# Evolution of the chromosome complement in Odonata[1])

by

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So far the chromosome complements of some 240 odonate species have become known. This figure represents approximately 4% of the total number of species described. The distribution of chromosome numbers within the order is given in Table I. Haploid chromosome numbers range from 3 tot 15; n = 13 being considered as the type number of the order (sensu WHITE 1954). It is found in some 58% of the species examined.

Table I

| Taxonomic group | Species examined | Type No | Number of species with the haploid complement (n) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 3 | 3-4 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 13-14 | 14 | 15 |
| O r d e r | 236 | 13 | 1 | 1 | | 1 | 1 | 1 | | 4 | 4 | 5 | 30 | 138 | 2 | 46 | 2 |
| ZYGOPTERA | 70 | 13? | | | | | 1 | | | 1 | | | 2 | 31 | | 34 | 1 |
| Platystictidae | 1 | 13? | | | | | | | | | | | | 1 | | | |
| Protoneuridae | 2 | 14 | | | | | | | | | | | | | | 2 | |
| Platycnemididae | 4 | 13 | | | | | | | | | | | | 4 | | | |
| Coenagrionidae | 31 | 14 | | | | | | | | | | | | | | 31 | |
| Pseudostigmatidae | 2 | ? | | | | | 1 | | | | | | | | | | 1 |
| Megapodagrionidae | 5 | 13 | | | | | | | | | | | | 5 | | | |
| Lestidae | 8 | 13 | | | | | | | | | | | | 8 | | | |
| Pseudolestidae | 1 | 9? | | | | | | | | 1 | | | | | | | |
| Polythoridae | 2 | 12? | | | | | | | | | | | 2 | | | | |
| Calopterygidae | 14 | 13 | | | | | | | | | | | | 13 | | 1 | |
| ANISOZYGOPTERA | 1 | 13? | | | | | | | | | | | | 1 | | | |
| Epiophlebiidae | 1 | 13? | | | | | | | | | | | | 1 | | | |
| ANISOPTERA | 165 | 13 | 1 | 1 | | 1 | | 1 | | 3 | 4 | 5 | 28 | 106 | 2 | 12 | 1 |
| Gomphidae | 22 | 12 | | | | | | | | | 2 | 2 | 18 | | | | |
| Petaluridae | 3 | 9? | | | | | | | | 2 | 1 | | | | | | |
| Aeshnidae | 21 | 14 | | | | | 1 | | | | 1 | 1 | | 4 | 2 | 12 | |
| Cordulegasteridae | 2 | 13 | | | | | | | | | | | | 2 | | | |
| Corduliidae | 7 | 13 | | | | | | | | | | 1 | | 6 | | | |
| Libellulidae | 110 | 13 | 1 | 1 | | 1 | | | | 1 | | 1 | 10 | 94 | | | 1 |

Several investigators have discussed the evolution of odonate chromosome numbers. Some expressed the opinion that the chromosome numbers lower than the type number came about by fusion of elements of the ancestral karyotype (OKSALA 1943, SESHACHAR & BAGGA 1962, CUMMING 1964a, 1964b), others considered the m-chromosome as an autosome undergoing a gradual diminution in volume until it eventually disappears (OGUMA 1930, DASGUPTA 1957). The latter hypothesis became known as the m-chromosome theory and is the only one so far available dealing with the karyotype evolution of the whole order.

Four main objections could be raised against these hypotheses: (1) they either do not consider or misinterpret the phylogenetic position and structural advancement (specialisation) of the taxonomic groups involved, (2) they are taking as starting point for evolutionary speculations the family type numbers, giving them *eo ipso* the meaning of ancestral numbers, (3) they fail to account for chromosome numbers exceeding the family type number, and (4) the m-chromosome theory is

built up on an *ad hoc* assumption of gradual diminution and eventual disappearance of one autosome after another, which is in contradiction with the observation that the total chromosome length in, say, n = 14 species is about the same as in n = 3 species.

We propose a new hypothesis in which both phylogenetic and cytological data are being taken into account.

Combining the family type numbers with the geological age of the families involved, the following pattern can be established:

(1) More than 90% of the species belonging to families known already from the Mesozoic epoch possess chromosome numbers lower than the type number of the order (Gomphidae, Petaluridae);

(2) This percentage amounts to about 10% among the families known from the Tertiary onwards only (Pseudolestidae, Polythoridae, Aeshnidae, Corduliidae and Libellulidae);

(3) All species belonging to families in which no fossil representatives are known possess chromosome numbers equal to or higher than the type number of the order.
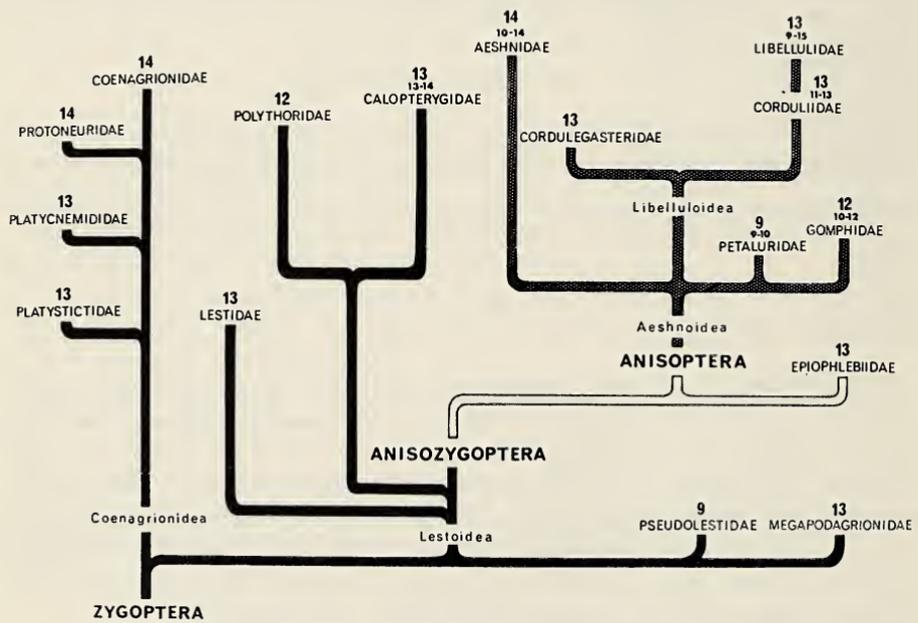


Fig. 1. FRASER's phylogenetic tree, limited to the cytologically examined families. Figures indicate the family type numbers and the range of numerical variation (if any). Secondary complements below n = 9 are not included.

