism	Keith N. Frayn	9781009108522
Understanding Fertility	Gab Kovacs	9781009054164
Understanding Forensic DNA	Suzanne Bell and John M. Butler	9781009044011
Understanding Natural Selection	Michael Ruse	9781009088329
Understanding Life in the Universe	Wallace Arthur	9781009207324
Understanding Species	John S. Wilkins	9781108987196

Understanding the Christianity–Evolution Relationship	Michael Ruse	9781009277280
Understanding Living Systems	Raymond Noble and Denis Noble	9781009277365
Understanding Reproduction	Giuseppe Fusco and Alessandro Minelli	9781009225939
Forthcoming:		
Understanding Charles Darwin	Erik L. Peterson	9781009338592
Understanding Creationism	Glenn Branch	9781108927505
Understanding the Nature–Nurture Debate	Eric Turkheimer	9781108958165

Understanding Reproduction

GIUSEPPE FUSCO
University of Padova

ALESSANDRO MINELLI
University of Padova

CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE
UNIVERSITY PRESS

Shaftesbury Road, Cambridge CB2 8EA, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314–321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre,
New Delhi – 110025, India

103 Penang Road, #05–06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of Cambridge University Press & Assessment,
a department of the University of Cambridge.

We share the University's mission to contribute to society through the pursuit of
education, learning and research at the highest international levels of excellence.

www.cambridge.org
Information on this title: www.cambridge.org/9781009225939

DOI: 10.1017/9781009225922

First published 2023

A catalogue record for this publication is available from the British Library.

A Cataloging-in-Publication data record for this book is available from the Library of Congress.

ISBN 978-1-009-22593-9 Paperback

'Fusco and Minelli provide a very clear and accessible overview of the strange and wonderful diversity of reproductive strategies and mechanisms in animals, plants and other organisms. They explain key concepts, define important terms, and place reproductive modes within an ecological and evolutionary context. This book will be a useful reference for biologists, students and even curious non-specialists.'

Russell Bonduriansky, University of New South Wales, Australia

'As a plant biologist, I often find myself trying to explain reproduction in plants as though they are somehow an anomaly rather than just another way of reaching the same goal following first principles. This perception of anomaly comes from a pedagogical bias of teaching reproduction as "sex in mammals". This book ties together concepts regardless of organism, drawing clear lines between a complex diversity of patterns and their underlying reproductive processes.'

Chelsea D. Specht, Barbara McClintock Professor in Plant Biology, Cornell University, USA

Cambridge University Press & Assessment
978-1-009-22593-9 — Understanding Reproduction
Giuseppe Fusco , Alessandro Minelli
Excerpt
More Information

Contents

978-1-009-22593-9 — Understanding Reproduction
Giuseppe Fusco , Alessandro Minelli

Foreword

Everybody has heard of reproduction; it has to do with sex and sexes, but not always. When it comes to humans, it is at the same time both an interesting and a taboo topic. Teachers may find it easier to teach about reproduction in plants rather than animals, and students may be puzzled when they are told that the beautiful flowers they have in that vase in their living room are in fact reproductive organs – I do not think that anyone would like the idea of having the reproductive organs of animals exposed in a vase in the living room! But this also shows the biased way in which we think about reproduction, taking ourselves and other animals – particularly mammals – as the starting point of any such discussion. But as Giuseppe Fusco and Alessandro Minelli show in this marvellous and informative book, there is a lot more to sex and reproduction than what we are usually familiar with. The present book is a real journey during which the authors masterfully describe and explain the diversity of forms of sex and reproduction across the whole tree of life. Reading this book will make you perceive sex and reproduction in a new way, far removed from the anthropocentricism that usually characterizes our perceptions of the subject. One message of the book is that we cannot draw on nature in order to make decisions about what is normal or abnormal when it comes to human sex and reproduction. What happens regularly in some groups may never happen in others; what could be considered as ordinary in some cases might be exceptional for others. Life has evolved a variety of ways for reproduction to occur, and Fusco and Minelli are to be commended for bringing us such a rich view of this complex topic in a single concise volume.

