

Introduction

A cat gives birth to her kittens, two earthworms mate and exchange sperm, a bee brings the pollen collected from the stamens of a buttercup to the pistils of another buttercup – diverse scenes from the same biological phenomenon, reproduction.

Reproduction is the subject of this book. At first sight, it seems to be a well-defined subject of study, which includes everything concerning the ways, times and mechanisms by which living beings produce their descendants. We all have an intuitive idea of what reproduction is, but this is likely to be based on the behaviour of a few organisms (especially animals) familiar to us. In fact, by widening our perspective on reproduction to less well-known organisms, up to and including the whole of the living world, we reach a point where the boundaries of reproductive phenomena become less and less distinct and finally blend into other aspects of biology. If we think we have a clear idea of the boundary between reproductive and growth processes based on what we know about humans or giraffes, the distinction between the two processes becomes more difficult to define for a strawberry plant or a marine annelid. If it seems easy to establish with reasonable clarity the identity of the individual that reproduces in the case of an eagle or a mosquito, in the case of a coral it is far from obvious where the boundaries between two individuals lie. Not to mention an ant colony – not a good choice of system to reassure us in our belief that we can always easily distinguish between the reproduction of an individual and the reproduction of a society.

These difficulties are unavoidable, and the iterated introduction of *ad hoc* definitions is an exercise in taxonomic arbitrariness.

Of course, we cannot do without definitions if we want to communicate, but the boundaries we establish from time to time between the objects of our study will not always and necessarily correspond to ‘natural’ boundaries emerging unequivocally from the biology of the organisms we study. There is no other way out, then, than to take a pragmatic approach. Definitions help, but they only work within delimited areas, beyond which they can be more of a hindrance than a help. That’s life.

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Along our journey we will meet many problems of boundaries and definitions precisely because this book deals with reproductive phenomena in all kinds of living beings: the binary fission of a unicellular alga, the stolon of a sequoia that separates it from the mother plant, the mating between two kangaroos, the production of spores by a mushroom, the encounter between the pollen of a thistle and the ovule of a conspecific plant, and more. We try to present all these phenomena using a common language for all living beings, at least in what are the most general aspects of their reproductive biology. This is not always easy, because in the specialized literature concerning the different groups the reproductive phenomena are often described from non-overlapping perspectives, using only marginally congruent terminology.

Against this background we have had to make choices in establishing the structure of this book and the boundaries of its subject matter.

A first and most fundamental choice was to limit the treatment to a ‘phenomenology of reproduction’. We fully acknowledge the interest of many other topics – e.g. the adaptive value of different reproductive modes or strategies and the possible scenarios of their evolution, or the vast subject of sexual selection – but we had to leave them out, because they would easily form the subject of another book. Reading tips will be provided for these topics.

A second, unavoidable basic question for a book on the reproduction of living beings is to decide who the living are. Trying to answer this question would lead to a very different book, and we therefore made a choice in line with the pragmatic approach outlined above. Although reproduction can unite material systems of different kinds, here we deal only with living beings in the strict sense, that is, with biological systems made up of one or more cells. Therefore, viruses, prion proteins and transposable genetic elements are excluded. We mention their reproduction only occasionally, when it is relevant to the reproductive phenomena of living beings in the strict sense.

There are, then, many possible ways of classifying different reproductive modes. And there are many different criteria, all equally justifiable, that could be applied to give a relative weight to each of the many topics into which the subject is divided. We give some prominence to those aspects of reproduction that have appreciable effects on evolutionary processes. For example, the association between the genetic system and the reproductive system of an organism determines the quantity and structure of individual variation that is produced in each generation – and this, in turn, constitutes the raw material on which natural selection and other mechanisms of evolutionary change operate.

Without a doubt, the theme of reproduction opens up a huge number of other biological themes, from ecology to applications in medicine, agriculture and animal husbandry, but we have to leave these subjects to other books.

Other aspects of the delimitation of the subject matter to be discussed depend on the taxonomic group considered. The whole life cycle of a living organism can be seen as a set of processes that contribute to a more or less faithful production of copies of itself. There is no aspect of the life of an organism that is not related to reproduction, directly or indirectly. Traditionally, however, under *reproductive strategies* (or *reproductive modes*) we refer only to certain aspects of genetics (e.g. sex chromosomes), anatomy (e.g. reproductive organs), physiology (e.g. sex hormones), life cycle (e.g. reproductive phases), or behaviour (e.g. courtship) that seem more directly involved in reproduction. These aspects vary greatly from species to species. It is not surprising, therefore, that textbooks on systematic biology offer very different contents, in the sections dedicated to the reproduction of each group of organisms. Examples are the structure of the flower in the case of plants, the origin of the gonoducts in annelids, the molecules involved in chemical communication between partners in insects, the strategies of courtship in birds, the duration of gestation in mammals.

