CYTOGENETIC STUDIES IN THE ORDER ODONATA

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PREFACE

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TABLE OF CONTENTS

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INTRODUCTION

In the past 60 years descriptions of the karyotypes of something over 100 species of Odonata have appeared. Most of the work has been purely descriptive but some of it has included interpretation and analysis. Although the early work contributed little to the understanding of structural and behavioral details of odonate chromosomes in modern terms, a pattern of morphological uniformity throughout the order became apparent.

The first worker to make a comprehensive study of dragonfly chromosome was McGill (1904, 1907; Lefevre and McGill, 1908) who studied spermatogenesis of Anax junius, though Carnoy (1885) had reported some apparently erroneous chromosome numbers for Calopteryx virgo some years earlier. Oguma reported chromosome numbers for eight species in one paper (1915) and mentioned several of these again while adding one more species in a later paper (1917). In both of these reports Oguma described the odonate karyotypes very briefly and these descriptions were presented along with a few from other groups of insects. Smith (1916) gave a rather extensive description of spermatogenesis in Sympetrum semicinctum and a briefer account of spermatogenesis in Libellula basalis. The next contribution came from Fuchsowna and Sawczyncska (1928) who described the chromosomes of Aeshna grandis and Libellula quadrimaculata.

Oguma (1930) then described the karyotypes of 16 species, some of which he had dealt with earlier (1915, 1917). His approach was somewhat different, however, in the 1930 paper. He picked closely related groups of species to see how much variation there is between closely related species. He concluded that sometimes the karyotypes of closely related species are indistinguishable and sometimes there are observable differences. This conclusion has been borne out frequently in later work. Oguma (op.cit.) also introduced the term "m-chromosome" to odonate karyotype studies, and it has proved to be a useful one. In the Odonata, the smallest pair of autosomes may be called m-chromosomes if their size makes them distinctive.

Oguma and Asana (1932) dealt with the chromosomes of two species of dragonflies from India, and then Asana and Makino (1935) described the karyotypes of ten other Indian species. A total of ten species of Japanese Odonata were cytologically described in a series of papers by Kichijo (1930, 1941, 1942a, 1942b) and at about the same time Makalovska (1940) described the karyotypes of 17 European species, one of which had appeared in the earlier literature.

In recent years the number of karyotypes described for the Odonata has grown rapidly and the concept of uniformity has been reinforced. However, a few exceptions to the established pattern have been noted. Ray Chaudhuri and Dasgupta (1949) in their description of the chromosomes of six Indian species recorded the first described XO sex determing mechanism. Toyoshima and Hirai (1953) gave a brief account of the chromosomes of four Japanese species, and Hirai (1956) redescribed

these and added two more. Wolfe (1953) presented data on the karyotype of Uropetala carovei in a comprehensive paper on the biology of the genus Uropetala in New Zealand. In a series of papers Omura (1949, 1952, 1953, 1955, 1957) discussed the chromosomes of 15 species of Japanese Odonata and presented additional information on several already described. Dasgupta (1957) described the chromosomes of 30 species of Indian Odonata.

Particularly important from the standpoint of developing the most widely held present views on the morphology and behavior of odonate chromosomes is the series of papers by Oksala (1939, 1943, 1944, 1945, 1948, 1952). These have been especially valuable in building a theoretical framework against which future observations could be tested.

From the papers cited above has come a general picture of the nature of odonate chromosomes as follows: They are fairly uniform in size with most of the members of the karyotype, except as noted below, not distinguishable from each other. Usually, the X-chromosome can be identified. There is frequently an autosome distinctly smaller than any of the others and this is called the m-chromosome by most authors. Often also there are one or two of the largest autosomes distinguishable on the basis of size. There is little numerical variation. The largest haploid number described for the order prior to the present paper was 14, and the smallest prior to 1962 was 9. The uniformity within families is even more striking. The chromosomes are reported to be monocentric and metacentric (Oksala, 1943, 1948, 1952). There is an X0 type of sex determination with two exceptions having been

noted to date (Ray Chaudhuri and Dasgupta, 1949); Seshachar and Bagga, 1962). Odonata have post-reductional meiosis in both sexes (Oksala, 1943, 1945, 1948). The situation with respect to chromosome morphology in the Odonata is well summed up by Oksala (1952, p. 450-51):

> The chromosome complements of the different species of Odonata are on the whole uniform. The haploid numbers of some 40 European species which have been cytologically examined by the present author are 12, 13, and 14. Genera and even families are characterized by a certain number, deviations from this rule being rare exceptions. The male is always heterogametic, representing the X0 type.
>
> Differences in size between the chromosomes of a complement are slight. Sometimes, however, the largest or the smallest chromosome, or both, can be distinguished from the others. All of the species in which spermatogonial or somatic mitoses have been studied possess chromosomes of one type only. This is metacentric with arms of exactly the same length, if microscopic evidence is to be relied upon. In the species of the genus Aeshna this fact has been verified by a detailed analysis made earlier (Oksala, 1943).

Exceptions to the generalizations listed above have been reported from time to time, but they have been sufficiently unusual or doubtful to remain exceptions. As such they have failed to change in any serious way the conception of the nature of odonate chromosome proposed by Oksala.

The summary of opinion by Oksala, if confirmed, would make the Odonata the only organisms, plant or animal, to combine post-reductional meiosis with monocentric chromosomes (Battaglia and Boyes, 1950); consequently they are of rather unusual cytogenetic interest. The concept of monocentric post-reductional chromosomes has been challenged on theoretical grounds by several workers (Hughes-Schrader, 1948; Lima-de-Faria, 1949; Castro, 1950), but these merely serve to heighten the cytogenetic interest in this group.

Three basic problems have emerged from the work of odonate cytology, although each of these is interrelated. These are: 1. The problem of chromosome numbers — why is there a pattern of uniformity with striking deviations from it? What is the mechanism for evolutionary change in chromosome numbers and what is the adaptive significance for such change? 2. The problem of the kinetochore — what is the real nature of the odonate kinetochore? 3. The problem of post-reductional meiosis — does the concept have any validity? Does it occur in the Odonata as defined by Oksala (1943, 1948), and if not, how should it be defined?

An attempt has been made to answer these questions, and one section of this paper is devoted to each one of the basic problems.

MATERIALS AND METHODS

The material described in this work was collected in Bolivia, Central America, Jamaica, Florida, and Texas. Testes were removed from the living adult males in such a way that a good taxonomic specimen was retained. These specimens are kept in a permanent collection and each can be correlated with a permanent cytological preparation. In field collections, the testes were fixed in Bauer's modification of Bouin-Allen's fixative (Bauer, 1931), were washed in distilled water, and then were stored in 80% ethyl alcohol. Some of the locally collected material was squashed in aceto-orcein with or without sodium citrate pre-treatment. Fixed and stored material was paraffin embedded, sectioned at 10-12 microns and Feulgen stained or was stained and made into Feulgen squash preparations.

Bright field observations were made with a Leitz Ortholux microscope using a 90X apochromatic oil immersion objective with a numerical aperture of 1.32. Observations were made in phase contrast using a Zeiss apochromatic 100X oil immersion objective with a numerical aperture of 1.32 and a Zeiss VZ phase contrast condenser. Original photographs were made with a Leitz Aristophot camera on 4 x 5 inch sheet film at a magnification of 3000 diameters. In reproduction these photographs are reduced to about 2250 diameters. Some retouching has been done on the photographs, but in all cases several photographs are available of the same figure at different focus, and all elements retain their original shape and size.

Approximately 400 cytological preparations and examinations were made of some 150 species, although some of these did not yield useful data.

The taxonomic arrangement is, with minor modifications, that proposed by Fraser (1957). However, one new subfamily is proposed and Calopterygidae is used in place of Fraser's Agrionidae. Species which are undescribed or are of doubtful taxonomic status are designated with numbers.

CHROMOSOME NUMBERS

The Evolution of Chromosome Numbers in the Odonata

Work in odonate chromosome numbers published through 1961 tended to indicate that numerical evolution is extremely conservative in this group. In the suborder Zygoptera all haploid numbers noted were either 13 or 14 (see Table 1). Furthermore, all species described of the family Coenagriidae had an n of 14 and all other Zygoptera had an n of 13. Thus through 1961 there was no described numerical variation within the families of Zygoptera (see Table 2). Three of the seven families of the suborder Anisoptera which had species cytologically described showed some variation, but even in these there is clearly one dominant type number for each family. Deviations from the type number are not common (see Table 1); the family Gomphidae is the only one in which they exceed 10% (27.3%). The percentage of deviations from the type number of 12 in the family Gomphidae is lowered by data presented in this paper to 19%. It is possible that there will be a further decrease in percentage as more data become available. Of the 79 species of Anisoptera which are listed in Table 1, only about 10% (8) deviate from the most common number for their respective families. The number of species which deviate from the type number by more than one approximates 2.5%. Through 1961 there were no published records of species which deviated in chromosome number from the family type number by more than two.

Several workers have attempted to draw phylogenetic implications from differences in chromosome numbers reported for the Odonata (Dasgupta, 1957; Oguma, 1930). Others have expressed doubts that such attempts have any validity due to the small amount of variation which had been reported in odonate karyotypes (Oksala, 1952). The argument for phylogenetic significance seems to be that since odonate karyotypes appear to be very conservative, whatever variation does show up in consistent patterns is quite significant. This reasoning apparently does have validity at the family level in spite of the striking variations which will be described below. The pattern of family type numbers is unmistakable (Table 1) and is further reinforced by data presented in this paper.

The Occurrence of Species of Odonata with Unusually Low Chromosome Numbers

The existence of species of Odonata which do not fit the usual pattern of little variation from a family type chromosome number was first brought to my attention in a personal communication from Mr. R. W. Cruden who had discovered a species of Corduliidae with a haploid number of seven. The type number for this family is 13. He had made counts only at diplotene and expressed the opinion that verification was needed (Cruden, 1961). Subsequently, I discovered several unrelated species of dragonflies with strikingly low chromosome numbers, and one such species has been reported from India (Seshachar and Bagga, 1962). While it remains an unusual phenomenon, there is no longer any question of the occurrence of these low numbers in species of several

families of the order. The term "low n" is used in this paper to refer to a species or population of Odonata the chromosome number of which is about half or less of the type number for the family to which the species belongs. Species whose chromosome number is greatly reduced, but does not approach half of the type number for the family are termed "intermediate cases." Obviously, these two categories blend with each other and with more normal karyotypes, and almost every conceivable degree of numerical reduction probably exists in odonate karyotypes.

The first published report of a case which unquestionably fits into the low n category was that of Hemianax ephippiger (Burmeister) which has a haploid number of seven (Seshachar and Bagga, 1962). This is half of the type number for the family Aeshnidae to which this species belongs.

