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CONSIDERATIONS ON THE EVOLUTION OF THE CHROMOSOME COMPLEMENT IN ODONATA[1]

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The views of earlier authors on the karyotypic evolution in dragonflies are criticised and a new hypothesis is proposed. It is based on integration of independent karyological, morphological and paleontological evidence, is accounting for the origin of any chromosome number, and is in agreement with the evidence found and the opinions expressed so far on the course of the karyotype numerical evolution in the other insect orders possessing holokinetic chromosomes.

It seems most likely that the present numerical variation in odonate karyotypes has developed through the occurrence of breaks (leading to haploid numbers 10 to 15) and fusions (leading to the complements 3 to 7) in ancestral forms which had n = 9.

Low-n complements have been reported for tropical species only, whereas secondarily reduced high-n complements so far have been recorded only in dragonflies from the Temperate Region.

The biological significance of the karyotype variation within a species is considered and a list of the known dragonfly hybrids is given.

Introduction

Several investigators have discussed the evolution of odonate chromosome numbers. Some expressed the opinion that chromosome numbers lower than the type number (sensu WHITE, 1954) came about by fusion of elements of the ancestral karyotype (OKSALA, 1943; SESHACHAR & BAGGA, 1962; CUMMING, 1964 a, 1964 b). Others considered the micro-chromosome found in many species 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

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so far available dealing with the karyotype evolution of the whole order.

In our opinion 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 and therefore do not agree with geological and phyletical evidence, (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, (4) the m-chromosome theory is built on an ad hoc assumption of gradual diminution and eventual disappearance of one autosome after another, which cannot be proved and therefore this theory cannot be regarded as satisfactory. If other, known or observable factors can be found which in a simple way explain the evolutionary process in the karyotype revealed by geological and other evidence, they are to be preferred to ad hoc assumptions.

It is worthwhile to examine the possibilities of building up an evolutionary hypothesis, which would be reasonable from the cytological point of view and would provide a chance for testing by other evidence. It is necessary, therefore, to consider the available data in some detail.

Numerical Variation in the Chromosome Complement

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 1. Haploid numbers range from 3 to 15. In general, however there is little numerical variation in the dragonfly chromosome complements. The haploid numbers 12, 13 and 14 are represented in more than 90% of the Odonata examined, $n = 13$ being considered as the type number of the order. It is found in some 58% of the species studied cytologically.

TABLE 1

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
Order	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

Chromosome Numbers of Odonata in View of the Paleontological Record and the Zoogeographical Evidence

Among all cytologically examined families only *Gomphidae, Petaluridae* and *Cordulegasteridae* are known from the Mesozoic beds, whereas the true *Platycnemididae, Coenagrionidae, Megapodagrionidae, Lestidae, Pseudolestidae, Polythoridae, Calopterygidae, Aeshnidae* (?), *Corduliidae* and *Libellulidae* were either never found or did not appear until the Tertiary epoch. It is probable, however, on the basis of the morphological structure of their oldest known fossil forms, that some of the latter families had their direct ancestors in the Late or in the Middle Mesozoic. This applies particularly to the *Megapodagrionidae, Lestidae, Pseudolestidae* and *Aeshnidae.*

As an auxiliary method the zoogeography is also of considerable importance for the estimation of the relative phylogenetic value of some taxonomic groups. Of particular interest is the paleogenic fauna (sensu TILLYARD, 1914, 1917), which has to be discussed here since certain cytologically examined families could be classified as its elements.

Only two species belonging to a single genus of *Epiophlebiidae* are known from Japan and the Himalayas respectively. This is almost certainly the very last stage in the distribution of a very archaic group. According to ASAHINA (1954) the family is most clearly related to the anisozygopterous Heterophlebioidea of the Lias period. It was placed into this superfamily by TILLYARD & FRASER (1938–1940) and FRASER (1957), but ASAHINA (1954) formed a new superfamily to contain the only two known species. In view of the high chromosome number of *Epiophlebia* (*E. superstes* Calvert, $n = 13$; OGUMA, 1951) and in connection with the parallel between high chromosome numbers and high degree of advancement (to be discussed below) it is interesting to note that many of the extinct species of Heterophlebioidea often show, in some characters, a more advanced feature than the recent *Epiophlebia.*

The *Petaluridae* are another very ancient, once flourishing and widespread family, which today has a typically paleogenic distribution (Japan, Australia, New Zealand, South- and North America). This distributional pattern combined with their archaic morphological structure, affords convincing evidence that the family is but a remnant of an earlier fauna. This is the smallest anisopterous group, the adults of which possess a mixture of gomphid, aeshnid and cordulegasterid characters with a hint of libellulidan families. It contains nine recent species belonging to five genera classified into two subfamilies. The fossil genera are known from the Jurassic period (Solenhofen).