Kostas Kampourakis, Series Editor

Preface

We all have an intuitive idea of what reproduction is and how it occurs in the living world. Images that might come to mind are those of a lioness licking her cubs, a puffball mushroom that explodes releasing spores, two damselflies copulating on a reed leaf, a bumble bee that brings the pollen collected from the stamens of a snapdragon to the pistils of another and possibly many others. All of this is right, but there is so much more than that. Common understanding of reproduction and reproductive processes is biased towards the behaviour of organisms (especially animals) more familiar to us. At variance with other fields of biology such as development or evolution, in this area of biology there are no widespread 'misconceptions', but rather a lack of appreciation of the amazing diversity of the phenomena of reproduction and sex. These are often unexpectedly different from what everybody knows from humans or other vertebrates. The variation lies not only in the way parents provide care for offspring, but in whether or not they do; not only in how males court females, but in who courts whom. There is variation in the number of sexes, the number of parents, what eggs do with sperm, whether offspring are the same kind of animal, or plant, as their parents.

Inspired by a graduate textbook we published in 2019, *The Biology of Reproduction*, to which this book owes most of its field-specific contents, we will address all the main facets of this large chapter of the life sciences – asexual reproduction, parthenogenesis, sex determination, reproductive effort and much more – with a coverage across the tree of life that extends across all the main groups: animals, plants (including 'algae'), fungi, protists and bacteria. While dealing with subjects as varied as the binary division of unicellular algae, the splitting of a strawberry's stolon from the mother plant, the mating of squid, the production of spores by boletus mushrooms, or the paternal care of Darwin's frog, we will try to present all these phenomena using a common language for all living beings, at least for the most general aspects of their reproductive biology, thus overcoming the diversity of the technical terminology still alive in different disciplinary traditions, such as in botany, zoology, microbiology and transmission genetics.

This is not a book of curiosities. How do porcupines do it? (in some way). How long is a baleen whale's penis? (very long). How many times can a lion copulate in a single day? (several). What we propose here is a planned journey through what we may call a 'phenomenology of reproduction'. The first chapter will prepare the ground with some preliminary concepts. There, we will also explain the difference between investigating sex and reproduction across the whole tree of life and in relation to our own species, where psychology and social sciences get involved. After an exploration of the great diversity of life cycles (Chapter 2), we will start with reproduction that does not involve sex (Chapter 3), before moving on in Chapter 4 to sexual reproduction, then to sexual reproduction in its most canonical form, where the parents are two (Chapter 5), and then to other, less well-known forms of sexual reproduction, where the parent is one, or nearly so (Chapter 6). In the last two chapters we will have a look at how sexual traits develop (Chapter 7), before closing with the broad subject of reproductive strategies (Chapter 8).

We will not systematically discuss the evolution and the adaptive value of different reproductive modes or strategies, but our classification of reproductive phenomena largely reflects the way these are relevant in evolutionary ecology and evolutionary developmental biology. During the journey we will encounter, along with more 'regular' reproductive modes, offspring produced solely for the purpose of nourishing their siblings, plants that entrust their pollen to bats, animals that have not known sex for tens of millions of years, insects with very many X and Y sex chromosomes, apparently immortal trees and bugs that are generated by mothers that are still to be delivered by their own mother. In the very last part of the book, we will see cases where there are doubts on how many individuals, either parents or offspring, have to be counted and cases at the border of what we can call reproduction, bearing a closer resemblance to the development or the growth of an individual.

Let's start our exploration of this overwhelming variety of forms through which reproduction has evolved along the larger and smaller branches of the great tree of life.

Acknowledgements

We are grateful to Katrina Halliday and Kostas Kampourakis for inviting us to write this book.

Along the way to publication, we enjoyed the precious assistance of Olivia Boult, Kostas Kampourakis, Jessica Papworth, Jenny van der Meijden and Hugh Brazier.

