Preface

The mechanisms that determine sex have been intriguing biologists for a long time. One reason may lie in the widespread occurrence and fundamental importance of sex throughout all forms of life. Another may stem from the profound sympathy we share with our fellow scientists for categories and numbers: clear-cut male and female phenotypes render studies on sex ratios and sex determination both tractable and appealing. Still another might simply be that we, biologists, share with our fellow humans an obsession for sex, hard-wired in our brains.

In 1983, James Bull supplied evolutionary biologists with a state-of-the-art synthesis on the 'Evolution of Sex Determining Mechanisms'. From his own words, writing this book was motivated by the author's astonishment in face of the bewildering variety of sex-determination systems. He intended his review to provide both an account of this variety, and a discussion of the processes that might have generated it. Accordingly, the first and largest part comprised a review of the main systems described so far, their occurrence throughout the animal kingdom, and a discussion of the possible transitions and evolutionary paths among them. The second part was more specifically devoted to the evolution of sex chromosomes, including a discussion of the possible role of sex-antagonistic selection in driving their dynamics. Bull's thorough synthesis successfully integrated current knowledge on the patterns of sex-determination systems and the processes driving their evolution; his book was very influential and is still much quoted.

More than 30 years have now passed, and, surprisingly, no full account of the field has been published since this landmark publication. The present book intends to fill this gap. In some way, it is an updating of Bull's work. We will re-appreciate and further expand several important insights from his book; we share, among others, the central idea that seemingly discrete sex-determination systems are connected by an underlying continuum. The proximate and ultimate causes driving transitions along this continuum are certainly key issues to address; this is the topic of our final chapter (Chapter 7), which expands in particular on the prominent role of genetic conflicts in this context. Along the same line, our Chapter 4 (quantitative genetics of sex determination) opposes the classical dichotomous view of environmental versus genotypic sex determination as distinct and mutually exclusive processes. In line with Bull's (1983) concept of 'sex tendency' (itself an extension of Bridges' (1925) genic balance theory), we rather see sex as a threshold trait, underlain by continuously distributed liability factors, under both genetic and environmental influence. Our Chapter 5 on the evolution of sex chromosomes updates and expands the second part of Bull's book. We further detail the selective forces acting on non-recombining genomic regions and document recent advances in the genomic aspects of Y- and W-chromosome degeneration. We also discuss recent insights in the distinct evolutionary fates of recombining sex chromosomes (X, Z, and pseudo-autosomal regions), as well as on other sex-limited chromosomes (U and V) evolving under haplo-genotypic sex determination.

Such common themes are to be expected: we evidently share Bull's astonishment of the bewildering diversity and impressive dynamics of sex-determination systems. Accounting for such dynamics and diversity naturally emerges as a central goal of any book with an evolutionary perspective on the topic. However, whereas many crucial questions raised in his time

remain open issues today, much progress has also been made in domains that were largely unexplored (or even unforeseen) some 30 years ago. Hence, there are necessarily differences in scope.

One such difference concerns the phylogenetic coverage of our book. Bull's review was essentially limited to animal sex determination. Angiosperms were briefly mentioned, mostly through a list of families in which male or female heterogamety had been documented, and the suggestion that, due to the haploid phase of their life cycles, plants might provide good models to test theories on the evolution of sex chromosomes. In the 1980s, the eukaryote radiation outside animals, land plants and higher fungi, was largely *terra incognita* (the 'protist' black box). Since then, the full extension and richness of living forms has been progressively unveiled; land plants, animals, and fungi now appear as the emerging tips of an iceberg of eukaryotic variety. Importantly, meiotic sex turns out to be one of the unifying features of this radiation: the same genes controlling meiosis have been found in all main eukaryotic lineages. Details of sexual cycles have been described in increasing numbers of lower fungi, chlorophytes, rhodophytes, phaeophytes, diatoms, oomycetes, alveolates, amoeobozoa, and many other basally diverged lineages. Deciphering the structure and function of mating types has provided new perspectives on the origin of the male and female sexes. Our Chapter 2 (including both a printed part and electronic supplements) accounts for this newly discovered world. We cover the diversity of eukaryotes and propose a typology for sexual cycles; we delineate the similarities and differences between sexes and other mating categories, discuss ultimate causes for their emergence, and suggest possible evolutionary scenarios to connect the dots: how did, for instance, the mating types found in haplontic unicellular lineages evolve towards the diplo-genotypic sex determination found in multicellular plants or animals?

Other obvious developments concern the molecular mechanisms of sex determination. Bull's (1983) fourth chapter mostly focused on a list of few genes known at that time to affect sex determination in three laboratory models (mice, *Drosophila*, and *Caenorhabditis*), with a description of the phenotypes of some mutations. Since then, biology has undergone its molecular and genomic revolutions. Large arrays of new laboratory tools now allow functional analysis of the gene cascades and feedback loops that, from the initial triggers to the downstream effectors, determine the sexual fate of cell lineages. The genetic pathways of sex determination have been dissected in much detail, not only in classical laboratory models, but also in increasing numbers of non-model animals, plants, algae, and fungi. We now know a lot about the molecular mechanisms that determine differentiation of floral meristems and self-incompatibility systems in angiosperms, or mating-type signalling and zygote formation in fungi or algae. Our Chapter 3 summarizes recent advances on the molecular mechanisms that orchestrate sexual cycles; besides their intrinsic interest, such mechanisms also matter because they provide crucial insights in transition processes.

Our book also extends and refines the concept of sex determination. For reasons presented in Chapter 1, we think that the field of sex determination is not limited to the initial triggers that decide sexual fates in gonochoric animals or dioecious angiosperms, but also includes the range of developmental processes of the male and female functions (often referred to as 'primary sex differentiation', or 'sex development' in Bull's words). In line with this extensive definition of the field, we also discuss the processes of sex differentiation in sequential and simultaneous hermaphrodites.

Finally, we further expand the scope of the topics covered, by indulging in a few incursions upstream and downstream of sex determination itself, into domains that were explicitly avoided in Bull's book. Placing sex determination in a broader context, our Chapter 1 will briefly present current thinking about what sex is and why it evolved, and how sexes relate to mating types and other mating categories such as self-incompatibility systems or induction types. Our Chapter 6 will outline the consequences of specific sex-determination systems for the evolution of life histories, genetic systems, sex allocation, sexual selection, and speciation. We found it useful to delineate how these aspects feed back on each other in an evolutionary context.

Our book is thus meant as a contemporary overview and a comprehensive treatise of patterns and processes of sex determination for the beginning of this century. It makes also clear that the field is now expanding at an unprecedented pace. With the ongoing popularization of genomic tools, and the rapid development of next-generation sequencing techniques, we expect a flurry of important new discoveries in the coming years, which promise to drastically affect our vision of the field. It is highly unlikely that another 30 years will pass until the next synthesis on sex-determination systems becomes necessary.

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