A low n Species in the Zygoptera

Genus Mecistogaster

On April 12, 1960, a single specimen of a species of the genus Mecistogaster (family Pseudostigmatidae) was taken by the writer on a small stream in thick forest about 4 km. northwest of Carinavi in the province of Nor Yungas of the Department of La Paz in Bolivia. The stream on which the specimen was taken was called "Cañada Naranjacada" the the local residents. Two days later on another stream 1 km. northwest of Carinavi a second specimen of Mecistogaster was taken. Differences in the thoracic color pattern and in the proportions indicated even in the field that two species were involved, although Mecistogaster

is an extremely variable group. The first specimen was designated in the field "Mecistogaster sp. #1" and the second was designated "Mecistogaster sp. #2" (see Figs. 1 and 2). The taxonomic status of these two species is such that they still cannot be assigned specific names and the field designations are thus retained here. The testes of both specimens were removed and prepared as described above. Karyotypes are as follows:

Mecistogaster sp. #1.

n = 15, $2n\sigma^{\prime}$ = 29. The karyotype is very similar to many others described for Odonata except that the haploid number is 15. This is the highest chromosome number yet reported for the order. There is an m-chromosome which forms a bivalent about the same size as the univalent X-chromosome in polar view of metaphase I (Figs. 3a, 3b). Sex determination is of the usual X0 type. The X-chromosome moves early toward one pole of the spindle at metaphase II (Figs. 4a, 4b). Spermatogonial metaphases show 29 chromosomes in polar view (Fig. 5).

Mecistogaster sp. #2.

n = 6, $2n\sigma^{\prime}$ = 12. This is an apparent low n species although the type number for the family Pseudostigmatidae cannot be determined from the material available. Six bivalents are visible in polar view of metaphase I (Figs. 6a, 6b), whereas in metaphas II, polar view, six dot-like elements appear (Figs. 7a, 7b). There is no indication of an X-chromosome preceding to one pole of the spindle nor is there any indication of an unequal or heteromorphic double chromatid in lateral view of metaphase II. In fact, no X-chromosome can be found at any

stage, and no unequal bivalent is apparent at metaphase I which could be interpreted as evidence for a neo-XY system. However, it is probable that the original X-chromosome is fused with two or several autosomes and constitutes such a small proportion of the mass of the new chromosome that the neo-XY system, even though it exists, is not easily demonstrated cytologically. Twelve chromosomes are always visible in clear polar views of spermatogonial metaphases (Figs. 8a, 8b). The lack of an obvious X-chromosome and the very low chromosome number of this species suggest that Mecistogaster sp. #1 has the more "normal" karyotype and is probably closer to the type number for the family. If this is true, Mecistogaster sp. #2 is clearly a low n species.

Low n Species in the Anisoptera

The low n species reported by Seshachar and Bagga (1962) belongs to the subfamily Anactinae of the family Aeshnidae, wherease the low n species discovered by Cruden (1961) occurs in the family Corduliidae. Three low n species from the family Libellulidae have come to light in my own material. The first two of these are from the genus Orthemis which is in the subfamily Libellulinae. The other one is from the genus Macrothemis which is here placed in a different subfamily, Dytheminae, subf. nov.[1] The karyotypes of species closely related to the low n

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1. In Fraser's reclassification of the order Odonata (1957) the arrangement of the Libellulidae is modified from Ris (1909). Most of Ris' groups have become subfamilies of Fraser. However, Fraser completely left "Gruppe IX" of Ris out of the reclassification and none

species are described in both genera. These species, which are presented for comparative purposes, occupy the same geographic region as the low n species and have karyotypes which are relative typical for the family Libellulidae.

Genus Orthemis

Orthemis is a common genus throughout the neotropical area, being represented by about one dozen species. In eastern Bolivia at least four species of this genus fly together along the rivers and larger streams. Two of these species, Orthemis biolleyi Calvert and Orthemis ferruginea (Fabricius) are relatively robust and resemble each other greatly in general form (Figs. 9, 13). The other two species, Orthemis levis Calvert and Orthemis cultriformis Calvert, are more slender and likewise appear quite similar to each other in flight (Figs. 17, 21).

Orthemis biolleyi Calvert

$n = 12$, $2n\,\sigma = 23$. In polar view of metaphase I (Figs. 10a, 10b) there are 11 bivalents and the univalent X-chromosome visible. There is no obvious m-chromosome. The X-chromosome approaches some of the smaller bivalents in size, and in some figures it is hard to distinguish from them. This chromosome, when distinguishable, always seems to occupy a position in the outer ring of chromosomes in metaphase I.

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of the included genera are mentioned in that work. Fraser indicated (1959) before his death that the omission had been inadvertent and that a new subfamily should be set up to include these six new world genera. He suggested that the name Dytheminae be used because Dythemis is the oldest

In polar view of metaphase II, 11 dot-like elements are visible (Figs. 11a,11b). In lateral view of metaphase II, the X-chromosome may be seen preceding the others to one pole (Figs. 12a,12b). The karyotype is very similar to those of most Libellulidae, except that there is no obvious m-chromosome and that the number is one less than the type number for the family.

Orthemis ferruginea (Fabricius)

n = 5, 2n ♂ = 10 (Bolivia); n = 12, 2n ♂ = 23 (Texas). This species was described more than 180 years ago from "America." It is currently recognized as a wide ranging species which occurs in the southern United States, the Antilles and Mexico south to Uruguay and Chile. It appears that eventually what is now considered one species will have to be divided up and placed under more than one specific name. The cytological data presented here apply to the population from eastern Bolivia, around Buena Vista, and to the population from central Texas.

The Texas population has a karyotype virtually indistinguishable from that of O. biolleyi from Bolivia. There is no obvious m-chromosome and the haploid number is 12. Sex determination is of the usual X0 type.

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included generic name. The name Dytheminae is used here to correspond to "Gruppe IX" of Ris (1909) and thus would include: Dythemis Hagen, 1961; Scapanea Kirby, 1889; Paltothemis Karsh, 1890; Brechmorrhoga Kirby, 1894; Macrothemis Hagen, 1868; and Gynothemis Calvert, 1909. Diagnosis of the subfamily Dytheminae may be found in Ris (1909, pp. 33-34).

The Bolivian population of O. ferruginea is a low n population. The four specimens examined in this study from near Buena Vista all have identical karyotypes. In polar view of metaphase I (Figs. 14a, 14b), five bivalents are seen, which are all about the same size. In polar view of metaphase II, five dot-like elements appear (Figs. 15a, 15b). In lateral view of metaphase II, the double chromatids are aligned as in other species of Odonata, but no X-chromosome can be seen at this or any other stage (Figs. 16a,16b).

Orthemis levis Calvert

n = 3, 2n♂ = 6; n = 4, 2n♂ = 8 (Heterozygotes: n = 3, 2n♂ = 7 in MI and MII and in spermatogonial metaphase respectively). Two specimens of O. levis were examined from the population of this species around Buena Vista in Bolivia. Both were numerical heterozygotes, resulting presumably from the fusion of an n = 3 gamete with one for which n = 4. The species is thus low n, but the frequency of the n = 3 and the n = 4 karyotypes in the population cannot be determined on the basis of the small sample available.

In polar view of metaphase I there are three bivalents which may be arranged in various configurations (Figs. 18a,18b). The bivalents are distinguishable from each other on the basis of size, and in these numerical heterozygotes the longest has two constrictions or weakly stained areas instead of the usual median one. The median constriction of odonate bivalents has been interpreted by Oksala (1943) as being the terminalized single chiasma of the bivalent. If, as the same author states occurs in rare instances, two chiasmata form and

terminalize to opposite ends of the chromosomes, a ring bivalent is formed which lies in the plane of the equatorial plate (Oksala, 1943). These ring bivalents have also been seen in low n species of Odonata where they are apparently more frequent than in species with normal karyotypes (Fig. 18b; see also Figs. 6b and 7). In my material, the tripartite bivalent is interpreted as being the result of two chromosomes each pairing with homologous portions of a fused chromosome. Each forms one chiasma which terminalizes to its end of the fused chromosome. The tripartite bivalent is thus a true bivalent in that only two sets of homologous genes are present. Metaphase II shows two dot-like elements in polar view (Figs. 19a, 19b) and in lateral view the double chromatids are balanced in the spindle (Figs. 20a, 20b). No X-chromosome is seen at any stage, nor are there any heteromorphic elements which can be correlated with sex determination. It appears that sex determination occurs as in the other low n species where a definite X-chromosome cannot be found.

Orthemis cultriformis Calvert

n = 12, 2n♂ = 23. In metaphase I, polar view, there are 11 bivalents and the univalent X-chromosome. The X-chromosome is easily identified by its shape and peripheral position. The chromosomes are graded in size from several which are relatively large to a smallest autosome which may be called the m-chromosome (Figs. 22a, 22b). In metaphase II, polar view, eleven dot-like elements are seen and, here also, the m-chromosome can be identified by its size (Figs. 23a, 23b). In lateral view of metaphase II the X-chromosome precedes

the others to one pole of the spindle (Figs. 24a,24b). O. cultriformis differs in karyotype from O. biolleyi chiefly in having a readily distinguishable m-chromosome.

Genus Macrothemis

At least three species of the genus Macrothemis (Libellulidae: Dytheminae) occur together in eastern Bolivia. Macrothemis musiva (Hagen) is a very slender species; Macrothemis hemichlora (Burmeister) is in some ways morphologically intermediate; and Macrothemis mortoni Ris is the most robust (Figs. 25,29 and 33).

Macrothemis musiva (Hagen)

$n = 13$, $2n\,\sigma^{\prime} = 25$. In polar view of metaphase I there are 12 bivalents and the univalent X-chromosome. An m-chromosome is present and the m-bivalent is slightly smaller than the X-chromosome (Fig. 26). In metaphase II twelve dot-like elements are usually seen (Fig. 27, left hand figure). Occasionally the X-chromosome does not precede the others to the pole, and 13 dot-like elements are seen in polar view (Fig. 27, right hand figure). In metaphase II, lateral view, the X-chromosome usually precedes the others to one pole of the spindle (Fig. 28).

Macrothemis mortoni Ris

$n = 13$, $2n\,\sigma^{\prime} = 25$. In metaphase I, polar view, 12 bivalents and the univalent X-chromosome are seen (Fig. 34). The m-bivalent is very small, about half the size of the X-chromosome at metaphase I. In polar view of metaphase II there are twelve dot-like elements, the

m-chromosome being very small (Fig. 35). In metaphase II, lateral view, the X-chromosome is seen preceding to one pole of the spindle (Fig. 36). The principal difference between the karyotype of Macrothemis mortoni and that of M. musiva is that in the former the m-chromosome is relatively much smaller. The whole karyotype appears smaller and more compact in M. mortoni. This is consistent in the specimens I have examined, but I do not know why this occurs. Both karyotypes are very typical of the Libellulidae.

Macrothemis hemichlora (Burmeister)

$n = 3$, $2n\sigma = 6$. This is a low n species and in metaphase I, polar view, only three bivalents are seen (Fig. 30). One of the bivalents is somewhat smaller than the other two. The terminalized chiasma of Oksala (1943) can be easily seen as a median constriction or lightly stained area in each of the bivalents. In metaphase II, polar view, three rounded elements appear (Fig. 31). In metaphase II, lateral view, the double chromatids line up as in other species, but no X-chromosome or heteromorphic double chromatid can be seen (Fig. 32). No X-chromosome can be seen at any stage. Presumably the original X-chromosome is fused to a group of autosomes, and constitutes such a small proportion of the neo-XY system that it is not easily demonstrated cytologically. The karyotype of M. hemichlora differs from that of Orthemis levis in that no tripartite bivalent can be seen in polar view of metaphase I or at any other stage.

Examples of Intermediate Cases of Numerical Reduction

Three cases of reduced chromosome number have been found in material from Bolivia in which the chromosome numbers do not differ sufficiently from their respective family type numbers to be called low n species. Nevertheless, these differences from type numbers are striking compared to variations which have been reported in the past. These three species are called intermediate cases, although it is recognized that no definite boundaries can be drawn for these various classes of numerical reduction. Related species from the same geographic region which have typical karyotypes are discussed for comparison.