The *Megapodagrionidae*, as defined at present, are morphologically archaic and have a very scattered and cosmopolitan distribution. The family is, however, in our opinion, in need of a revision, therefore it seems preferable to delay the zoogeographical classification.

For similar reasons we refrain from the zoogeographical classification of the *Pseudolestidae*. The family has been split up into three subfamilies, containing two fossil and seven recent genera with coenagrionidan, megapodagrionidan and amphipterygidan characters. The fossils were recovered from the Eocene and Miocene beds of North America, while the recent genera occur in the West Indies, Costa Rica, Suriname, Oriental region and Australia.

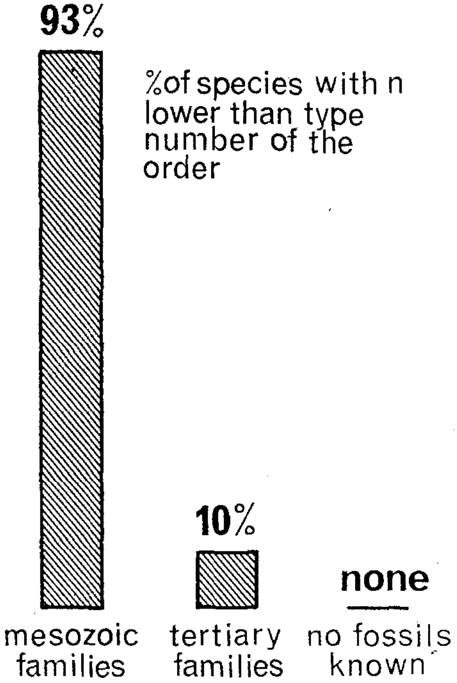
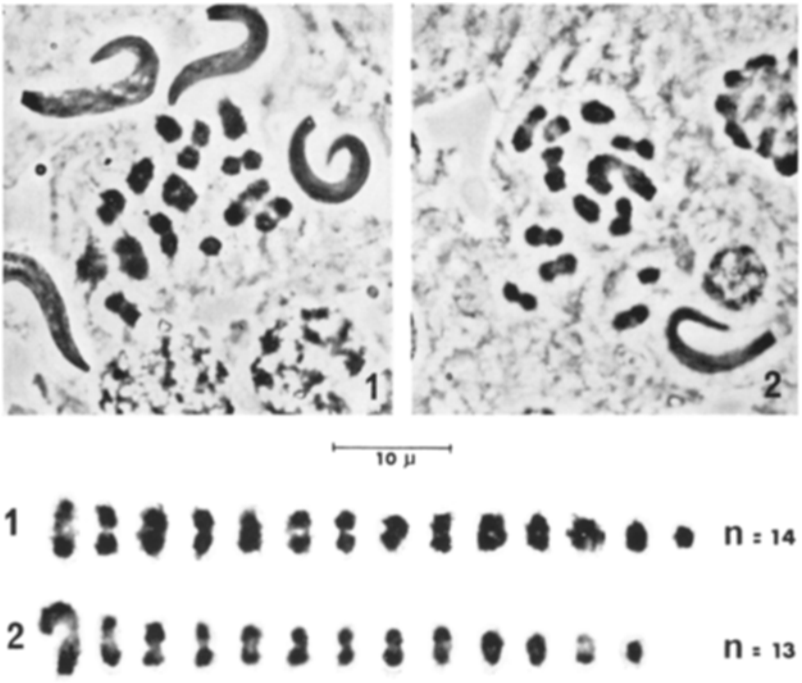


Fig. 1. Chromosome numbers in relation to geological age of the cytologically examined dragonfly families.



Aeshna grandis (L.) (De Bilt, Netherlands). Primary spermatocyte metaphase, polar views. 1. Normal, n = 14, complement. 2. The sex-element attached to an autosome, resulting in an n = 13 complement and in a reversion to the neo XX/XY sex determining mechanism. Note the double length of the first bivalent (× 1500).

