Chapter 1
Chromosomes of Hymenoptera

Abstract Karyotypic features of the order Hymenoptera are reviewed. Main genetic features of the life cycle, i.e. arrhenotoky (sometimes changed to thelytoky) and haplodiploidy, are discussed. Models of sex determination in Hymenoptera are listed. Diversity of chromosome numbers, including ploidy levels, and general chromosomal morphology in the order are briefly reviewed. Various structural features of mitotic chromosomes (chromosome size, centromere position and centromere index, euchromatic and heterochromatic segments, nucleolus organiser, etc.) including different banding techniques, such as C-, AgNOR-, G- and restriction banding, fluorochrome staining and in situ hybridisation (FISH, chromosome painting) are described. Details of meiosis as well as the structure of meiotic chromosomes of Hymenoptera are reviewed. The diversity of chromosome sets in various hymenopteran taxa (including types of chromosomal rearrangements detected in the order) is shown. Taxonomic and phylogenetic implications of karyotypic analysis of Hymenoptera are described.

Keywords Chromosomes · Hymenoptera · Karyotype · Phylogeny · Taxonomy

1.1 Karyotype Structure of Hymenoptera

1.1.1 Main Genetic Features of Life Cycle

The mechanism of sex determination in Hymenoptera attracted researchers’ attention for a long time. In the middle of the nineteenth century Dzierzon (1845, cited in Crozier 1975) suggested that arrhenotoky, i.e. development of males (in contrast to females) from unfertilised eggs, was characteristic of the honeybee (Apis mellifera Linnaeus). Cytological proofs of this hypothesis, however, were obtained only at the borderline between the nineteenth and twentieth centuries (Paulcke 1899, Petrankewitsch 1901). Data on arrhenotoky in other Hymenoptera appeared at approximately the same time (Wheeler 1903, 1904, Castle 1904), although acceptance of its widespread occurrence in the order lasted for dozens of years (Sanderson 1932, Heimpel and de Boer 2008).
The second genetic characteristic of the hymenopteran life cycle that is also tightly bound to arrhenotoky is haplodiploidy, i.e. presence of haploid males and diploid females in the overwhelming majority of those insects. This means that at least the large part of the male’s tissues (including gametes) remains haploid, and therefore an abortive meiosis without decrease in chromosome number takes place there. This fact has been first discovered by Meves (1904, 1907) in *A. mellifera* and then repeatedly confirmed in other members of the order Hymenoptera (Sanderson 1932, 1988, Torvik-Greb 1935, Koonz 1936, 1939, Schmieder 1938, Mackay 1955, Smith and Peacock 1957, Sharma et al. 1961, etc.).

As mentioned above, arrhenotoky is characteristic of many hymenopterans, although thelytoky (i.e. development of the purely female offspring from unfertilised eggs; White 1973) is detected in some insects belonging to this group (Heimpel and de Boer 2008). Thelytoky does not usually occur in all members of certain taxa; on the contrary, it can be found sporadically in many groups, and arrhenotokous and thelytokous populations of the same morphospecies often coexist (Hung et al. 1988, Stouthamer and Kazmer 1994, Belshaw et al. 1999, Jeong and Stouthamer 2005, Lattorff et al. 2005). The only exception from this rule is gall wasps of the family Cynipidae. In many Cynipidae, alteration of the so-called sexual and parthenogenetic generations is observed within the life cycle. The parthenogenetic generation consists of females of two types that lay unfertilised eggs. These two types differ in that females of the first type give rise only to males, whereas those of the second type give rise only to females of the sexual generation. In turn, offspring of the males and females of this generation are females of the parthenogenetic generation. Thelytoky in these forms as well as in some other species is therefore cyclical (Doncaster 1916, Crozier 1975, Quicke 1997). Another modification of the normal life cycle is found in the ants *Cataglyphis cursor* (Fonscolombe) and *Wasmania auropunctata* (Roger) in which workers are produced by sexual reproduction, but new queens are almost exclusively produced by thelytoky. Moreover, males of *W. auropunctata* also reproduce clonally because the maternal half of their genome is likely to be eliminated from diploid eggs (Pearcy et al. 2004, Fournier et al. 2005).

Although reports on the discovery of sex chromosomes in parasitic (Guhl and Dozortseva 1934, Dreyfus and Breuer 1944) and aculeate Hymenoptera (Kerr 1951) appeared up to the middle of the twentieth century, it is now considered proven that these chromosomes are absent from hymenopteran karyotypes (White 1973, Crozier 1975). Nowadays, it is widely accepted that sex determination in Hymenoptera occurs through allelic interactions modulated by ploidy levels of individuals (Snell 1935, Crozier 1971). If relatively rare mutations are excluded (see e.g. Beukeboom et al. 2007), hymenopteran females are usually diploid and their males are haploid, although diploid males were also detected in some species (Whiting and Whiting 1925, Speicher and Speicher 1938, 1940, Woyke 1969, Smith and Wallace 1971, Hung et al. 1972, Kerr 1974, Hedderwick et al. 1985, Tsuchida et al. 2002, Cowan and Stahlhut 2004, etc.). Although the single multiallelic locus, *csd*, was previously thought to be involved in sex determination in the Hymenoptera (Beye et al. 2003, Evans et al. 2004), this locus was recently found