Subfamily Aeshninae

Two of these intermediate cases occur in the genus Aeshna (Aeshnidae: Aeshninae). These were taken in Bolivia along with other members of the subfamily Aeshinae which have typical karyotypes. These two intermediate cases are discussed here with two cytologically typical members of the same genus and with one member of a closely related genus.

Coryphaeshna adnexa (Hagen)

n = 14, 2n ♂ = 27. In metaphase I, polar view, there are 13 bivalents and the univalent X-chromosome, which sometimes lies outside of the outer ring of bivalents (Fig. 37). There is no clear-cut m-chromosome, the smallest two bivalents being approximately equal in size and slightly larger than the X-chromosome. Metaphase II, polar view, shows 13 similar elements, and in lateral view, it can be seen that the X-chromosome goes to one pole in the usual manner (Figs. 38,39).

Aeshna peralta Ris

n = 14, 2n ♂ = 27. The karyotype of this species is similar to the preceding one except that an m-chromosome is distinguishable and forms a bivalent which is about the size of the X-chromosome in polar view of metaphase I (Fig. 40). Metaphase II is typical of Aeshna (Figs. 41,42).

Aeshna sp. near unicolor Martin

n = 14, 2n ♂ = 27. This is an apparently undescribed species which is sytematically near Ae. unicolor Martin. A single specimen was taken near Buena Vista in eastern Bolivia. Its karyotype is typical of Aeshna. An m-chromosome is distinguishable in polar view of metaphase I (Fig. 43). Metaphase is as in other species of Aeshna with the X-chromosome visible at one end of the spindle in lateral view (Figs. 44, 45).

Aeshna diffinis diffinis Rambur

n = 11, 2n ♂ = 21. In this species the haploid number has been reduced by three from the usual aeshnid karyotype, and consequently, it is intermediate between low n species and those with the family type number. In most species of Aeshna there is one bivalent in polar view which is larger than any of the others (Figs. 37,40). Sometimes two such bivalents occur (Fig. 43). In metaphase I, polar view, of this species there are four such especially large bivalents (Fig. 46). Three of these are probably due to the fusion of two chromosomes each of the original karyotype, and the fourth is probably what was originally the largest chromosome. Three fusions would lower the chromosome number

from the type number to the present n = 11. This species has an m-chromosome which in polar view of metaphase I forms a bivalent about the size of the X-chromosome (Fig. 46). Metaphase II, in polar view, shows ten elements as expected, and the X-chromosome reduces in a normal manner in this division (Figs. 47,48). Both polar and lateral views of metaphase II show a greater variation in the size of the double chromatids than is usually the case.

Aeshna intricata Martin

n = 10, 2n♂ = 19. This species is another which is intermediate between the extreme numerical reduction of a low n species and a typical karyotype. This description is based on a single specimen reared from a nymph taken on the altiplano in the Bolivian Andes at an altitude of 12,500 feet. Metaphase I in polar view shows five particularly large bivalents which perhaps represent four fusions plus the bivalent which was largest in the original karyotype (Fig. 49). The X-chromosome is the smallest element in the complement, the m-bivalent being about twice the size of the X-chromosome in this species (Fig. 49). There is quite a bit of variation in the size of the double chromatids in polar and lateral views of metaphase II. The X-chromosome reduces normally (Figs. 50, 51).

Genus Perithemis

Another intermediate case occurs in the genus Perithemis (Libellulidae: Diastatopinae). Five species of this genus occur in the Buena Vista region of Bolivia. Four of these five have typical karyotypes for the family Libellulidae; the fifth has a reduced chromosome number.

Perithemis mooma Kirby

n = 13, 2n♂ = 25. The m-bivalent is somewhat smaller than the X-chromosome in polar view of metaphase I (Fig. 52). Metaphase II is typical of Libellulidae in all respects (Figs. 53, 54).

Perithemis sp. #2

n = 13, 2n♂ = 25. This is an apparently undescribed species of Perithemis and its field designation is retained here. Its karyotype is as in the preceding species except that no m-chromosome is distinguishable (Figs. 55,56,57).

Perithemis cornelia Ris

n = 13, 2n♂ = 25. The karyotype is very similar to that of the previous species. Here also no m-chromosome can be distinguished (Figs. 58,59,60).

Perithemis electra Ris

n = 13, 2n♂ = 25. The karyotype of this species is as in Perithemis sp. #2 and P. cornelia. The X-chromosome behaves normally; no m-chromosome is distinguishable (Figs. 61,62,63).

Perithemis lais (Perty)

n = 9, 2n♂ = 17. This karyotype is intermediate between one typical of Libellulidae and one of a low n species. In metaphase I, polar view, five bivalents occur which are much larger than the other three. The X-chromosome is the smallest element of the karyotype. The smallest of the five large bivalents (in the center of the metaphase plate, Fig. 64) may represent what was the largest chromosome pair

of the original karyotype. The other four, still larger, bivalents seem to contain chromosomes which were derived from the fusion of two chromosomes of the original karyotype. Thus four fusions would have lowered the haploid number from 13 to its present nine. Eight elements are seen in polar view of metaphase II, and here again some variation in size is obvious (Fig. 65). Lateral view of metaphase II shows that the behavior of the X-chromosome remains unaffected by the fusions in the karyotype of this species (Fig. 66).

The Origin of Reduced Chromosome Numbers in the Odonata

It seems clear that odonate chromosome numbers which are distinctly lower than type numbers come about in the majority of cases by fusion of elements which were present in the ancestral karyotype. Oksala (1943, p. 58) in discussing the only species of Aeshna in his material which differs from the type number of 14, states:

> All species except Ae. coerulea have 13 autosome bivalents, one of which is distinctly larger than the others and one (the m-chromosome) distinctly smaller, Ae. coerulea has 12 bivalents; one of these is unusually large and evidently corresponds to two ordinary autosomes in other species; thus it has to be taken as the produce of some kind of fusion. (Italics mine.)

He does not speculate further about the kind of fusion involved.

Another kind of numerical reduction in Odonata has been suggested by Oguma (1930). He visualized the m-chromosome as an autosome which was undergoing gradual diminution in volume, and which was destined eventually to disappear entirely. In summarizing this

opinion he wrote:

> In this way, through gradual diminution and final disappearance of an autosome, the chromosome number in dragonflies becomes different from species to species.

Oguma's hypothesis may account for some minor variation in chromosome number in Odonata, but it must be rejected as a method of origin for the low n species for two reasons. First, loss of this amount of genetic material would not be feasible (e.g., the transformation from n = 13 to n = 3) and there is no evidence for such loss. And second, the production of the low n karyotypes is apparently not a very gradual process, but can occur relatively rapidly in evolution.

Data from a preliminary cytophotometric examination which I have made suggest that there is not an appreciable difference in the amount of DNA in the karyotypes of Macrothemis musiva (n = 13), M. mortoni (n = 13) and M. hemichlora (n = 3). Not enough work has been done at the present time to give data which are statistically significant. It is clear, however, that the reduction in chromosome number of all of the species which are discussed in this paper as low n species or intermediate cases is accompanied by the increase in size of some or all of the chromosomes which are present. This fact indicates that even if some loss of genetic material has occurred, fusion must be the primary means of reduction of chromosome numbers in this group.

The type of fusion involved must also be considered. Seshachar and Bagga (1962) suggest that the reduction of the chromosome number of Hemianax ephippiger from the type number of n = 14 to the present

number of n = 7 is the result of centric fusion. It is true that centric fusion is by far the most discussed type of fusion in the literature, and Oksala (1943) states that Odonata possess monocentric, metacentric chromosomes. From this it would appear that, given enough rearrangements, centric fusion would be a possibility, but a number of objections can be made both to specific suggested instances of centric fusion and to centric fusion as a general method of numerical reduction in the Odonata.

Seshachar and Bagga (1962) suggest that 13 centric fusions were involved in reducing the dipolid number of Hemianax ephippiger from 27 to 14. However, only one event of fusion would be required to lower the haploid number by one, and thus only seven fusions would have been necessary. Heterozygotes would persist for a while and then either the fused or unfused chromosome would be eliminated from the karyotype by selection unless some type of heterosis were involved. These authors (op.cit.) also suggest that the chromosomes which now exist in the karyotype of H. ephippiger are acrocentric. For this to be true an additional rearrangement would be required for each member of the karyotype after the centric fusion had taken place, and subsequently, the metacentric chromosomes would have to be removed by selection.

As the reduction in chromosome number becomes greater, as for example from n = 13 to n = 3, the number of rearrangements necessary for centric fusions to be the means of this reduction becomes almost insurmountable. Every pair of chromosomes would have to undergo a series of major rearrangements in sequence. If we start with metacentric

chromosomes, such as Oksala (1943) suggests occur in Odonata, the cycle of events necessary in each pair of chromosomes is as follows: 1. A pericentric inversion (2 breaks) or a homosomal shift in the kinetochore (3 breaks) to produce one acrocentric chromosome. 2. The pair would have to become homozygous for the acrocentric chromosome through selection. 3. A centric fusion would occur between one member from each of two pairs of chromosomes. 4. The resulting metacentric chromosome would have to become homozygous through selection, and the haploid number would thus be reduced by one. Before any further fusion could occur, the new chromosome would have to start at the beginning of the sequence again with a rearrangement to the acrocentric condition.

If centric fusion were the means of reducing chromosome numbers in Odonata, the specific changes in karyotype which resulted in the present n = 3 of Macrothemis hemichlora might be as follows: 12 members of the n = 13 karyotype undergo the four step process outlined above, and the resulting six centric fusions give an n = 7 karyotype. Then six members of the n = 7 karyotype repeat the process and the resulting three centric fusions give an n = 4 karyotype. Two members of the n = 4 karyotype would go through the process once more and the centric fusion between them would give the final result of n = 3. The whole process would involve 20 pericentric inversions or similar rearrangements, and in each the acrocentric element would have to be made homozygous by selection. There would also be ten centric fusions and each of these would also have to become homozygous by selection for

the fused element. The karyotype would start with 12 pairs of metacentric autosomes and a metacentric X-chromosome, and, provided that the X-chromosome were included in the process, it would be reduced to three pairs of metacentric chromosomes. This process seems unduly complicated to have occurred rapidly and repeatedly as a regular feature of odonate karyotype evolution.

Theoretical problems also exist for the fusion of holokinetic chromosomes although not of the same magnitude as for monocentric ones. If the existence of telomeres is conceded, the dislocation hypothesis of Navashin (1932) should apply to changes in chromosome numbers in holokinetic as well as monocentric chromosomes. Troedsson (1944) has presented direct evidence to the contrary for fragmentations in compound sex chromosomes of some heteroptera, but this would involve the origin of new telomeres and not the elimination of old ones. She does not deal with the problem of the origin de novo of telomeres in her material, but presumably under some conditions this can happen. In a number of ascarid nematodes the ends of chromosomes are cast off in the cleavage divisions and the newly formed ends do not behave abnormally (Walton, 1924). It is also possible that for some reason telomeres may occasionally fail to function and that this may bring about direct terminal fusions, which in holokinetic chromosomes would be viable. However, I know of no evidence on this point, and I suggest that the more probable mechanism for these fusions is reciprocal terminal translocation between non-homologous chromosomes. Such a translocation could leave one long chromosome containing most of the

genetic material and a fragment containing two telomeres and little else. If the telomeres of holokinetic chromosomes are lacking in kinetic properties, such fragment would be quickly lost. It certainly would be lost as quickly as the fragment containing a kinetochore produced by a centric fusion. The resulting fused chromosome would have to become homozygous by selection before further fusion could be successful as in the case of centric fusion. However, no rearrangements would be necessary to prepare the chromosome for further fusion.