If FRASER's genealogical tree (1957), based on four fundamental structural characters, is combined with palaeontological records and cytological findings (Fig. 1), it provides evidence for the following conclusions:

(1) The chromosome numbers do reflect neither the phylogeny of the order nor the affinities between and within the families;

(2) Generally speaking, the geologically old groups, which in the present-day fauna are represented only by a small number of primitive, often discontinuously distributed species, possess low chromosome numbers, whereas advanced or geologically young families as a rule have numerically high complements, regardless their affinities and origin (*Epiophlebia* etc.).
Therefore,

(3) high chromosome numbers are an indication of a high degree of advancement and specialisation. This conclusion is of basic importance for the understanding of the karyotype evolution of the order.

The determination of the ancestral chromosome number is, in our opinion, the central problem.

Karyotypes of dragonflies can be divided roughly into two groups: (1) the "normal", high-n complements (n = 9 to 15), and (2) the low-n complements (n = 3 to 7). Between the two there is a clear gap, since no dragonfly is known with a haploid chromosome number of 8. Chromosome size in the hign-n species is approximately half that in the low-n species. The parallel between the increase in specialisation and the increase of the chromosome number is valid for the high-n complements only. The low-n species can be found in various systematic groups, of any type number. This has been demonstrated most clearly by the discovery of a normal-n and a low-n population of one and the same species (*Orthemis ferruginea* (Fabr.)), n = 12 and n = 5 (CUMMING 1964a, 1964b). This being so, the low-n karyotypes are of secondary origin and do not offer any base for the determination of the ancestral chromosome number.

Among the high-n complements, on the other hand, the lowest number n = 9, seems actually the most probable approximation to the ancestral chromosome number of the Odonata. On palaeontological grounds one could suggest that this number represents the true ancestral complement of the order. It is found in the families Pseudolestidae and Petaluridae. The latter family is doubtless the most archaic and phylogenetically the most primitive among living dragonflies. Another primitive and early side line are the Gomphidae the chromosome number of which
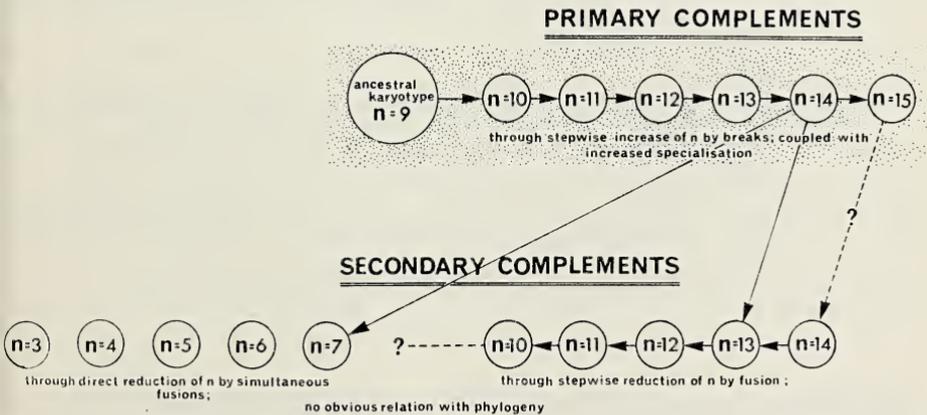


Fig. 2. Explanation in text.

in many species deviates but slightly from the supposed ancestral number. Among the more specialised forms, only one case of n $=$ 9 is known (*Perithemis,* Libellulidae).

It seems most likely that the present numerical variation in odonate karyotypes has developed by the occurrence of breaks leading to haploid numbers 10 to 15 and by fusions leading to haploid numbers 3 to 7 in ancestral forms which had a chromosome number n $=$ 9.

The high-n karyotypes are not homogenous by origin either. Fusion of two or a few elements gives rise to secondary high-n types (14 $\rightarrow$ 13 $\rightarrow$ 12 etc.). In many such cases the fusion can be traced because the fused chromosomes are significantly longer than the other chromosomes of the set. If only two chromosomes are fused, the sex chromosome is usually involved, and a neo-XX/XY sex determination mechanism replaces the usual XX/XO type. The fusion is not always found in all populations of the same species, nor does it always occur in all cells of one individual (*Aeshna grandis* (L.), etc.).

Figure 2 illustrates our hypothesis of karyotype evolution in dragonflies. It has the advantage of (1) being based on independantly obtained evidence regarding phylogenetical position and karyotype; (2) being able to account for any chromosome number.

Nothing can be said at present regarding the nature of breaks and fusions. The diffuse nature of the centromere however, makes the survival of chromosome fragments possible.

It is interesting to note that low-n complements were found in tropical species only, whereas secondarily reduced high-n complements so far have been recorded only in dragonflies from the Temperate Region.

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Dagvlinder op licht. In 1967 zat omstreeks 1 uur op een nacht bij windstil weer een *Thecla betulae* L. bij de lamp.

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