SEX CHROMOSOMES AND SEX DETERMINING MECHANISMS IN ODONATA, WITH A REVIEW OF THE CYTOLOGICAL CONDITIONS IN THE FAMILY GOMPHIDAE, AND REFERENCES TO THE KARYOTYPIC EVOLUTION IN THE ORDER

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The morphological and kinetical features of the odonate sex chromosomes are reviewed and trends of the evolution of different modes of sex determination in the order are considered. The cytological conditions in the family Gomphidae are of particular importance for the understanding of the evolution of sex determination in dragonflies and are discussed in detail.

The original mode of sex determination in Odonata is of the XO/XX type, the male being the heterogametic sex, and is observed in all primary complements (cf. KIAUTA, 1967) regardless of the chromosome number viz. the degree of phylogenetic advancement and specialisation achieved by the taxons concerned.

The mean length of the sex chromosome and the ratio between the longest autosomal bivalent and X are not characteristic at superspecific taxonomic levels. In the male the sex chromosome is usually positively heteropycnotic at all spermatocyte stages, save metaphase and anaphase, whereas in the female it is nearly without exception isocyclic. The first maturation division is equational for X, the second is reductional.

In secondary complements a neo-XY sex determination occurs, in those cases where the original X was involved in a fusion with an autosome. Its occurrence is not related to phylogeny.

The neo-XY condition is often reversible: it occurs in some cells (or stages) while not in others of the same individual. If stabilised, it tends to evolve further, as it was demonstrated in Gomphidae, into a secondary XO type. The process has three stages, with an intermediate neo-X neo-neo-Y sex determination and a final numeric reduction of the diploid complement by two elements.

It was demonstrated, that the present type number of Gomphidae is of secondary rather than of primary origin.

Introduction

So far the chromosome complements of nearly 400 dragonfly species
belonging to 17 families of the three living suborders have been examined. Though incomplete, the reviews by Cumming (1964a) and Crudên (1968) include most of the hitherto published evidence on the odonate chromosome numbers. Sex chromosomes are recognizable in species assigned to all families studied, but no special attention has ever been payed either to the morphological and kinetical features of the sex chromosomes, or to the general aspects of the sex determination in the order. The sole exceptions are the publications by Oguma (1930), Oksala (1943), Seshachar & Bagga (1962), Kiauta (1967, 1968b) and Kiauta & van Brink (1968).

The more primitive type of sex determining mechanism in organisms is the XY-XX mode, from which it is supposed that the other mechanisms have been derived (White, 1954; Saëz, 1963; Darlington, 1965). In dragonflies, however, the combination XY-XX has secondarily originated from the XO-XX type. The latter is met with in most of the odonate species examined. The male is the heterogametic sex.

McGill (1904) was the first to note the sex element ("accessory chromosome") in Anax junius (Drury). She did not yet recognize its proper sexual nature; nevertheless, she described and figured correctly its postreductional conduct during meiosis. The latter has been confirmed by numerous subsequent workers, but two exceptions to the general rule were published by Smith (1916) and Makalowskaja (1940).

Lefèvre & McGill (1908) were the first to suggest a possible sexual character of the "accessory chromosome" in Anax junius (Drury). But it was Smith (1916) who ultimately recognized it as the sex element in Sympetrum semicinctum (Say).

The neo-XY-XX mode of sex determination was discovered in dragonflies by Makalowskaja (1940). Although she properly described and figured the situation in Aeshna grandis (L.) and A. juncea (L.), she apparently did not understand the phenomenon. Oksala (1943) dealt in extenso with the behaviour of the sex chromosomes in neo-XY complements of several species of the same genus. Several more cases of this mode of sex determination were brought on record by Ray Chaudhuri & Das Gupta (1949), Omura (1955), Seshachar & Bagga (1962) and Crudên (1968).