Thus in the series of fusions resulting in the present karyotype of Macrothemis hemichlora, 10 rearrangements would be necessary in holokinetic chromosomes (terminal heterosomal translocations) with subsequent stabilization of the rearranged chromosomes in the karyotype. In monocentric chromosomes the same transformation would require 30 major rearrangements (10 centric fusions and 20 pericentric inversions or shifts) and these would each also require selection for homozygosity of the rearranged chromosome. Independent evidence for the lack of a localized kinetochore in Odonata makes it appear that the former course was more likely the actual one taken.

Adaptive Significance of Low Chromosome Numbers

The Odonata are an ancient group which is systematically very distinct from other modern orders of insects. The paleontological history of the order as it is now defined extends back to the Permian (Tillyard, 1925), and the present day forms retain many primitive features.

This archaic aspect, combined with the reported uniqueness and uniformity of odonate karyotypes, has made it tempting to think of the Odonata as living cytological fossils. According to this view, the evolution of the odonate genetic system is passively conservative; that it is well adapted to the needs of a conservative group; and that it has perhaps not changed much since the Paleozoic. If this concept were reliable, the Odonata could be expected to provide data of great importance in the study of the evolution of genetic systems.

The discovery of the low n species changes this picture of passively conservative karyotype evolution in the Odonata considerably. These striking changes in an established pattern are obviously adaptive or they could not have survived. The fact that such extreme changes are possible indicates that the original pattern is not as passive as might have been assumed, but that it is maintained by some selective advantage. These low n karyotypes also indicate that changes in the original pattern can be rapid and profound when adaptive considerations require it.

The recombination index of a species is an important attribute of its genetic system (Darlington, 1937; White, 1954). A balance must be achieved between genetic variability on one hand and biological efficiency and stability on the other. It is likely that organisms evolve a recombination index which suits their evolutionary needs. As the chiasma frequency per bivalent seems to be fairly well fixed in Odonata by the mechanics of post-reductional meiosis (Oksala, 1943,1945), the only effective way to change the recombination index is to change the

chromosome number.[2] It is suggested that the recombination indices have been stabilized at levels which are selectively adaptive for the various families of Odonata, and this leads to the relative uniformity of karyotypes clustered around family type numbers. If it is true that these recombination indices are adaptive to the particular kind of ecology and natural selection encountered in the dragonflies, then they can only be changed for some good reason. In this case the good reason must be to gain a selective advantage or allay a selective disadvantage which is of greater immediate evolutionary importance than the maintenance of an optimum recombination index.

Whatever the adaptive considerations of an abrupt change in the recombination index, one immediate consequence of a low n karyotype is apparent. This is the complete reproductive isolation from closely related populations with normal karyotypes. This would come about whenever more than two chromosomes would have to pair with a single one in a numerical heterozygote. Any time the chromosome numbers of two populations vary by more than two to one, this three or more to one pairing would be inevitable in some chromosomes of the hybrid.

In the simplest case involving monocentric chromosomes where the fused element was derived as described earlier, and involved what

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2. If Oksala's data (op.cit.) are accepted, the recombination index for male Odonata would always be the $2n\,\sigma^{\prime}$ number, and for females it would be the 3n number. For example, when the chromosome number changes from n = 13 to n = 3, the male recombination index would change from 25 to 6 and that of the female would change from 39 to 9.

was originally three chromosomes, the fused chromosome would be the result of four overlapping pericentric inversions and two translocations. Synapsis of this chromosome with the three original chromosomes would at best be incomplete and would result in a very complicated tangle containing four kinetochores. Three of these would have to segregate from the other one to produce viable gametes, and the problem of spindle orientation, it can be presumed, would be a difficult one. Also, since almost all of the fused chromosome lies within one or more pericentric inversions, any crossover would almost certainly lead to deficiencies and duplications.

In holokinetic chromosomes two to one pairing between fused and unfused elements of the karyotype would lead to viable gametes. This two to one numerical heterozygosity must be a normal step in the evolution of low numbers in the Odonata and one case of it (Orthemis levis) has been found in the material from Bolivia. Three to one pairing would probably lead to complete inviability as in the case of monocentric chromosomes. This is true because in a three to one pairing three chiasmata would have to form to hold the bivalent together at metaphase I. Only two of these could terminalize and the other would have to remain in the center of the bivalent. This would not allow normal spindle orientation at either division of meiosis and would appear to lead to inevitable deficiencies and duplications.

It may be significant that all of the low n species reported in this paper occupy habitats where they come into contact with other closely related species of the same genus. In many cases the related species

can be seen flying together. It has been suggested on theoretical grounds (Dobzhansky, 1940) that when two populations have diverged sufficiently so that hybrids are less well adapted than either parent, selection would act to build effective mechanisms for genetic isolation. Koopman (1950) showed that this actually occurs in the course of several generations in laboratory populations of Drosophila pseudoobscura and D. persimilis. Subsequently the reinforcement of genetic isolating mechanisms has been suggested by the data from several studies of natural populations (e.g., Blair, 1955,1958).

The data on the low n species of Odonata are not sufficient to say whether reinforcement of genetic isolation is the adaptive factor which would account for the evolution of an apparently less satisfactory recombination index. Certainly the genetic isolation resulting from these fusions would be very effective.

Chromosomal Polymorphism

Chromosomal polymorphism in natural populations has not to my knowledge been previously reported for the Odonata, but it is a regular feature of the karyotypes of some species of several other groups (Stone, 1949; Patterson and Stone, 1952; White, 1954,1956). It is clear that numerical polymorphism such as has been described in this paper for Orthemis levis must be a normal event in the evolution of lower chromosome numbers in Odonata. However, in the usual karyotypes, the chromosomes are so small that the interpretation of a heterozygous individual would be very difficult. The possibilities that numerical heterozygotes

may be maintained by heterosis and that numerical polymorphism may be related to geographic or ecological factors must wait for future studies.

Data on Chromosome Numbers of Other Species of Odonata

Original cytological data are presented in Table III for 107 species of Odonata of which 106 have not been previously studied cytologically. Two previous descriptions of the chromosomes of Pantala flavescens (Fabr.) from India appear identical, not only with respect to the chromosome number but also to the very small size of the m-chromosome, to the observations made in this study on the same species from Bolivia.

Table III includes cytological data for 30 species of Zygoptera; 30 have been previously described by other workers. As there is no overlap, 60 species of Zygoptera are now cytologically known. Table IV lists all odonate species for which chromosome numbers could be obtained either through original observations or from the literature. The literature contains descriptions of representatives of four families and eight subfamilies of Zygoptera. Information is presented in this study for an additional six families and ten subfamilies. Thus cytological information is now available for representatives of ten families and 18 subfamilies of Zygoptera.

The pattern of little variation from a family type number is reinforced by the new data in spite of the first two reported cases of numerical variation within families of Zygoptera. Eight of the ten families within this suborder which have representatives known cytologically show no

numerical variation and there is still no numerical variation in 16 of the 18 subfamilies. This situation is now more significant because the number of species for which data are available is much greater than previously. The 29 species which have been cytologically studied to date in the family Coenagriidae all have a haploid number of 14. The two cytologically described species of the family Protoneuridae also have a haploid number of 14, but with one exception there are no other species known to have this number in the Zygoptera. The families Platystictidae, Platycnemididae, Megapodagriidae and Lestidae all have, so far as is known, a haploid number of 13. The two cytologically known species of Polythoridae both have a number of 12. The family Calopterygidae seems to have a type number of 13 as eleven out of 12 species of the two subfamilies have this number. Hetaerina rosea Selys has a number of 14 and thus is the only known exception to the typical number in this family. This is a particularly interesting case because it is one of only two in the Odonata in which the number of a species exceeds the type number for the family. The other case is in the Libellulidae where Ray Chaudhuri and Dasgupta (1949) reported a haploid number of 14 for Neurothemis tulia tulia (Drury). These two cases do not agree with what appears to be the usual method of numerical change in the Odonata, that is, reduction from a type number by fusion of elements of the karyotype.

The status of the species reported for the family Pseudolestidae cannot be determined from the material available. The haploid number of nine may be the type number for this family or may be the result of

an isolated case of intermediate numerical reduction from some higher number. Also it will be necessary to do more work to understand the situation in the Pseudostigmatidae. It is assumed that the type number for this family is near the n = 15 of Mecistogaster sp. #1, but this cannot be proved without the study of considerably more material.

The pattern of numerical constancy has also been reinforced in the Anisoptera, although a number of striking deviations from type numbers are reported. Data for a total of 77 species of Anisoptera are presented in this study and 76 of these had not been previously studied. Seven families of Anisoptera have cytologically described representatives and no data are presented here for families which were previously unknown. Twenty-four subfamilies of Anisoptera now have representatives cytologically known; four of these subfamilies are newly represented in this study. The amount of deviation from type numbers has become much more uniform for families in which a number of species are represented. The percentages of cytologically described species which deviate from family type numbers for families of Anisoptera in which seven or more species have been studied are:

Gomphidae	19%
Aeshnidae	22%
Corduliidae	17%
Libellulidae	17%

These figures include all low n species and intermediate cases of numerical reduction which have been reported. In Libellulidae the number of species involved is 103 of which 18 deviate from the type number of

13. It appears that the amount of deviation from type numbers within families of the Anisoptera is tending to stabilize at near 20%. This is not true, however, at the subfamily level. For example, deviation within subfamilies from the family type number varies from 0% to 100% in the Gomphidae and from 0% to 33% in the Libellulidae.

THE KINETOCHORE

The nature of the kinetochore or centromere is one of the most important cytological problems in the Odonata and has been the subject of some controversy. Oksala is one of the modern workers who has come out strongly in favor of a localized kinetochore, but his conclusions have been questioned by other workers. Battaglia and Boyes (1955) say of Oksala's work, "Concerning Odonata, Oksala's evidence for the existence of post-reduction is acceptable, however, the real nature of the centromere and certain problems of meiosis require clarification." Hughes-Schrader (1948), Lima-de-Faria (1949) and Castro (1950), among others, have objected to the localized kinetochore on theoretical grounds, but have presented no data to support their conclusions. Oksala is thoroughly committed to the localized kinetochore and he has studied a large amount of odonate material of both sexes. In his most recent paper on the subject (Oksala, 1952) he states his case in these terms:

> The centromere is situated in a clear median constriction. The chromosomes are also often typically bent at this point. The direct microscopic evidence thus argues in favour of a localized centromere in the Odonata. The postreductional type of meiosis characteristic of these insects has, however, caused certain authors to doubt the presence of a localized centromere in this group. Although the monocentric character of the chromosomes has not been experimentally proved so far, the empirical facts presented above are against its being diffuse. Another question is whether the localized centromere of the dragonflies is in all respects comparable with the centromere of, say, the Orthoptera or Diptera. These questions must, however, be passed over in this connection.