Several colleagues and friends have contributed significantly to the genesis (or generation) of this work, either helping with our previous book, *The Biology of Reproduction* (2019), to which the contents of this book owe so much, or directly commenting, providing information or help on specific issues in this one, or both: Wallace Arthur, Loriano Ballarin, Giorgio Bertorelle, Ferdinando Boero, Roberto Carrer, Maurizio Casiraghi, James DiFrisco, Andrea Di Nisio, Diego Fontaneto, Carlo Foresta, Cora Fusco, Clelia Gasparini, Adriana Giangrande, Diego Hojsgaard, Marta Mariotti, Koen Martens, Francesco Nazzi, Pietro Omodeo, Marco Passamonti, Andrea Pilastro, Valerio Scali, Emanuele Serrelli, Irene Stefanini, Antonio Todaro and Vera Tripodi.

Mariagiulia Sottoriva produced all the final artwork, and significantly contributed to designing its adaptation for the present book from more technical sources. We thank her for her patience in dealing with our not always clear ideas on what the final artwork should be.

1 Individuals and Reproduction

Forms of Persistence

Ever since living beings arose from non-living organic compounds on a primordial planet, more than 3.5 billion years ago, a multitude of organisms has unceasingly flourished by means of the reproduction of pre-existing organisms. Through reproduction, living beings generate other material systems that to some extent are of the same kind as themselves. The succession of generations through reproduction is an essential element of the continuity of life. Not surprisingly, the ability to reproduce is acknowledged as one of the most important properties to characterize living systems. But let's step back and put reproduction in a wider context, the endurance of material systems.

Compared to material systems belonging to the domain of inanimate matter, such as rocks and minerals, living beings are material systems with a relatively modest degree of physical persistence: their existence depends on some capacity for 'renewal' through time. This renewal occurs at different levels of their organization and at different time scales with respect to the lifetime of the individual organism.

At the level of their most basic components, all living beings are subject to a considerable flow of matter through growth and metabolism, which has profound effects on their constitution at the molecular level. At each breath, about 10^{21} oxygen atoms, which for a while have been part of our body, abandon us in the form of CO_2 and H_2O molecules, while as many new oxygen atoms, in form of O_2 molecules from the air, become part of us. These 'new' atoms have certainly belonged to countless other living beings – microorganisms, plants, dinosaurs, bugs and multitudes of past and present humans, including ourselves some time ago. There are so many atoms even in a small chunk of matter, that this kind of atomic promiscuity is a statistical certainty. It has been calculated that more than 90% of our atoms are replaced every year. At any time, our bodies take in new atoms from the air we breathe, the food we eat, and the liquids we drink. These atoms are incorporated into our cells and fuel the chemical processes that keep us alive. This happens in all living beings, although to a variable extent, depending on the species and the life stage. For example, there is very little molecular turnover in the resting spores of many bacteria, which can remain dormant for thousands of years.

At a higher level of their organization, all living beings renew whole parts of their body during life. Unicellular organisms can renew subcellular structures, and, more prominently, multicellular organisms can renew entire cells. The turnover rate of our cells (calculated for an adult human male of 170 centimetres and 70 kilograms) varies among tissues, from 0 (cells never replaced, like most brain neurons) to 210 billion cells per day (red blood cells), for a total of 330 billion cells per day, corresponding to about 80 g of mass. About 86% of these cells are blood cells, and most of the remainder belong to the wall of the stomach and the gut. Our red blood cells persist in circulation for only about 3–4 months in an adult individual, before being phagocytized by other circulating cells, so they must be continuously replenished through cell proliferation and differentiation. The epithelial cells of our intestine are renewed every 4–5 days, so we renew more than 30 g of our gut (about 40 billion cells) per day. This kind of renewal at the cellular level is even more conspicuous in case of injuries to the body that are repaired through healing or regeneration, as when a lizard loses its tail.