If the taxonomic classification of the latter two families were to remain definite, there is scarcely any doubt that they should be classified as paleogenic faunal groups.

Combining the family type numbers with the geological age of the families involved, the following pattern can be established (Fig. 1):

(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, 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.

Affinities within the Order in the Light of the Cytological Evidence

There is a great controversy as to the classification, origin and affinities of the fossil and recent Odonata. Fraser's genealogical scheme of affinities (FRASER, 1957) is doubtless the best interpretation of the inner relationships of the order so far at our disposal. His genealogical tree is based on four fundamental structural characters, viz. the presence or absence of the primary antenodals, the recession of the *Riii* and *Riv* to the proximal position of nodus, the mutual position of eyes and the nature of the ovipositor.

The main features of FRASER's genealogical tree could be summarised as follows:

(1) The Anisozygoptera are not placed at the point of the original divergence of the Zygoptera and Anisoptera, but are considered as an advanced stage of zygopteran evolution, which finally led to the modern Anisoptera.

(2) Zygoptera have the most primitive origin of the recent Odonata.

(3) *Coenagrionidae*, although at present the most advanced and dominant family of the suborder, have an independent origin, which is more ancient than that of any other present-day dragonflies.

(4) The Anisoptera are direct descendants of the Anisozygoptera.

(5) *Aeshnidae* and *Libellulidae* represent the most advanced and successful forms of the present-day Odonata.

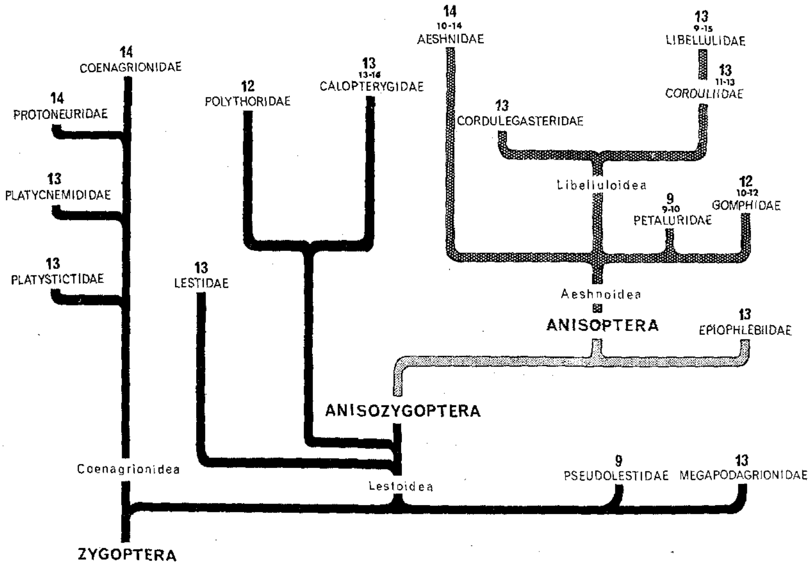


Fig. 2. FRASER's phylogenetic tree, limited to the cytologically examined families. Figures indicate the family type numbers and the range of numerical variation (if any). The secondary complements below n = 9 are not included.

If FRASER's scheme is combined with cytological findings (Fig. 2), the following features can be pointed out:

(1) In all of the most advanced, at present dominant and specialised families (*Coenagrionidae*, *Aeshnidae*, *Libellulidae*) the high chromosome numbers prevail. A high number should be considered, therefore, as an indication of advancement.

(2) Bearing this in mind, the *Protoneuridae* are more specialised than any other family of the group, save the *Coenagrionidae* (cf. also LIEFTINCK, 1953).

(3) Among the Lestoidea the *Lestidae* are more advanced than usually supposed, and *Pseudolestidae* are the most primitive family of the living Zygoptera.

(4) *Polythoridae* are more generalised than any other cytologically examined family derived from the amphipterygidan stock, but, unfortunately, nothing is known of the cytology of the *Amphipterygidae* themselves.

(5) Although an ancient form, *Epiophlebiidae* represent a rather

advanced side line of the Anisozygoptera. They should be considered as an autogenic relic of a paleogenic group.

(6) Aside from various morphological characters, the cytological evidence too, shows the highly heterogeneous nature of the superfamily Aeshnoidea, including the advanced and often specialised *Aeshnidae* and the primitive and archaic *Gomphidae* and *Petaluridae.*

(7) *Libellulidae* are cytologically very uniform and, in general, advanced and often specialised.