Even here we could not escape space constraints, and owing to the specificity of some aspects we had to leave these out, despite their interest. For example, we refer only in passing to many topics in vertebrate ethology such as courtship and parental care, or to the physiology of the production of seeds and fruit in plants. Suggested readings will also be provided for these topics.

One last note concerns taxonomy. For our broad-spectrum taxonomic treatment it was necessary to adopt a classification scheme that is up to date as far as possible, but at the same time reasonably consolidated. For convenience of exposition, not all taxonomic groups we discuss are strictly monophyletic. Among the most common paraphyletic or polyphyletic groups that we mention are prokaryotes (eubacteria plus archaea), protists (unicellular eukaryotes), polychaetes (a paraphyletic grouping of annelids), crustaceans (in the traditional sense that excludes insects), reptiles (in the traditional sense that excludes birds), algae (photoautotrophic protists, rodophytes, phaeophytes, chlorophytes and other minor groups), bryophytes (non-tracheophyte embryophytes), pteridophytes (non-spermatophyte tracheophytes), gymnosperms (non-angiosperm spermatophytes) and plants in the widest sense (algae of various groups plus embryophytes). The appendix at the end of the book provides a phylogenetic classification of the taxa mentioned in the text.

Here, finally, is a preview of the contents of the chapters that follow.

In Chapter 1 we introduce some fundamental concepts, starting with a tentative definition of reproduction that will be revised and enriched in the

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following chapters, and with the traditional distinction between sexual and asexual reproduction. We address the delicate issues relating to the notions of biological individual, generation and life cycle (but we refrain from discussing these topics from a philosophical perspective). We also deal with the not always clearly defined relationship between reproductive and developmental processes, in particular those related to regeneration.

Chapter 2 is devoted to the relationships between reproduction and life cycle. We start by illustrating the classical division of life cycles on the basis of the alternation of nuclear phases (haplontic, diplontic, haplodiplontic). Then we move on to the alternation between sexual and asexual generations (metagenetic cycles), amphigony and parthenogenesis (heterogonic cycles), gonochoric and hermaphrodite (heterogenic cycles), solitary and colonial, unicellular and multicellular. We conclude with short sections on the alternation of generations dependent on seasonal polyphenism and the different ways in which different reproductive phases can be distributed within one generation.

Chapter 3 is dedicated to the natural history of reproduction. A first section on asexual reproduction deals with the different forms of cell division in unicellular prokaryotes and eukaryotes. A short interlude introduces the notion of sex (itself in some respects problematic) and describes sexual phenomena uncoupled from reproductive processes, both in prokaryotes and in unicellular eukaryotes. The main types of sexual reproduction (gametogamy, gamontogamy, autogamy) are described, as are the distinction between sexes and mating types and the different ways in which the individual sexual condition (e.g. unisexual or hermaphrodite) can be distributed within the population. Short paragraphs are devoted to secondary sexual characters and to conditions such as aneuploidy, gynandromorphism and intersexuality. Attention is then shifted to the reproductive organs of the metazoans and the morphology of eggs and spermatozoa, and also to the reproductive organs of plants and the morphology of their gametes. Finally, the fate of gametes is described, both in typical biparental reproduction, with particular regard to its ecological context, and in uniparental sexual reproduction (self-fertilization, parthenogenesis, gynogenesis, androgenesis and hybridogenesis).

The short Chapter 4 deals with investment in reproduction by organisms, first considering the destiny and care of the products of reproduction and the alternative between oviparity and viviparity, followed by a brief mention of the forms of parental care given to the offspring by one or other parent, or both. Some energetic and metabolic aspects of reproduction, in particular vitellogenesis in animals and the formation of endosperm in flowering plants, are also considered, concluding with a short section on the various strategies of

parental investment, including different fecundity/fertility levels, considered against different environmental contexts.

Chapter 5 deals with the genetics and cytogenetics of reproduction, starting again from asexual reproduction. Genetic variation due to new mutations, recombination, stochastic segregation or epigenetic causes is discussed. Moving to sexual reproduction, we discuss mechanisms of genetic exchange in the prokaryotes, but eventually focus more closely on sexual reproduction in the eukaryotes. First, the various sources of genetic variation (independent assortment of chromosomes and chromatids, crossing over and gene conversion at meiosis, syngamy) are discussed, thus addressing the genetics of hereditary transmission through different modes of sexual reproduction (amphigony, self-fertilization, meiotic and ameiotic parthenogenesis, gynogenesis, hybridogenesis, androgenesis). The last paragraphs of this chapter are devoted to sexual leakage and some special cases of sex in eukaryotes (conjugation in ciliates, parasexual cycle in fungi, chimerism).

In Chapter 6 we discuss the determination of sex and mating type, considering both genetic systems of sex determination and those dependent on environmental factors such as temperature or interactions with conspecific individuals, to end with cases of maternal determination of sex and so-called mixed sex-determination systems. We devote only brief notes to sexual differentiation, to conclude with the mating types of fungi and protists.

In Chapter 7 we present an overview of the reproductive phenomena that occur in the different phyla.