Finally, since living beings are mortal (a topic we will discuss in detail before the end of this chapter), there is a population-level renewal, through reproduction. The plants that cover the slopes of a mountain are probably not the same individuals that covered those slopes a thousand years ago. A pine tree, before dying and disappearing as an individual material system, can generate other pines, and the pine forest endures, at least for a while, certainly for much longer than the time the single pine tree persists. On the longest time scale, living systems compensate by means of reproduction for their limited capacity for individual persistence.

All these forms of renewal in living beings contrast with the apparently unchanging shape of the mountain on which our pine forest sits. On the time scale of the life of the forest, the mountain has largely maintained its constitution down to the single atoms, most of which are the same and have remained in the same spatial relationships, the latter affected only to a negligible degree by movements of blocks of rock along fault lines and the surface phenomena of erosion and transport.

An exploration of this third way of living renewal–the reproductive processes – is the subject of this book, while the objective of this chapter is to equip ourselves with some conceptual tools that will be needed along our journey. To help the reader manage the diversity of organisms we will mention in the following pages, a quick guide to the diversity of life is provided in Box 1.1, while some basic biological knowledge needed to appreciate the diversity of reproductive process can be found in the last section of this chapter.

Box 1.1 A Classification of Living Organisms

To help readers move through the variegated landscape of our broad-spectrum taxonomic treatment, we outline here a classification scheme that is as up to date as possible. For convenience of exposition, we have nevertheless saved a few old names that have disappeared from current classifications because the groups they identify have been acknowledged not to be monophyletic, that is, to include all and only the descendants of a common ancestor. For example, while vertebrates are confirmed as a monophyletic group, invertebrates are simply all animals that are not vertebrates. Other commonly used names that do not correspond to monophyletic taxa are protists (unicellular eukaryotes), polychaetes (annelids other than oligochaetes, the latter including earthworms and leeches), crustaceans (in the traditional sense that excludes insects), algae, bryophytes, pteridophytes and even reptiles in the usual sense that excludes birds.

The primary taxonomic division of living beings is between prokaryotes and eukaryotes. Prokaryotes, most of which are unicellular, include the true bacteria, within which are classified also the blue-green algae, and a diverse group known as the archaea. Unicellular organisms also account for a huge and diverse set of eukaryotes, only a few of which have close affinities to multicellular ones, such as *Volvox* or *Chlamydomonas* with the true plants, or diatoms with the brown algae.

Most unicellular eukaryotes, and a few multicellular ones that are closely related to some of them, are informally called protists. Free-living aquatic photosynthesizing protists are often called algae, an informal group that includes also aquatic photosynthesizing multicellular organisms; based on their pigments, red, brown and green algae are distinguished.

The most familiar groups of eukaryotes are the land plants, the fungi and the animals.

The simplest kind of land plants (or embryophytes) are mosses and liverworts, traditionally grouped as bryophytes; they lack the vessels for the transport of sap that characterize the remaining land plants, therefore called vascular plants or tracheophytes. These comprise, in turn, horsetails and ferns, collectively called the pteridophytes, and a much larger group, the seed plants or spermatophytes. Some of the latter, the gymnosperms, including conifers, lack true flowers and produce naked ovules; their sister group are the flowering plants, or angiosperms. Here, ovules mature within the ovary, and thus the seeds are enclosed in a fruit.

Long classified with plants, but closer instead to animals, are the fungi. These include a modest number of unicellular forms (yeasts) and a huge diversity of multicellular organisms. Devoid of the pigments that characterize algae and other plants, fungi are mostly exploiters of decaying matter, or symbionts associated with the roots of plants, or parasites. The main fungal taxa are ascomycetes, basidiomycetes and zygomycetes.

Within animals (or metazoans), some 30 highest-level groups or phyla are currently accepted. Sponges are mainly marine, but a few live in freshwater. Other marine groups are the diaphanous ctenophores or comb-jellies, and nearly all cnidarians (sea anemones, corals, medusae). Many free-living members of the platyhelminths or flatworms are also marine, but the group includes freshwater forms such as planarians. Flatworms include also two large groups of parasites, the digeneans or flukes and the cestodes or tapeworms.