Another interesting genealogical tree has been produced by ANDO (1962). It is based on embryological characters and deviates from FRASER's conception.

It is interesting that ANDO too, on embryological grounds, regarded *Lestidae* as a rather specialised family, but, contrary to the cytological evidence, he considered *Calopterygidae* and *Coenagrionidae* as being more generalised than *Lestidae.* Further he has stressed that *Megapodagrionidae* are akin both to *Lestidae* and *Epiophlebiidae.* The cytological evidence supports this view only to the extent that the chromosome numbers of these families are the same. As to Aeshnoidea he considered *Aeshnidae* and *Petaluridae* to be closely related to each other, but *Gomphidae* should form a separate branch. The cytological evidence does not support this view.

BULLENS (1966) recently outlined an interesting genealogical scheme based upon structure of the larval gizard of nine major families. She considered *Coenagrionidae* as highly specialised, but placed *Lestidae* at the base of the line branching from *Platycnemididae* and leading over *Lestidae, Aeshnidae* and *Cordulegasteridae* towards the *Libellulidae,* and *Petaluridae. Gomphidae* constitute a side line of BULLENS' concept, the very base of which is formed by the *Calopterygidae.*

The above evidence leads to the following important 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 high chromosome numbers, regardless of 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 m-Chromosome Theory

The m-chromosome theory as first proposed by OGUMA (1930) and further developed by DASGUPTA (1957) is the only available hypothesis dealing with the karyotype evolution of the whole order.

DASGUPTA visualised the karyotype evolution as a result of the gradual diminution and final disappearance of one autosome after another, the intermediate stage being indicated by the presence of a pair of m-autosomes (= micro-chromosomes – due to their inferior size when compared to the other autosomes). In this way DASGUPTA was, of course, forced to take for the ancestral number the complement $n = 14$ ($= 13\,a + X$), the highest chromosome number known at that time in the order. This complement appears as type number in the most advanced families *Coenagrionidae* and *Aeshnidae*, which were therefore interpreted as the most primitive ones.

The m-chromosome theory is, in our opinion, not tenable because of (1) its interpretation of the course of evolutionary development in the direction from high-n to low-n complements, resulting in the consequent assumption of the phylogenetic primitivity of the families that actually are most advanced (as proven in many ways by non-cytological evidence) and (2) because of the ad hoc assumption of gradual disappearance of one autosome after another, which is in contradiction with the observation that the total chromosome length in $n = 14$ species is about the same as in $n = 3$ species. Besides, the gradual disappearance of one autosome after another would cause the loss of such an amount of DNA that it would hardly be feasible.

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

The Ancestral Chromosome Number

Karyotypes of dragonflies can be divided roughly in two groups (Fig. 3): (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 number of 8.

Chromosome size in the high-n species is approximately half that in the low-n species.

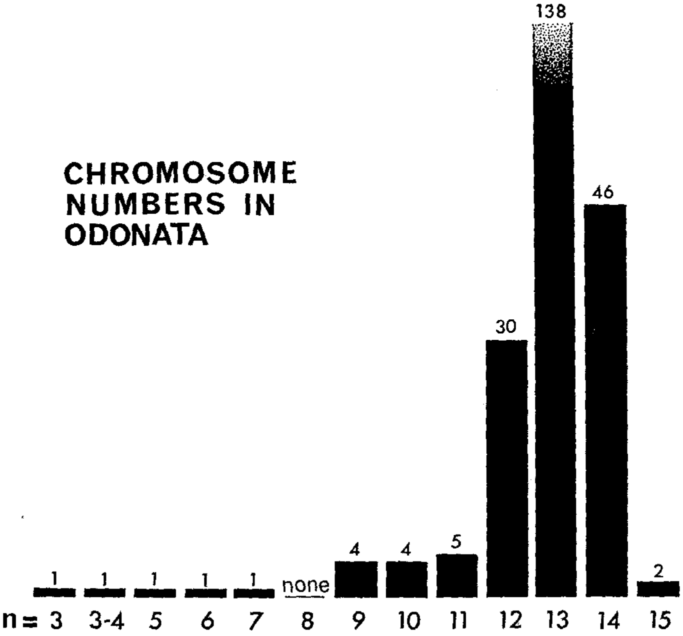


Fig. 3. Histogram of the haploid chromosome numbers in Odonata.