The nature of the kinetochore in Odonata is of great importance in defining post-reductional meiosis in organisms in general. Odonata

are the only large group of organisms which are reported to combine post-reductional meiosis with a localized kinetochore. Rishikesh (1959) reported post-reduction for sex chromosomes of Anopheles stephensi, but the type of phenomenon described is excluded from the definition of post-reduction by several workers (Oksala, 1948; Battaglia and Boyes, 1955). If the kinetochore of Odonata is not localized, no known organism with post-reduction has a localized kinetochore and the type of reduction cannot be defined in terms of the kinetochore as done by Oksala (1948). It is important, then, to look at the nature of the odonate kinetochore rather carefully.

Oksala's Evidence for Monocentric Chromosomes

Oksala (1943) had two lines of evidence for the monocentric nature of odonate chromosomes. First, in some spermatogonial metaphases the chromosomes appeared bent in the middle in polar view and there seemed to be a constriction at the point of the bend. And second, in lateral view of metaphase I in some preparations, he could apparently see two spindle fibers going to each pole from each bivalent. It is true that both of these types of evidence may be observed in favorable preparations. They have been seen many times in my own material. Of these two kinds of evidence, Oksala considered the second, the double spindle fibers in metaphase I, to be the most conclusive. Taken alone, without further evidence, the arguments of Oksala would seem to lead to the conclusion that odonate chromosomes are, indeed, monocentric.

Additional Evidence from the Present Study

Two developments have contributed additional information on the odonate kinetochore. One of these is the discovery of species with strikingly low chromosome numbers, the low n species. The other is the use of the phase contrast microscope on Feulgen squash material as well as on sectioned material. The low n species contribute information in four ways. The first type of information comes from the relatively large size of the low n chromosomes. It can be seen that these chromosomes proceed to the poles in a parallel manner at anaphase I, and at the anaphse of spermatogonial metaphase (Fig. 67). If the chromosomes were monocentric, one would expect the arms of these long chromosomes to drag behind in a much more obvious way. The second bit of information also comes from the relatively large size and easy visibility of the low n chromosomes. It can be seen that the spindle fibers appear to attach along the length of these large chromosomes and not from one point. Spermatogonial chromosomes are very large and easy to see, but do not show a structure which can be interpreted as a median kinetochore. The third point to be considered is the difficulty of evolving the low n karyotypes in an organism with monocentric chromosomes. It is clear that the low chromosome numbers in the low n species come about by fusion of elements which are present in the ancestral karyotype. If the chromosomes were monocentric, each fusion would have to involve the loss of one kinetochore, and would thus have to be in this way similar to a centric fusion. If odonate chromosomes were monocentric, the process of fusion necessary to

produce a change in chromosome number from n = 13 to n = 3 would be extremely complicated. The required steps have been listed earlier in this paper (p. 25).

The fourth line of evidence coming from the low n species is based on White's (1954, p. 196) suggestion that the size of the spindle apparatus and cell may be a determining factor in changes in chromosome number. He postulates that even if a rearrangement is satisfactory from the standpoint of genic balance, it still must not diminish the efficiency of the mitotic or meiotic mechanism in a purely mechanical way. White states:

> Thus a rearrangement which gave rise to a chromosome twice the normal length might impair the anaphase disjunction process quite seriously, since any particular type of spindle probably cannot cope with more than a certain length of chromosome.

Most or all of the chromosomes in the low n species are at least twice the normal length of those of closely related species. Moreover, measurements indicate that there is no significant difference in the size of the spindles or cells. I suggest that the limitation proposed by White (loc. cit.) does not apply to holokinetic chromosomes. In this type of chromosome all parts of the chromosome proceed to the poles in a more or less parallel manner, and therefore no difficulty in anaphase disjunction should be encountered with longer chromosomes.

The fifth line of evidence bearing on the nature of the odonate kinetochore coming from the present study is the most conclusive of all and it helps explain the evidence obtained by Oksala. This comes from phase contrast observation of thin Feulgen squash preparations. The

two spindle fibers which may be seen proceeding to each pole from each bivalent at metaphase I may also be seen proceeding from each chromosome at spermatogonial metaphase (Fig. 68) and from each double chromatid at metaphase II (Figs. 69,70). Moreover, the double spindle fibers are not close enough together to be interpreted as a compound spindle fiber from a localized kinetochore (Fig. 69). There is no model for meiosis with chromosomes which possess a single localized kinetochore in which two separate spindle fibers proceed to each pole at metaphase II. It is similarly inconceivable that the localized kinetochore would allow such a situation at spermatogonial metaphase.

The best interpretation of these data seems to be that the two spindle fibers which now can be seen at all divisions are the borders of regions of kinetic activity for a particular chromosomal element or the optically observable edges of a broad band of spindle fibers which attach along the entire chromosome. As for the clear constrictions observed by Oksala in somatic chromosomes, it seems likely that the chromatids separate in the centers first and that an optical slice through such a figure gives the impression of a median constriction.

The conclusion seems inescapable that the chromosomes of Odonata are holokinetic, that is, that they lack a localized kinetochore. The most conclusive single piece of evidence is that of the double spindle fibers seen at metaphase II and in spermatogonial metaphase. The other evidence, while circumstantial, strengthens the case for holokinetic chromosomes. The classic method for conclusively proving the presence of holokinetic chromosomes is to use radiation to break the

chromosomes up and to observe the behavior of the fragments in mitosis or meiosis (Carlson, 1938; Rhoades and Kerr, 1949). This has not been successfully done in the Odonata. The ordinary species have chromosomes which are too small to lead to a meaningful conclusion. However, it is hoped that the low n species will provide material for useful radiation experiments in the future.

CHIASMATA, SPINDLE ORIENTATION AND REDUCTION

Chiasmata

Chiasma formation is difficult to study in Odonata in its early stages. There is some indication that in certain species several chiasmata may form in each bivalent (Figs. 71,72), but it is not possible to prove that these so-called "chiasmata" involve actual interchanges. At these stages it is difficult to separate true chiasmata from relational coiling. Some workers (e.g., Ray Chaudhuri and Dasgupta, 1949; Seshachar and Bagga, 1962) have given chiasma frequencies per bivalent which are greater than unity at various meiotic prophase stages of males, but this work does not throw much light on chiasma formation and behavior. Oksala (1943,1952) states categorically that in male odonata only one chiasma forms per bivalent. He gives statistics (1943) which show that only 0.01% of the bivalents in male Aeshna crenata form two chiasmata per bivalent and that the lack of a single chiasma is even rarer. Oksala's data, however, are based on later stages (diakinesis and metaphase I) which are scorable in sectioned material. The question as to whether multiple chiasmata in earlier stages might be resolved into a single apparent chiasma by diakinesis must remain for the present unanswered. Oksala (loc.cit.) states that the single chiasma formed in each male odonate bivalent terminalizes to the end of the bivalent and thus an end to end association of the chromosome is seen at metaphase I. This can be easily verified and is especially obvious in the low n species (Figs. 30,73).

Oksala (1945) further reports that in female Odonata, two chiasmata per bivalent form and that these terminalize to opposite ends of the bivalent to form a ring. The present study does not include material of females so I cannot verify this, but Oksala's data seem adequate to demonstrate his conclusion.

Whatever the number of actual interchanges or crossovers in the Odonata, then, the chiasma frequency at metaphase I appears to be one per bivalent in males and two per bivalent in females. This is the chiasma frequency which must be considered from the standpoint of the mechanics of spindle orientation and reduction.

The question as to whether chiasmata really terminalize in organisms with holokinetic chromosomes has been raised by Resende (1953). This worker claims that since in holokinetic chromosomes sometimes the ends of the chromosome lead the way to the poles, chiasmata should centralize rather than terminalize. This would lead to a breakage-fusion cycle which Resende claims is the regular part of the genetic system of these organisms. It can be cytologically demonstrated from the present material that Resende's hypothesis does not apply to the Odonata and in addition there are several theoretical flaws in Resende's scheme which should be pointed out. Resende assumes that it is the force of traction provided by the spindle fibers which leads to the terminalization of chiasmata. This is certainly not true of the Odonata and it is doubtful that it is true of any organism where true terminalization occurs. It can be seen in the Odonata that terminalization precedes separation on the spindle at metaphase I. Resende's hypothesis

would require an X-shaped figure at metaphase I with the arms of the X crossing in the equatorial plate (Fig. 74). In Odonata this situation does not occur. The figures are cross-shaped or rod-shaped (Fig. 75). The separation of a bivalent does not proceed from the ends toward the middle but from the middle toward the end (Fig. 76). This is also true of chromosomes of mitosis; separation of the chromatids is from the middle toward the ends of the chromosomes (Fig. 77).

Spindle Orientation

Other workers have tied the problem of reduction to spindle orientation (Oksala, 1943, 1948; Battaglia and Boyes, 1950), and spindle orientation has frequently been thought of in terms of the way the kinetochore is oriented relative to the spindle in the meiotic division (Oksala, 1948). In organisms which possess a localized kinetochore, the distinction between auto-orientation of the kinetochores of a bivalent and co-orientation of those kinetochores is valid and relatively easy to determine. If a kinetochore independently orients to the two poles of the spindle, then auto-orientation occurs. If, on the other hand, the two kinetochores of a bivalent, operating jointly, each orient to the opposite pole of the spindle, co-orientation occurs. Co-orientation is linked to reduction because it insures "disjunction of homologous chromosomes," and auto-orientation is linked to an equational division because it insures "division of sister chromatids" (Battaglia and Boyes, 1950). In organisms which lack a localized kinetochore, the problem is not as easy to define. It involves knowing whether whole chromosomes or pairs of homologous chromatids are oriented to separate poles

of the spindle at metaphase I. Some workers have given up attempting to make a distinction between auto-orientation and co-orientation in these forms. Ris (1942, p. 292) states:

> Where crossing over occurs the terms pre-reduction and post-reduction of chromosomes have lost any meaning though in organisms with a localized kinetochore one can still speak of pre-reduction and post-reduction of the kinetochore. In forms with a diffuse spindle attachment, however, the sister chromatids are not held together by an unsplit region of the chromosome and one must look for other criteria to describe the behaviour of the bivalents in the two divisions.

It is, however, clear that if a chromosome can be defined in the first meiotic division of organisms with holokinetic chromosomes, the situation where chromosomes are lined up on either side of the equatorial plate is co-orientation of chromosomes, and the situation where homologous chromatids are lined up on either side of the equatorial plate is auto-orientation of chromosomes. Monocentric chromosomes can be defined as everything attached to a single kinetochore and under this definition, if chiasmata terminalize, they do so to the ends of the chromosomes. Thus, it would be possible to define holokinetic chromosomes in bivalents at metaphase I as the structures to the end of which chiasmata terminalize. Auto-orientation may then be defined as spindle orientation in which chiasma terminalization of the bivalents is in a direction perpendicular to the axis of the spindle. Conversely, co-orientation becomes spindle orientation in which chiasma terminalization is in a direction parallel to the axis of the spindle (Figs. 78,79). The question of orientation would probably be impossible to resolve in organisms with holokinetic chromosomes in which there was no terminalization. To quote Oksala (1948, p. 110):

> The problem of reduction might become critical and even in principle impossible of decision if cases were found in which the centromeres were diffuse and in which the chiasma appeared in the middle of the chromosome not finally terminalized toward the end. In such a case it would be impossible to decide, not only in practice but even in principle, which of the four chromatids of a bivalent belonged to any chromosome; there would be no sense in bringing up the question of reduction at all.