A generally elongated body articulated into segments is the most obvious feature of annelids. These include terrestrial or freshwater groups like earthworms and leeches, but the majority is represented by the marine polychaetes. Other animal groups are often described as minor, because they include only a handful of species or because these are small and inconspicuous, or for both reasons, but we will nonetheless encounter them in our pages because of peculiarities of their reproductive biology.

Huge groups of invertebrates are the nematodes and the arthropods. Nematodes or roundworms include very many parasites, including *Ascaris*, but also free-living species such as *Caenorhabditis elegans*, one of the most popular model organisms studied in the laboratory. Arthropods, unmistakable for their segmented body provided with an exoskeleton and more or less numerous pairs of articulated appendages, including sensory (antennae), feeding (maxillae, mandibles) and locomotory (legs), are the largest of all animal phyla. They include the chelicerates, with scorpions and pseudoscorpions, mites and spiders; the many-legged myriapods; and the crustaceans, mainly aquatic, but with a successful branch of terrestrial forms (woodlice or land isopods). Other than the familiar decapods (crabs, shrimps, lobsters), crustaceans include many other groups such as cladocerans (*Daphnia*). Based on molecular evidence, insects are classified today by most authors as a specialized lineage of crustaceans.

Very unusual and diverse are the shapes of the echinoderms (e.g. starfishes and sea urchins), and those of tunicates, the sessile ascidians and the planktonic thaliaceans. Despite the obvious morphological distance, these latter groups of marine animals are closely related to vertebrates.

Within vertebrates, the old class of fishes has been long abandoned, their content being now distributed between several major groups: we will deal with representatives of the cartilaginous fishes (sharks, rays), crossopterygians (coelacanth) and numerous bony fishes. Of amphibians, we will mention both urodels (salamanders) and anurans (frogs and toads). Of reptiles other than birds, we will see the lineages of turtles, squamates (lizards, snakes) and crocodiles.

Following a simplified but up-to-date classification, the mammals mentioned in the text belong to the following groups: monotremes (platypus and echidnas), marsupials (kangaroo, wallaby, opossum) and placentals, to which we belong.

What Is Reproduction?

Let's adopt an informal common-sense concept of reproduction. In biology, we can define reproduction as *the process by which new individuals are generated from pre-existing individuals*. Implicitly, it is assumed that the 'new individuals' are materially derived from pre-existing ones, or parents. This concept of reproduction has deep roots in human history, as it emerged by obtaining increasingly detailed knowledge of the life cycles of the plants and animals most familiar to us, ourselves included. This simple definition, as trivial as it may seem, nonetheless allows us to leave out other possible forms of generation that are not found in living beings.

A long tradition that remained alive until the nineteenth century accepted the possibility of *spontaneous generation*, that is, the direct formation of living organisms (the simplest ones at least) from inanimate matter, such as mud or rotting organic material. It was William Harvey (1578–1657), who in his *Exercitationes de generatione animalium* of 1651 first recognized a fundamental divide between the world of living beings and the rest of nature, based on a principle of generation: '*omnia ex ovo*', all living beings are born of an egg. Belief in spontaneous generation was progressively dismantled through the experimental work of scientists, among them Francesco Redi (1626–1697), who inflicted a mortal blow to the doctrine of spontaneous generation with his experiments designed to reveal whether 'any exudate from a rotten corpse, or any filth of something putrefied, generates worms'. Redi observed indeed that 'worms' (actually, insect larvae) developed in sealed glass flasks containing rotting pieces of meat or little dead animals, but only if, before sealing them, access to these flasks and their content was allowed to big flies, blue, green or grey, similar to those into which the 'worms' eventually transformed. Further important contributions were provided by Lazzaro Spallanzani (1729–1799), Franz Schulze (1815–1873) and finally Louis Pasteur (1822–1895), who definitively demonstrated that spontaneous generation does not occur, not even in microorganisms.