The parallel between the increase in specialisation and the increase of the chromosome number is apparent in the high-n species 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, 1964 a, 1964 b). This being so, the low-n complements are of secondary origin and do not offer any basis 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 of the ancestral chromosome number of the Odonata. On paleontological grounds one could suggest that this number represents the true ancestral number of the order. It is found in the most primitive families *Pseudolestidae* and *Petaluridae.* The latter family is doubtless the most archaic and phylogenetically the most primitive among living dragonflies. Similar is the case of the family *Pseudolestidae.* Another primitive and early side line are the *Gomphidae* in which chromosome numbers, in many species, deviate but slightly from the supposed ancestral number. Among the more specialised forms, only one case of n = 9 is known (*Perithemis lais* [Perty], *Libellulidae*). For these reasons it can be assumed that the complement n = 9 represents most probably the ancestral chromosome number of the order.

Proposed Hypothesis of the Karyotypic Evolution in Odonata

It seems most likely that the present numerical variation in odonate karyotypes has developed through the occurrence of breaks (leading to haploid numbers 10 to 15) and fusions (leading to haploid complements 3 to 7) in ancestral forms of n = 9.

The high-n karyotypes are not homogeneous in origin either. Fusion of two or a few elements gives rise to secondary high-n types (14 → 13 → 12, etc.). In many such cases the fusion can be traced because the fused chromosomes are significantly longer than the other elements of the set. If only two chromosomes have fused, the sex-chromosome is usually involved, and a neo-XX/XY sex-determining 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 (Pl. I).

This hypothesis of karyotypic evolution in dragonflies has the

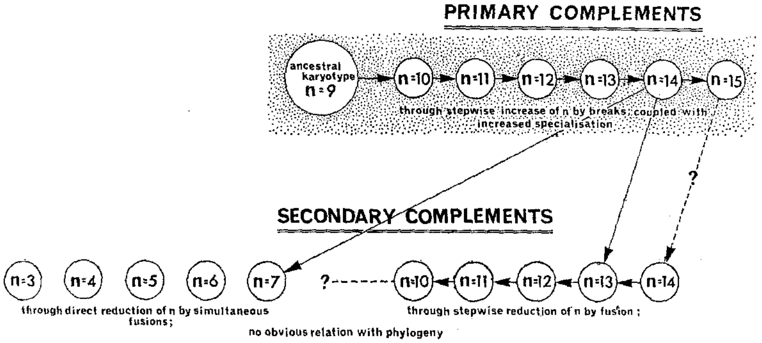


Fig. 4. Graphic interpretation of the proposed hypothesis. Explanation in text.

advantage of (1) being based on the integration of independent karyological, morphological and paleontological evidence, and (2) accounting for the origin of any chromosome number. Its graphical interpretation is given in Fig. 4.

Geographical Aspect of the Karyotype Evolution in Odonata

On the basis of the material so far examined an analysis of the geographical aspect is hardly justifiable. The material covers only Europe, the Far East, parts of tropical Asia, South America and a part of North America, wheras nothing is known on the cytology of African and Australian (continental) dragonflies. In spite of these gaps in our knowledge, a geographic pattern seems to be detectable.

The low-n complements have been reported for tropical species only, whereas secondarily reduced high-n complements so far have been recorded only in dragonflies from the Temperate Region.

This pattern should be understood as strictly provisional until the results of the future investigations will either confirm or deny it.

Biological significance of the karyotype variation within a species, with notes on species hybrids in dragonflies

Because of the lack of visible structural differentiation in dragonfly chromosomes, only gross rearrangements which led to changes in chromosome number could be observed. The biological significance of any rearrangements is reflected in their adaptive value and in the possible production of cytological isolation mechanisms between two karyologically different populations of the same species. Consequently, they are of great importance in the process of speciation. In this connection it is worthwhile to review the information on dragonfly hybrids.

Laboratory crossings of insects originating from karyologically different populations or belonging to different (infra) specific forms were, to our knowledge, never attempted with dragonflies (cf. interesting crosses made by KAWAGUCHI, 1923, between *Bombyx mori* and *B. mori mandarina*, which provided the evidence that the m-chromosome in this lepidopteron is but a part of a broken autosome).