Reduction in the Odonata

If we accept Oksala's definition of reduction, Odonata certainly have post-reductional meiosis. The original data of Oksala (1943) are valid in this connection, but perhaps not conclusive. Additional information from the low n species reinforces Oksala's conclusions considerably. First, with the larger and fewer bivalents, it is easy to verify that at metaphase I the chiasmata do terminalize in a direction perpendicular to the axis of the spindle. Polar views frequently show clear end-to-end association of chromosomes with terminalized chiasmata. Second, ring bivalents are more common in low n species than in those with normal karyotypes, and these ring bivalents are easier to observe. The rings clearly lie in the plane of the equatorial plate. On one occasion two adjacent polar views of metaphase I in Macrothemis hemichlora were observed (Fig. 80). These rings are in the equatorial plate of the metaphase figure. Third, in numerical heterozygotes, the chiasma terminalization is to opposite ends of the fused element, and the tripartite bivalent lies in the equatorial plate with both chiasmata visible (see Fig. 81, polar view of metaphase I of Orthemis levis). This means that the terminalization of chiasmata in metaphase I is perpendicular to the axis of the spindle. Therefore, auto-orientation

occurs in metaphase I, and the Odonata have post-reductional meiosis.

The Mechanics and Causes of Spindle Orientation and Post-Reduction

In considering the causes of post-reduction in Odonata, Oksala (1943) considered that it can be linked to Darlington's theory of precocity. Darlington's (1939) view is that the reduction (co-orientation) is caused by precocious development of the primary spermatocyte so that the kinetochore is incapable of division at the first meiotic division. The result is that the kinetochores co-orient in the first division and separate from each other. Oksala (1943) claims that in Odonata the development of the primary spermatocyte takes an unusually long time. This allows the kinetochores to be prepared for division (escape precocity) at metaphase I and auto-orientation results. Several flaws can be found in this reasoning, but the most important one is that Odonata have holokinetic chromosomes. Darlington's theory of precocity cannot operate in chromosomes without localized kinetochores.

It seems clear that the factor responsible for pre- or post-reduction in organisms with holokinetic chromosomes is spindle orientation in terms of the direction of terminalization. No definitive answer can be given as to the predisposing factors at this time, but several facts are suggestive. It is possible that chiasmata or the terminalization process itself may play a role in spindle orientation. Terminalized chiasmata always locate in the equatorial plate and this is true both for organisms with

holokinetic chromosomes and for those with a localized kinetochore. It is true not only of metaphase I in Odonata, but also of the half-chiasmata in metaphase II. The indication that the half-chiasmata are responsible for orientation of the double chromatids at metaphase II in odonate meiosis comes from the numerical heterozygote in Orthemis levis. The tripartite bivalent divides in the first meiotic division to give rise to two triple chromatids. If orientation of these triple chromatids were governed by kinetic factors alone, they might be expected to line up stretched out parallel to the axis of the spindle and this would lead to duplication and deficiencies in the gametes. Instead, they orient in a U-shape with the two half-chiasmata in the equatorial plate. It seems clear that the half-chiasmata have something to do with the orientation (Figs. 82,83).

Two unresolved problems which are necessary to understanding orientation and reduction in many organisms are the nature and structure of residual terminalized chiasmata and half-chiasmata and the nature of the force which leads to terminalization of chiasmata.

SUMMARY AND CONCLUSIONS

Chromosome numbers have been reported in the past for 109 species of Odonata from 11 families and 28 subfamilies. New data for 106 species presented in this paper bring the number of cytologically known species to 215 and the number of higher categories which are represented to 17 families and 42 subfamilies.

In the past the chromosome numbers which have been reported in the Odonata have been remarkably uniform, particularly within families. Much greater variation occurs in the material described in this paper, but the concept of family type numbers is strengthened by the new data. Deviations from type numbers are very unusual in the Zygoptera. In families of Anisoptera in which more than seven species are known, the deviations from type numbers approximate 20%.

As odonate karyotypes are uniform not only with respect to chromosome number but also to chromosome morphology and behavior, the concept of passively conservative chromosome evolution in the Odonata has been expressed. Karyotype evolution in general has in the past been considered by some workers to be actively adaptive (McClung, 1938). The discovery of the low n species of Odonata makes it appear that this more dynamic concept of the evolution of genetic systems fits the Odonata. The karyotypes are capable of extreme changes when influenced by adaptive considerations.

One adaptive factor in odonate karyotype evolution is the recombination index. Recombination indices in Odonata vary only with changes in chromosome number because chiasma frequency per bivalent is relatively fixed. It is suggested that the relative constancy of odonate chromosome numbers is determined in part by an adaptive recombination index.

Low n species are defined as species with about half or less the family type chromosome number. Four such species are described in this paper. Also three cases of intermediate reduction of chromosome numbers are noted. It is suggested that these species tolerate an adaptively less satisfactory recombination index to gain some other selective advantage. One possibility for such a selective advantage is the reinforcement of genetic isolating mechanisms.

Chromosomal polymorphism in natural populations has not been previously reported in the Odonata. One case of numerical polymorphism is reported in this paper. This type of numerical heterozygosity is likely a necessary step in the evolution of lowered chromosome numbers. The discovery of cases of this type in ordinary odonate karyotypes is hindered by the small size of the chromosomes. The case reported here is Orthemis levis. The two individuals examined were both heterozygous for n = 3 and n = 4 karyotypes. It may be expected that more cases of this type will be reported in the future as techniques for observing them become more refined.

The nature of the kinetochore in Odonata is a problem which has aroused much interest of cytogeneticists because of its theoretical implications. Oksala, who has done most of the critical work on the

chromosomes of this group, claims that the chromosomes are monocentric. Evidence is presented in this paper which indicates that the chromosomes are not monocentric but holokinetic. This finding means that there are no known organisms which have auto-orientation of localized kinetochores at metaphase I of meiosis. The precocity theorty of Darlington (1939) does not seem to determine, as Oksala (1948) suggested, whether a localized kinetochore will undergo auto- or co-orientation. The relationship between holokinetic chromosomes and auto-orientation in the first meiotic metaphase is not as well understood. Auto-orientation occurs in metaphase I of some organisms which have holokinetic chromosomes. It has not been determined whether, as suggested by Battaglia and Boyes (1950), it must occur in these organisms.

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Table 1

CHROMOSOME NUMBERS OF ODONATA
REPORTED THROUGH 1961

TAXA	HAPLOID NUMBERS					
	9	10	11	12	13	14
Suborder ZYGOPTERA						
Platycnemididae					2	
Coenagriidae						20
Pseudagriinae						9
Coenagriinae						7
Ischnurinae						3
Agriocneminae						1
Lestidae					2	
Calopterygidae					6	
Suborder ANISOPTERA						
Gomphidae		1	2	8		
Gomphinae		1	2	6		
Ictinogomphinae				1		
Hageninae				1		
Petaluridae	2					
Aeshnidae					1	11
Brachytrinae						1
Aeshninae					1	7
Anactinae						2
Gynacanthaginae						1

Continued

Table I (continued)

TAXA	HAPLOID NUMBERS					
	9	10	11	12	13	14
Cordulegasteridae					2	
Corduliidae					6	
Corduliinae					5	
Epophthalmiinae					1	
Macrodiplacidae					2	
Libellulidae			1	2	39	1
Libellulinae					13	
Brachydiplactinae					3	
Sympetrinae			1	1	11	1
Leucorrhininae					4	
Tritheminae				1	2	
Rhyotheminae					2	
Pantaliinae					4	

The figures in this table represent the number of species in the listed taxa which had been reported through 1961 to have these haploid chromosome numbers. Family totals are underlined. Families and subfamilies for which no numbers had been reported are not included.

Table II

SUMMARY OF CHROMOSOME NUMBERS REPORTED FOR FAMILIES OF ODONATA THROUGH 1961

Family	Range of n	Most common n (type number)
Platycnemididae	13	13
Coenagriidae	14	14
Lestidae	13	13
Calopterygidae	13	13
Gomphidae	10-12	12
Petaluridae	9	9
Aeshnidae	13-14	14
Cordulegasteridae	13	13
Corduliidae	13	13
Macrodiplacidae	13	13
Libellulidae	11-14	13