Material systems that are not considered living organisms, or do not qualify as living cellular systems – for instance, viruses, prion proteins (prions) and transposable DNA sequences (transposons) – can reproduce in some sense, although differently from living organisms. An important difference with respect to organismal reproduction is that these systems can replicate without contributing constitutive matter to their descendants. In other words, the causal link between 'parents' and 'offspring' does not pass through the transformation of a part of the body of the parent into the offspring. For instance, prions are proteins with a special conformation, capable of inducing other molecules of the same protein, but with a different three-dimensional structure, to take their own conformation. In this way, prions start a chain reaction that leads to their multiplication in an infectious way. Some prions are associated with pathological conditions of the mammal nervous system – for instance, bovine spongiform encephalopathy (BSE), also known as mad cow disease. Another example is offered by retroviruses, such as human immunodeficiency virus (HIV). When infecting a cell, the virus induces it to produce copies of its genetic material and the molecules for its shell, the capsid. However, neither the genetic material nor the proteins of the capsid of the 'offspring generation' are derived from parental molecules. The parent virus is causally responsible for the production of a new viral unit, but does not contribute any of the matter of which it is made.

Apart from these other forms of reproduction, two different aspects of population renewal contribute to biological reproduction. One is that 'new individuals' are added to the set of existing ones. In this *demographic* aspect of reproduction, 'new' should be understood as a quantitative addition to the entities that already exist. The other is the production of 'individuals that are new', compared to the existing ones. In this *innovative* aspect of reproduction, 'new' should be understood as qualitatively different from the pre-existing entities. According to the demographic concept, focus is on replacing the individuals that inevitably perish, thus maintaining or possibly increasing the size of the population. In contrast, according to the innovative concept, focus is on the appearance of 'something new under the sun', thus allowing the population to change through the generations – that is, to evolve.

These two distinct aspects of reproduction are found together in some forms of reproduction, for instance, in the most common instances of sexual reproduction, but not in all. As we will see, some modes of reproduction lead to a renewal only in the demographic sense, while innovation, although eventually occurring in all organisms, is not necessarily associated with reproduction.

Asexual and Sexual Reproduction

Traditionally, a primary distinction is traced between *asexual* and *sexual* reproduction. This division, as the two terms suggest, is based on the characterization and involvement of the so-called *sexual processes*.

At the genetic level, *sexual processes* are biological processes through which new combinations of genetic material are created from distinct sources. These can occur through the union of genetic material of different provenance, as in the fusion of the gametes of two individuals, but also through the reassortment of genetic material of different origin, like the reshuffling of the two sets of chromosomes during meiosis (*recombination*) for producing gametes or spores. Novel genetic assets can be obtained also in other ways. One is *horizontal gene transfer*, where genetic material is moved from one individual to another that is not its offspring (and not even necessarily of the same species), to be incorporated in the latter's genome. This sexual process occurs regularly in prokaryotes, but it is common among eukaryotes and between prokaryotes and eukaryotes as well. Sexual processes, sometimes dubbed simply *sex*, for short, are thus distinguished, in principle at least, from the processes of change of genetic information that occur in a single individual without the contribution of DNA from other sources, as in gene mutations. In the case of eukaryotes, for simplicity, in this book we will discuss the genetic aspects of reproduction at the level of the nuclear genome, overlooking the dynamics internal to the genomes of the organelles (mitochondria and plastids).

These phenomena of genetic reassortment may or may not be associated with reproduction. A classic example of sex dissociated from reproduction is offered by ciliates, a group of unicellular protists to which paramecia belong. Ciliates commonly practise a form of sex called *conjugation*. Two individuals (conjugants) unite temporarily, exchange genetic material through a sort of reciprocal fertilization, then separate again. The result of this exchange is a pair of independent individuals (ex-conjugants), genetically different from the conjugants. Note that the number of individuals has not changed through sex: two conjugants in, two ex-conjugants out.

Thus, in ciliates it is possible to have reproduction without sex, when a paramecium simply splits into two (binary fission, Chapter 3), or sex without reproduction, when two paramecia unite, exchange genetic material and then separate, both genetically renovated (conjugation).