In nature interspecific copulation is prevented by mechanical, geographical, ecological and ethological (territoriality) isolation mechanisms. Nevertheless, it happens occasionally that interspecifically mixed pairs succeed in achieving the copulatory position, but such pairs greatly outnumber the actually recorded hybrids.

To our knowledge the following intermediate specimens were so far reported as hybrids:

(1) *Coenagrion pulchellum* (v.d. Lind.) × *C. puella* (L.). A male hybrid is described and illustrated by BILEK (1963).

(2) *Enallagma civile* (Hagen) × *E. carunculatum* Morse. WILLIAMSON (1906) examined 500 males of these species, originating from a locality where these damselflies were extremely abundant, and found 20–30 clearly intermediate specimens. They were not described morphologically.

(3) *Gomphus lividus* Sel. × *G. graslinellus* Walsh. A male hybrid was described and figured by WILLIAMSON (1903). MUTTKOWSKI (1910) assigned a specific name (*G. williamsoni*) to it. The intermediate character of the single known individual is very clear and no other such specimen has ever been found. Its hybrid nature can be therefore, safely assumed.

(4) *Gomphus crassus* Hagen × *G. fraternus* (Say). WILLIAMSON (1906) recorded intermediate, specifically indeterminable specimens, taken in a locality where the above mentioned species were very abundant, and which are most probably hybrids. They were not described morphologically.

(5) *Aeshna* (*Hesperaeschna*) *confusa* Ramb. × *Ae.* (*Neureclipa*) *diffinis* Ramb.

A probable male hybrid was recorded and partially described by CALVERT (1956) on the basis of a personal communication by René Martin.

(6) *Anax imperator* Leach × *A. parthenope* Sel.

A male hybrid described and figured by BILEK (1955).

The general features of these few known hybrids could be summarised as follows:

(1) All of them are species hybrids, although the parents may belong to different subgenera.

(2) All hybrids of which the sex has been reported are males.

(3) In the case of *Coenagrion* the chromosome number and the gross morphology of karyotype are the same in the two parent species.

This is almost certainly true also for the *Enallagma* and *Anax* hybrids. An equal chromosome number is fairly probable in the case of *Gomphus* as well, but a certain numerical variation within the genus should be taken into account.

The supposed hybrid of *Aeshna* would be particularly interesting. The chromosome number of the nominate form *diffinis* is n = 11, but nothing is known on the cytology of *Ae. confusa*. The numerical variation among the cytologically examined species of the genus is rather broad (from n = 10 to 14).

The subgeneric affinities within the genus *Aeshna* were reconstructed by WALKER (1912) and CALVERT (1956). Their genealogical tree, however, does not agree with our general observations as recorded in the present paper and according to which the specialised forms have higher chromosome numbers than the more primitive ones. The so far examined *Aeshna*-subgenera have the following chromosome numbers: *Marmaraeschna:* n = 10, *Neureclipa:* n = 11, *Aeshna, Coryphaeschna* and *Hesperaeschna:* n = 14.

Review of the Evidence on the Chromosome Evolution in other Insect Orders Possessing a Diffuse Centromere

The course of the karyotype numerical evolution in Odonata, as suggested in this paper, is in close agreement with the evidence found and the opinions expressed so far on the subject in the other insect orders possessing holokinetic chromosomes (Dermaptera[?], Mallophaga, Siphunculata, Heteroptera, Homoptera, Lepidoptera, Trichoptera, some Coleoptera[?]). The following similarities with the pattern of the chromosome evolution in Odonata could be pointed out:

(1) Chromosome fusions and transversal fragmentations are suggested to be generally responsible for the variation in chromosome numbers in all insect orders possessing a diffuse kinetochore. They can cause a numerical variation at any taxonomic level (SHINJI, 1931; HALKKA, 1959; GUPTA, 1964; BROWN, 1965; SUOMALAINEN, 1966; UESHIMA, 1966).

(2) Family type numbers are detectable in most Homoptera and Heteroptera, but are lacking in the Lepidoptera and in Trichoptera. In the last two orders mentioned the DNA contents of the karyotype

should be measured. It is likely that a family pattern could be found in this way.

(3) The parallel between the increased specialisation and/or advanced phylogenetic position on one hand, and the increased chromosome number on the other, exists at least in some homopteran groups (*Aphididae*, e.g. SHINJI, 1931) and in Heteroptera (e.g. LESTON, 1957). The reverse situation has never been proved for any of the groups so far studied cytologically.

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