Preface

One of the most important topics in evolutionary biology concerns the origin and evolution of sex-determining systems and sex chromosomes. Certain plant species display younger sex-chromosome systems in different evolutionary stages. It is thought that the same evolutionary forces described for animals are operating in plants. However, in opposition to the situation in animals, sex-determining mechanisms seem to be more flexible, and most species with separate sexes have evolved directly from ancestors with both sex functions. These features make plants excellent models for studies on sex determination. In this context, early evolved plant-sex chromosomes have given rise to many studies in recent years. In this book, the most recent findings are highlighted and reviewed, focusing specifically on model species, including Carica papaya, Fragaria virginiana, Silene latifolia and Rumex acetosa.

Chapter 1 - Sex chromosomes are thought to have evolved from an autosomal pair through the accumulation of sex-determining genes and the disruption of X-Y recombination that ultimately led to the formation of heteromorphic sex chromosomes. Early evolved plant-sex chromosomes have given rise to many studies in recent years, which have proved chromosomal rearrangements and repetitive-DNA accumulation crucial events that play an important role in sex-chromosome evolution. In this review, the authors combine evidence gathered by different approaches and report the most recent findings in three model species on plant sex-chromosome analyses, including different levels of sex-chromosome differentiation: *Carica papaya*, homomorphic sex chromosomes; *Silene latifolia*, heteromorphic and undifferentiated; and *Rumex acetosa*, heteromorphic and highly differentiated.

The data are discussed in the light of plant sex-chromosome differentiation and evolution.

Chapter 2 - Sex chromosomes evolved from a pair of autosomes. During their evolution, suppression of recombination occurred in the sex determining regions, the nonrecombining regions then expanded resulting in the production of the heteromorphic sex chromosomes. In humans and *Drosophila melanogaster*, the sex chromosomes developed about 300 million years ago (mya) and 60 mya, respectively. By contrast, plant sex chromosomes are comparatively new; the papaya sex chromosomes developed 2–3 mya, and the sex chromosomes of the dioecious *Silene latifolia* arose 10–20 mya. The study of these young sex chromosomes allows us to understand the early steps of sex chromosome evolution. Repetitive sequences are thought to be involved in preventing recombination and in causing the expansion of the nonrecombining regions. Moreover, the location of repetitive sequences could provide clues into large-scale chromosomal rearrangements. In the last decade, many repetitive sequences have been characterized in *S. latifolia* and they have been used as probes for fluorescent *in situ* hybridization. These studies showed that large rearrangements were involved in sex chromosome evolution in *S. latifolia*, and that Y chromosome-specific repetitive sequences accumulated during its evolution. Together with the data from the genetic mapping of sex chromosome-linked genes, these results are very informative for understanding the structure of the sex chromosomes and the process of their evolution.

Chapter 3 - According to the currently accepted model, sex chromosomes evolve from a pair of autosomes via a series of step-wise expansions of the non-recombining region on the Y chromosome (NRY), creating 'evolutionary strata', followed by degeneration of genes trapped in the NRY. This model is based on the analysis of ancient (over 200 million year [MY] old) sex chromosomes of mammals and birds, as well as recent translocations of autosomes to sex chromosomes (neo-sex chromosomes) in *Drosophila*. Much less is known about plant sex chromosomes, with the bulk of data coming from only two species, *Silene latifolia* and *Carica papaya*, and even for these best studied plants, less than a dozen sex-linked genes have been identified and analysed. Here the author critically discusses the main conclusions from the data available. In particular, he stresses that the evidence for 'evolutionary strata' and for genetic degeneration of Y-linked genes in plants is relatively weak. Thus, it is premature to extend the 'animal model' of sex chromosome evolution to plants, as the evolutionary trajectory of plant sex chromosomes may differ from that in animals.

Sex chromosomes are peculiar structures present in most animal and some plant genomes [1]. Although they evolved many times independently, their properties are quite similar in different groups of organisms. The chromosome restricted to one sex (Y in male- or W in female-heterogametic species) lacks recombination and is genetically degenerate, while its counterpart (X or Z, respectively) is present in both sexes, actively recombines in the homogametic sex and is relatively gene-rich. Independent evolution of similar structures in different organisms provides a wealth of material for evolutionary genetic studies seeking to understand the origin and evolutionary forces involved in sex chromosome evolution.

Chapter 4 - Papaya is a semi-woody tree that produces fruit rich in vitamins and minerals. It is trioecious with male, female, and hermaphrodite plants. Though many theories have been suggested in the past, papaya sex is determined by a pair of nascent sex chromosomes; females have two X chromosomes, males have an X and a Y, and hermaphrodites have an X and a Y^h, which varies slightly from the male Y. Any combination of the Y and Y^h genotype, YY, Y Y^h, or Y^h Y^h, is lethal. The X and Y chromosomes have a small non-recombining region in the centromeric and pericentromeric region. The hermaphrodite-specific region of the Y^h chromosome (HSY) is gene poor and has an increased amount of retroelements and chromosomal rearrangements compared to its X counterpart and the genome wide average. The X and Y chromosomes were estimated to have diverged relatively recently about 2-3 million years ago (MYA), and even more so for the Y and Y^h (73,000 years ago). Physical maps of the HSY and the corresponding X region have been produced and sequenced, showing the HSY sequence has expanded. Genes in these regions are being mined with a special focus on identifying the two sex determination genes, one promoting maleness and one suppressing femaleness. The impact of identifying the sex determination genes would be high for both the commercial production of papaya and the field of sex chromosome evolution.

Chapter 5 - *Fragaria* is an exceptional model system for understanding sexual system and sex chromosome evolution. The genus hosts the entire range of sexual systems, as well as novel features, such as diversity of ploidy levels and the presence of female heterogametey. Comparative genetic mapping has revealed the autosomal ancestor of sex chromosomes in two species and exposed the evolutionary lability of sex-determining chromosomes in this young system. Recent QTL analyses have allowed the first glimpse of the genomic architecture of secondary sexual dimorphism and point the way for future work aimed at understanding the driving forces behind sex chromosome initiation and turnover. The genus is also poised to aid in answering the question of how genome doubling and merger facilitates the initiation of polymorphic sexual systems and the development of sex chromosomes.

Chapter 6 - The origin and evolution of sexual dimorphism and the sex-determining mechanisms are major topics in Evolutionary Biology on which many studies have focused in recent decades. Among flowering plants, the origin of dioecy has resulted from quite recent events, occurring independently in about 7% of the genera. However, only a moderate number of dioecious plant species exhibit chromosome-mediated sex-determination systems. The genus *Rumex* (*Polygonaceae*), with monoecious, gynodioecious, hermaphroditic, and polygamous representatives, and with dioecious species bearing sex chromosomes in different evolutionary stages (homomorphic, XX/XY, XX/XY$_1$Y$_2$), has considerably contributed to shed light on this topic. Although still patchy, current knowledge on sex-chromosome evolution has greatly benefited from analyses on species of this group, for which the most significant findings are reviewed in this chapter.