Table III

ORIGINAL CYTOLOGICAL DATA FOR THE ODONATA

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Suborder ZYGOPTERA				
Family Platystictidae Subfamily Palaemnematinae				
Palaemnema paulina (Drury)	Costa Rica	13	present	
Family Protoneuridae Subfamily Protoneurinae				
Epipleoneura sp. no. 1	Bolivia	14	none	based on counts from metaphase II
Neoneura rubriventris Selys	Bolivia	14	present	
Family Coenagriidae Subfamily Amphicneminae				
Diceratobasis macrogaster (Selys)	Jamaica	14	present	
Subfamily Ischurinae				
Acanthagrion ascendens Calv.	Bolivia	14	present	
Acanthagrion chacoense Calv.	Bolivia	14	present	
Aeolagrion foliacum Sjostedt	Bolivia	14	none	
Ischnura fluviatilis Selys	Bolivia	14	none	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Ischnurinae				
Ischnura sp. nr. ultima Ris	Bolivia	14	none	
Tigriagrion aurantinigrum Calv.	Bolivia	14	none	
Subfamily Agriocneminae				
Ceratura capreola Hagen	Bolivia	14	none	
Subfamily Arginae				
Argia sedula (Hagen)	Florida	14	none	
Family Pseudostigmatidae				
Mecistogaster sp. no. 1	Bolivia	15	present	
Mecistogaster sp. no. 2	Bolivia	6	none	Apparent low n species
Family Megapodagriidae Subfamily Megapodagriinae				
Megapodagrion macropus Selys	Bolivia	13	none	$2n\sigma^{\prime} = 25$ with X-chromosome largest element.
Megapodagrion setigerum Selys	Bolivia	13	none	
Subfamily Argiolestinae				
Heteragrion flavidorsum Calv.	Bolivia	13	none	
Heteragrion inca Calvert	Bolivia	13	present	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Argiolestinae				
Philogenia carrillica Calvert	Costa Rica	13	present	
Family Lestidae Subfamily Lestinae				
Lestes forficula Rambur	Jamaica	13	present	
Lestes vidua Hagen	Florida	13	present	m-chromosome minute
Family Pseudolestidae Subfamily Pseudolestinae				
Hypolestes clara (Calvert)	Jamaica	9	none	
Family Polythoridae Subfamily Polythorinae				
Cora irene Ris	Bolivia	12	present	
Polythore boliviana (MacLach.)	Bolivia	12	present	
Family Calopterygidae Subfamily Calopteryginae				
Calopteryx maculata (Beauvois)	Florida	13	present	
Subfamily Hetaerininae				
Hetaerina americana (Fabr.)	Texas	13	present	
Hetaerina charca Calvert	Bolivia	13	present	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Hetaerininae				
Hetaerina rosea Selys	Bolivia	14	present	
Hetaerina sanguinea Selys	Bolivia	13	none	
Hetaerina titia (Drury)	Texas	13	present	
Suborder ANISOPTERA				
Family Gomphidae Subfamily Gomphinae				
Erpetogomphus designatus Hagen	Texas	12	present	
Erpetogomphus diadophis Calvert	Texas	12	none	
Gomphus pallidus Rambur	Florida	12	none	
Subfamily Epigomphinae				
Epigomphus llama Calvert	Bolivia	10	none	
Subfamily Gomphoidinae				
Aphylla edentata Selys	Bolivia	12	none	
Aphylla producta Selys	Bolivia	12	none	
Gomphoides sp.	Bolivia	12	none	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Gomphoidinae				
Phyllocycla sp.	Bolivia	12	none	
Progomphus intricatus Hagen	Bolivia	12	none	
Progomphus phyllochromus Ris	Bolivia	12	present	
Family Petaluridae Subfamily Petalurinae				
Tachopteryx thoreyi (Hagen)	Texas	10	present	
Family Aeshnidae Subfamily Aeshninae				
Aeshna d. diffinis Rambur	Bolivia	11	present	
Aeshna intricata Martin	Bolivia	10	present	
Aeshna peralta Ris	Bolivia	14	present	
Aeshna sp. nr. unicolor Martin	Bolivia	14	present	
Coryphaeschna adnexa (Hagen)	Bolivia	14	none	
Family Corduliidae Subfamily Corduliinae				
Tetragoneuria petechialis Muttkowski	Texas	11	none	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Family Libellulidae Subfamily Libellulinae				
Cannaphila vibex (Hagen)	Bolivia	13	present	m-chromosome minute
Dasythemis esmeralda Ris	Bolivia	13	present	
Libellula axilena Westwood	Florida	12	none	
Libellula incesta Hagen	Florida	13	none	
Orthemis biolleyi Calvert	Bolivia	12	none	
Orthemis cultriformis Calvert	Bolivia	12	present	
Orthemis ferruginea (Fabr.)	Bolivia	5	none	low n population
Orthemis ferruginea (Fabr.)	Texas	12	none	
Orthemis levis Calvert	Bolivia	3-4	none	low n population
Subfamily Diastatopidinae				
Diastatops intensa Ris	Bolivia	13	present	
Diastatops obscura (Fabr.)	Bolivia	13	present	
Perithemis cornelia Ris	Bolivia	13	none	
Perithemis domitia (Drury)	Jamaica	13	present	
Perithemis electra Ris	Bolivia	13	none	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Diastatopidinae				
Perithemis lais (Perty)	Bolivia	9	none	
Perithemis mooma Kirby	Bolivia	13	present	
Perithemis seminole Calvert	Florida	13	present	
Perithemis sp. no. 2	Bolivia	13	none	
Zenithoptera viola Ris	Bolivia	13	present	
Subfamily Brachydiplactinae				
Micrathyria atra Martin	Bolivia	13	present	
Micrathyria didyma (Selys)	Jamaica	13	present	
Micrathyria hageni Kirby	Jamaica	13	present	
Micrathyria iheringi Santos	Bolivia	12	present	
Micrathyria laevigata Calvert	Bolivia	13	present	
Micrathyria ocellata dentiens Calvert	Bolivia	13	present	
Micrathyria sp. nr. eximia Kirby	Bolivia	11	none	
Micrathyria sp. ungulata group	Bolivia	12	none	
Micrathyria spuria (Selys)	Bolivia	13	present	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Sympetrinae				
Erythemis attala (Selys)	Bolivia	13	none	
Erythemis plebeja (Burm.)	Bolivia	13	none	
Erythrodiplax b. basalis (Kirby)	Bolivia	13	none	
Erythrodiplax castanea (Burm.)	Bolivia	12	none	
Erythrodiplax connata fusca (Rambur)	Bolivia	13	none	
Erythrodiplax fervida (Erichson)	Jamaica	13	present	
Erythrodiplax justiniana (Selys)	Jamaica	13	present	
Erythrodiplax media Borror	Bolivia	11	present	
Erythrodiplax melanorubra Borror	Bolivia	13	present	
Erythrodiplax paraguayensis (Forster)	Bolivia	12	present	
Erythrodiplax umbrata (Linn.)	Bolivia	13	present	
Erythrodiplax unimaculata (De Geer)	Bolivia	13	present	
Lepthemis vesiculosa (Fabr.)	Bolivia	13	none	

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Sympetrinae				
Pachydiplax longipennis (Burm.)	Florida	13	present	
Rhodopygia cardinalis (Erichson)	Bolivia	13	present	
Tarnetrum illotum (Hagen)	Jamaica	13	present	
Subfamily Leucorrhinae				
Cannacria herbida (Gundlach)	Jamaica	13	present	
Subfamily Dytheminae				
Brechmorrhoga nubecula Ramb.	Bolivia	13	present	
Brechmorrhoga pertinax peruviana Ris	Bolivia	13	none	
Dythemis cannacrioides Calv.	Bolivia	12	present	
Dythemis multipunctata Kirby	Bolivia	13	present	
Dythemis rufinervis (Burm.)	Jamaica	13	present	
Macrothemis hemichlora (Burm.)	Bolivia	3	none	low n population
Macrothemis mortoni Ris	Bolivia	13	present	
Macrothemis musiva (Hagen)	Bolivia	13	present	
Scapanea frontalis (Burm.)	Jamaica	13	present	m-chromosome minute

SPECIES	LOCALITY	n	m-chromosome	REMARKS
Subfamily Pantaliinae				
Miathyria marcella (Selys)	Bolivia	13	present	
Pantala flavescens (Fabr.)	Bolivia	13	present	m-chromosome minute
Pantala hymenaea (Say)	Bolivia	13	present	
Tauriphila australis (Hagen)	Bolivia	13	present	
Tramea abdominalis (Rambur)	Bolivia	13	none	
Tramea carolina (Linn.)	Florida	13	none	
Tramea cophysa Hagen	Bolivia	13	present	