Sexual processes, associated or not with reproduction, are found in virtually all major lineages of living beings. Note that in the scientific literature about the genetics of reproduction, 'to have sex' generally means 'to carry out a sexual process', not 'to mate'. That a mating may not result in reproduction is probably quite obvious to everybody.

Reproduction can thus be qualified as sexual or asexual based on the involvement of potentially independent sexual processes. Accordingly, sexual or asexual are in principle attributes of reproduction, but not attributes that apply to a given organism, since many organisms can reproduce in both ways.

Asexual reproduction (in plants, also called *vegetative reproduction*) is a mode of *uniparental reproduction* (i.e. reproduction from a single parent) that does not involve sexual processes or the production of gametes, not even in derived or residual form. As a first approximation, asexual reproduction generates individuals genetically identical to each other and identical to the parent, thus forming what is termed a clone (Chapter 3), and for this reason it is also called clonal reproduction. However, asexual reproduction in some cases fails to produce perfectly clonal descendants, while sexual reproduction occasionally has a clonal outcome.

Asexual reproduction is the most common form of reproduction among unicellular organisms, prokaryotes and eukaryotes alike, but is also very common among multicellular organisms. For instance, many plants, for example most reeds, propagate by runners; many marine worms multiply by splitting into pieces; and some sea anemones generate new polyps through budding. In bacteria and some protists, this is the only mode of reproduction (*obligate asexual reproduction*). However, more often, asexual reproduction coexists with sexual reproduction, either as the only form of reproduction in a specific phase of an organism's life cycle (e.g. in the polyp phase of cnidarians with a typical metagenetic cycle; Chapter 2), or as a reproductive option (*facultative asexual reproduction*) co-occurring with the sexual one (e.g. in many plants). In any case, the obligate asexual reproduction of certain organisms does not rule out the possibility of these having sex that is not associated with reproduction, as mentioned above for the paramecium, and this is very common in prokaryotes.

Sexual reproduction is a form of reproduction that generates new individuals with a genetic make-up resulting from the association and/or the reassortment of genetic material of different origins. In the most canonical form of sexual reproduction, the genome of an offspring, in other words the totality of its genetic material, derives from the union of (partial) copies of the genomes of two parents through fertilization. Here two distinct sexual processes are involved: the recombination of each parent's genomes at meiosis during the production of gametes, and the combination of the genomes of the two gametes into the zygote's genome at syngamy. Sexual reproduction involving two parents is called *amphigony* or *biparental sexual reproduction*. However, there are also forms of *uniparental sexual reproduction* (Chapter 6), in which the genome of a single parent is modified and reorganized during the process that leads to the offspring generation, as in parthenogenesis (reproduction through eggs that do not need to be fertilized) or in self-fertilization (reproduction through eggs that are fertilized by the sperm of the same individual). Sexual reproduction is found in the vast majority of multicellular eukaryotes and in most protists, but it does not necessarily rule out other forms of sex or other forms of reproduction.

With reference to the demographic and innovative aspects of reproduction mentioned in the previous section, the demarcation between sexual and asexual reproduction we have just established entails both the possibility of innovation without reproduction and without demographic growth (through sex alone), and the possibility of reproduction with or without sex, and with or without the production of genetic novelty.

Unfortunately, a discordant terminology is in use, based on different opinions on where to draw the line between sexual and asexual reproduction. In particular, what is contentious is whether some forms of uniparental reproduction, such as parthenogenesis, should be considered as sexual or asexual, along with the species or the individuals that practise them. In this book we have adopted a terminology that takes into account both the role of sex and the processes by which gametes are formed. Cases of uniparental reproduction involving sexual processes (as in self-fertilization), or deriving from processes typical of sexual reproduction (such as egg formation in parthenogenesis), are treated in the context of sexual reproduction, even when they have a clonal outcome. However, this terminological inconsistency in the literature is a minor point in comparison to the fact that there are forms of reproduction that challenge inclusion in any rigid classification. In any case, the reader is alerted: sexual and asexual may mean different things to different people.