Table IV

SUMMARY OF CHROMOSOME NUMBERS OF ODONATA REPORTED IN THE LITERATURE TO DATE AND IN THE PRESENT PAPER

SPECIES	n	SOURCE
Suborder ZYGOPTERA		
Family Platystictidae Subfamily Palaemnematinae		
Palaemnema paulina (Drury)	13	Present study.
Family Protoneuridae Subfamily Protoneurinae		
Epipleoneura sp. #1	14	Present study.
Neoneura rubriventris Selys	14	Present study.
Family Platycnemididae Subfamily Platycnemininae		
Copera annulata (Selys)	13	Kichijo, 1941, 1942; Dasgupta, 1957.
Platycnemis pennipes Pall.	13	Oksala, 1945.
Family Coenagriidae Subfamily Amphicneminae		
Diceratobasis macrogaster (Selys)	14	Present study.
Subfamily Pseudagriinae		
Ceriagrion cerinorubellum (Brauer)	14	Dasgupta, 1957.
Ceriagrion coromandelianum (Fabr.)	14	Ray Chaudhuri and Dasgupta, 1949.
Ceriagrion rubiae Laidlaw	14	Asana and Makino, 1935.
Ceriagrion fallax Ris	14	Dasgupta, 1957.
Pseudagrion bengalense Laid.	14	Dasgupta, 1957.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Pseudagriinae		
Pseudagrion decorum (Rambur)	14	Dasgupta, 1957.
Pseudagrion microcephalum (Rambur)	14	Dasgupta, 1957.
Pseudagrion spenci Fraser	14	Dasgupta, 1957.
Pseudagrion rubiceps Selys	14	Dasgupta, 1957.
Subfamily Coenagriinae		
Erythromma najas Hansen	14	Makalovskaja, 1940.
Coenagrion pulchellum Vand.	14	Makalovskaja, 1940.
Coenagrion hastulatum Charp.	14	Makalovskaja, 1940.
Coenagrion armatum Charp.	14	Makalovskaja, 1940.
Coenagrion hieroglyphicum (Burm.)	14	Kichijo, 1941,1942.
Nehalennia speciosa (Charp.)	14	Oksala, 1945.
Pyrrhosoma nymphula (Sulz.)	14	Oksala, 1945.
Subfamily Ischurinae		
Acanthagrion ascendens Calv.	14.	Present study.
Acanthagrion chacoense Calv.	14	Present study.
Aeolagrion foliacum Calvert	14	Present study.
Enallagma cyathigerum (Charp.)	14	Makalovskaja, 1940; Oksala, 1945.
Ischnura elegans (v.d. Lind.)	14	Oksala, 1945.
Ischnura fluviatilis Selys	14	Present study.
Ischnura senegalensis (Rambur)	14	Kichijo, 1941,1942; Dasgupta, 1957.
Ischnura sp. nr. ultima Ris	14	Present study.
Tigriagrion aurantinigrum Calvert	14	Present study.
Subfamily Agriocneminae		
Agriocnemis selenion Ris	14	Kichijo, 1941,1942.
Ceratura capreola Hagen	14	Present study.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Arginae		
Argia sedula (Hagen)	14	Present study.
Family Pseudostigmatidae		
Mecistogaster sp. #1	15	Present study.
Mecistogaster sp. #2	6	Present study.
Family Megapodagriidae Subfamily Megapodagriinae		
Megapodagrion macropus Selys	13	Present study.
Megapodagrion setigerum Selys	13	Present study.
Subfamily Argiolestinae		
Heteragrion flavidorsum Calvert	13	Present study.
Hetaerina inca Calvert	13	Present study.
Philogenia carrillica Calvert	13	Present study.
Family Lestidae Subfamily Sympecmatinae		
Sympycna fusca (Lind.)	13	Kichijo, 1941,1942. Oksala, 1945.
Subfamily Lestinae		
Lestes forficula Rambur	13	Present study.
Lestes sponsa (Hansem)	13	Kichijo, 1941,1942. Makalovskaja, 1940.
Family Pseudolestidae Subfamily Pseudolestinae		
Hypolestes clara (Calvert)	9	Present study.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Family Polythoridae Subfamily Polythorinae		
Cora irene Ris	12	Present study.
Polythore boliviana (MacLac.)	12	Present study.
Family Calopterygidae Subfamily Calopteryginae		
Calopteryx atrata Selys	13	Oguma, 1930; Omura, 1957.
Calopteryx cornelia Selys	13	Oguma, 1930.
Calopteryx maculata (Beauvois)	13	Present study.
Calopteryx splendens (Harris)	13	Makalovskaja, 1940; Oksala, 1945.
Calopteryx virgo Linn.	13	Makalovskaja, 1940; Kichijo, 1942; Hirai, 1956; Omura, 1957.
Mnais costalis Selys	13	Oguma, 1930.
Mnais strigata Selys	13	Oguma, 1930; Omura, 1957.
Subfamily Hetaerininae		
Hetaerina americana (Fabr.)	13	Present study.
Hetaerina charca Calvert	13	Present study.
Hetaerina rosea Selys	14	Present study.
Hetaerina sanguinea Selys	13	Present study.
Hetaerina titia (Drury)	13	Present study.
Suborder ANISOPTERA		
Family Gomphidae Subfamily Gomphinae		
Erpetogomphus designatus Hagen	12	Present study.
Erpetogomphus diadophis Calv.	12	Present study.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Gomphinae		
Gomphus citimus tabei Asahina	11	Toyoshima and Hirai, 1953; Hirai, 1956.
Gomphus hakiensis Oguma	12	Kichijo, 1939.
Gomphus melaenops Selys	12	Toyoshima and Hirai, 1953; Hirai, 1956; Omura, 1957.
Gomphus melampus bifasciatus Asahina	10	Oguma, 1930; Toyoshima and Hirai, 1953; Hirai, 1956; Omura, 1957.
Gomphus pallidus Rambur	12	Present study.
Gomphus postocularis Selys	12	Omura, 1957.
Gomphus susukii Oguma	12	Oguma, 1930.
Gomphus unifasciatus Oguma	11	Oguma, 1930.
Nihonogomphus viridis Oguma	12	Omura, 1957.
Ophiogomphus serpentinus Charp.	12	Oksala, 1945.
Subfamily Epigomphinae		
Epigomphus llama Calvert	10	Present study.
Subfamily Ictinogomphinae		
Ictinogomphus rapax (Rambur)	12	Asana and Makino, 1935; Omura, 1949, 1952, 1953; Dasgupta, 1957.
Subfamily Gomphoidinae		
Aphylla edentata Selys	12	Present study.
Aphylla producta Selys	12	Present study.
Gomphoides sp.	12	Present study.
Phyllocycla sp.	12	Present study.
Progomphus intricatus Hagen	12	Present study.
Progomphus phyllochromus Ris	12	Present study.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Hageninae		
Sieboldius albardae Selys	12	Omura, 1957.
Family Petaluridae Subfamily Petalurinae		
Tachopteryx thoreyi (Hagen)	10	Present study.
Uropetala carovei Selys	9	Wolfe, 1953.
Subfamily Tanypterictinae		
Tanypteryx pryeri Selys	9	Kichijo, 1939.
Family Aeshnidae Subfamily Brachytrinae		
Boyeria maclachlani Selys	14	Omura, 1957.
Subfamily Aeshinae		
Aeshna coerulea (Strom.)	13	Oksala, 1943.
Aeshna crenata Hagen	14	Oksala, 1939,1943.
Aeshna cyanea Mull.	14	Oksala, 1943.
Aeshna d. diffinis Rambur	11	Present study.
Aeshna grandis Linn.	14	Makalovskaja, 1940; Oksala,1943,1945.
Aeshna intricata Martin	10	Present study.
Aeshna juncea Linn.	14	Makalovskaja, 1940; Oksala, 1943,1944.
Aeshna osiliensis fennica Valle	14	Oksala, 1943,1944.
Aeshna peralta Ris	14	Present study.
Aeshna subarctica elisabethae Djak	14	Oksala, 1943.
Aeshna viridis Eversm	14	Oksala, 1943.
Aeshna sp. nr. unicolor Martin	14	Present study.
Coryphaeshna adnexa (Hagen)	14	Present study.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Anactinae		
Anax junius (Drury)	14	McGill, 1904; Lefevre and McGill, 1908.
Anax parthenope julius Brauer	14	Omura, 1957.
Hemianax ephippiger (Burmeister)	7	Seshachar and Bagga, 1962.
Subfamily Gynacanthaginae		
Gynacantha japonica Bartenef	14	Omura, 1957.
Family Cordulegasteridae Subfamily Cordulegasterinae		
Anotogaster sieboldii (Selys)	13	Oguma, 1930.
Cordulegaster annulatus Latr.	13	Oksala, 1939.
Family Corduliidae Subfamily Corduliinae		
Cordulia aenea Linn.	13	Makalovskaja, 1940.
Somatochlora metallica (v.d. Lind)	13	Oksala, 1945.
Somatochlora uchidai Oguma	13	Oguma, 1915,1930.
Somatochlora viridinea Uhler	13	Oguma, 1915,1930.
Somatochlora flavomaculata Vanderl.	13	Makalovskaja, 1940.
Tetragoneuria petechialis Muttkowski	11	Present study.
Subfamily Epophthalmiinae		
Epophthalmia f. frontalis Selys	13	Dasgupta, 1957.
Family Macrodiplacidae Subfamily Macrodiplacinae		
Aethriamanta brevipennis (Rambur)	13	Dasgupta, 1957.
Urothemis signata (Rambur)	13	Dasgupta, 1957.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Family Libellulidae Subfamily Libellulinae		
Cannaphila vibex (Hagen)	13	Present study.
Dasythemis esmeralda Ris	13	Present study.
Lathrecista asiaica (Fraser)	13	Dasgupta, 1957.
Libellula angelina Selys	13	Oguma, 1915,1930.
Libellula axilena Westwood	12	Present study.
Libellula basalis MacLachlan	13	Smith, 1916.
Libellula incesta Hagen	13	Present study.
Libellula quadrimaculata L.	13	Oguma, 1915,1930; Makalovskaja, 1940; Omura, 1955.
Lyriothemis pachygastra Selys	13	Omura, 1955.
Orthemis biolleyi Calvert	12	Present study.
Orthemis cultriformis Calvert	12	Present study.
Orthemis ferruginea (Fabr.)		
Bolivia	5	Present study.
Texas	12	Present study.
Orthemis levis Calvert	3-4	Present study.
Orthetrum albistylum (Selys)	13	Oguma, 1917,1930; Omura, 1955.
Orthetrum cancellatum (Linn.)	13	Dasgupta, 1957.
Orthetrum glaucum (Brauer)	13	Dasgupta, 1957.
Orthetrum japonicum (Uhler)	13	Oguma, 1917,1930; Omura, 1955.
Orthetrum pruinosum neglectum (Rambur)	13	Dasgupta, 1957.
Orthetrum sabina (Drury)	13	Asana and Makino,1935; Ray Chaudhuri and Dasgupta, 1949.
Orthetrum triangulare melania Selys	13	Omura, 1955.
Potamarcha obscura (Rambur)	13	Asana and Makino,1935; Dasgupta, 1957.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Diastatopidinae		
Diastatops intensa Ris	13	Present study.
Diastatops obscura (Fabr.)	13	Present study.
Perithemis cornelia Ris	13	Present study.
Perithemis domitia (Drury)	13	Present study.
Perithemis electra Ris	13	Present study.
Perithemis lais (Perty)	9	Present study.
Perithemis mooma Kirby	13	Present study.
Perithemis seminole Calvert	13	Present study.
Perithemis sp. #2.	13	Present study.
Zenithoptera viola Ris	13	Present study.
Subfamily Brachydiplactinae		
Brachydiplax chalybea (Brauer)	13	Dasgupta, 1957.
Brachydiplax farinosa Kruger	13	Dasgupta, 1957.
Brachydiplax sobrina (Rambur)	13	Ray Chaudhuri and Dasgupta, 1949.
Micrathyria atra Martin	13	Present study.
Micrathyria didyma (Selys)	13	Present study.
Micrathyria hageni Kirby	13	Present study.
Micrathyria iheringi Santos	12	Present study.
Micrathyria laevigata Calvert	13	Present study.
Micrathyria ocellata dentiens Calvert	13	Present study.
Micrathyria sp. nr. eximia Kirby	11	Present study.
Micrathyria sp. ungulata group	12	Present study.
Micrathyria spuria (Selys)	13	Present study.
Subfamily Sympetrinae		
Acisoma p. panorpoides Rambur	13	Dasgupta, 1957.
Brachythemis contaminata (Fraser)	13	Asana and Makino, 1935; Dasgupta, 1957.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Sympetrinae		
Bradinopyga geminata (Rambur)	13	Dasgupta, 1957.
Crocothemis erythraea (Brulle)	13	Dasgupta, 1957.
Crocothemis servilia (Drury)	13	Asana and Makino, 1935; Ray Chaudhuri and Dasgupta, 1949; Omura, 1955.
Diplacodes trivialis (Rambur)	13	Asana and Makino, 1935; Dasgupta, 1957.
Diplacodes nebulosa (Fraser)	13	Dasgupta, 1957.
Erythemis attala (Selys)	13	Present study.
Erythemis plebeja (Burmeister)	13	Present study.
Erythrodiplax b. basalis (Kirby)	13	Present study.
Erythrodiplax castanea (Burmeister)	13	Present study.
Erythrodiplax connata fusca (Rambur)	13	Present study.
Erythrodiplax fervida (Erichson)	13	Present study.
Erythrodiplax justiniana (Selys)	13	Present study.
Erythrodiplax media Borror	11	Present study.
Erythrodiplax melanorubra Borror	13	Present study.
Erythrodiplax paraguayensis (Forster)	12	Present study.
Erythrodiplax umbrata (Linn.)	13	Present study.
Erythrodiplax unimaculata (De Geer)	13	Present study.
Lepthemis vesiculosa (Fabr.)	13	Present study.
Neurothemis tulia tulia (Drury)	14	Ray Chaudhuri and Dasgupta, 1949.
Pachydiplax longipennis (Burm.)	13	Present study.
Rhodopygia cardinalis (Erich.)	13	Present study.
Sympetrum eroticum (Selys)	11	Kichijo, 1942; Hirai, 1956.
Sympetrum flaveolum Linn.	13	Makalovskaja, 1940.
Sympetrum frequense (Selys)	12	Oguma, 1917, 1930.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Sympetrinae		
Sympetrum pedemontanum (Allioni)	13	Oguma, 1917,1930.
Sympetrum scoticum (Donov)	13	Makalovskaja, 1940.
Sympetrum semicinctum (Say)	13	Smith, 1916.
Tarnetrum illotum (Hagen)	13	Present study.
Subfamily Leucorrhininae		
Cannacria herbida (Gundlach)	13	Present study.
Leucorrhinia albifrons Burmeister	13	Makalovskaja, 1940.
Leucorrhinia dubia Vandl.	13	Oksala, 1945.
Leucorrhinia pectoralis (Charp.)	13	Oksala, 1945.
Leucorrhinia rubicunda Linn.	13	Makalovskaja, 1940.
Subfamily Tritheminae		
Pseudothemis zonata Burmeister	12	Omura, 1955.
Trithemis aurora Burmeister	13	Oguma and Asana,1932.
Trithemis pallidinervis (Kirby)	13	Asana and Makino,1935.
Subfamily Dytheminae		
Brechmorrhoga nubecula Rambur	13	Present study.
Brechmorrhoga pertinax peruviana Ris	13	Present study.
Dythemis cannacrioides Calvert	12	Present study.
Dythemis multipunctata Kirby	13	Present study.
Dythemis rufinervis (Burmeister)	13	Present study.
Macrothemis hemichlora (Burm.)	13	Present study.
Macrothemis mortoni Ris	13	Present study.
Macrothemis musiva (Hagen)	13	Present study.
Scapanea frontalis (Burmeister)	13	Present study.

Continued

Table IV (continued)

SPECIES	n	SOURCE
Subfamily Rhyotheminae		
Rhyothemis variegata (Joh.)	13	Ray Chaudhuri and Dasgupta, 1949.
Rhyothemis fuliginosa Selys	13	Toyoshima and Hirai, 1953; Omura, 1955; Hirai, 1956.
Subfamily Pantaliinae		
Miathyria marcella (Selys)	13	Present study.
Pantala flavescens (Fabr.)	13	Asana and Makino, 1935; Dasgupta, 1947; Present study.
Pantala hymenaea (Say)	13	Present study.
Tauriphila australis (Hagen)	13	Present study.
Tramea abdominalis (Rambur)	13	Present study.
Tramea basilaris burmeisteri Kirby	13	Dasgupta, 1957.
Tramea cophysa Hagen	13	Present study.
Tramea carolina (Linn.)	13	Present study.
Tramea limbata (Desj.)	13	Asana and Makino, 1935.
Tramea virginia (Rambur)	13	Oguma and Asana, 1932 (as T. chinensis); Dasgupta, 1957.

PLATE I

Chromosomes of two species of Mecistogaster

Figures 1, 3, 4, and 5 are Mecistogaster sp. #1.

Figures 2, 6, 7, and 8 are Mecistogaster sp. #2.

Figures 3 and 6 metaphase I, polar view.

Figures 4 and 7 metaphase II, polar view.

Figures 5 and 8 spermatogonial metaphase, polar view.

Figures 1 and 2 are actual size. The scale is in microns and is for Figures 3 through 8.

PLATE I

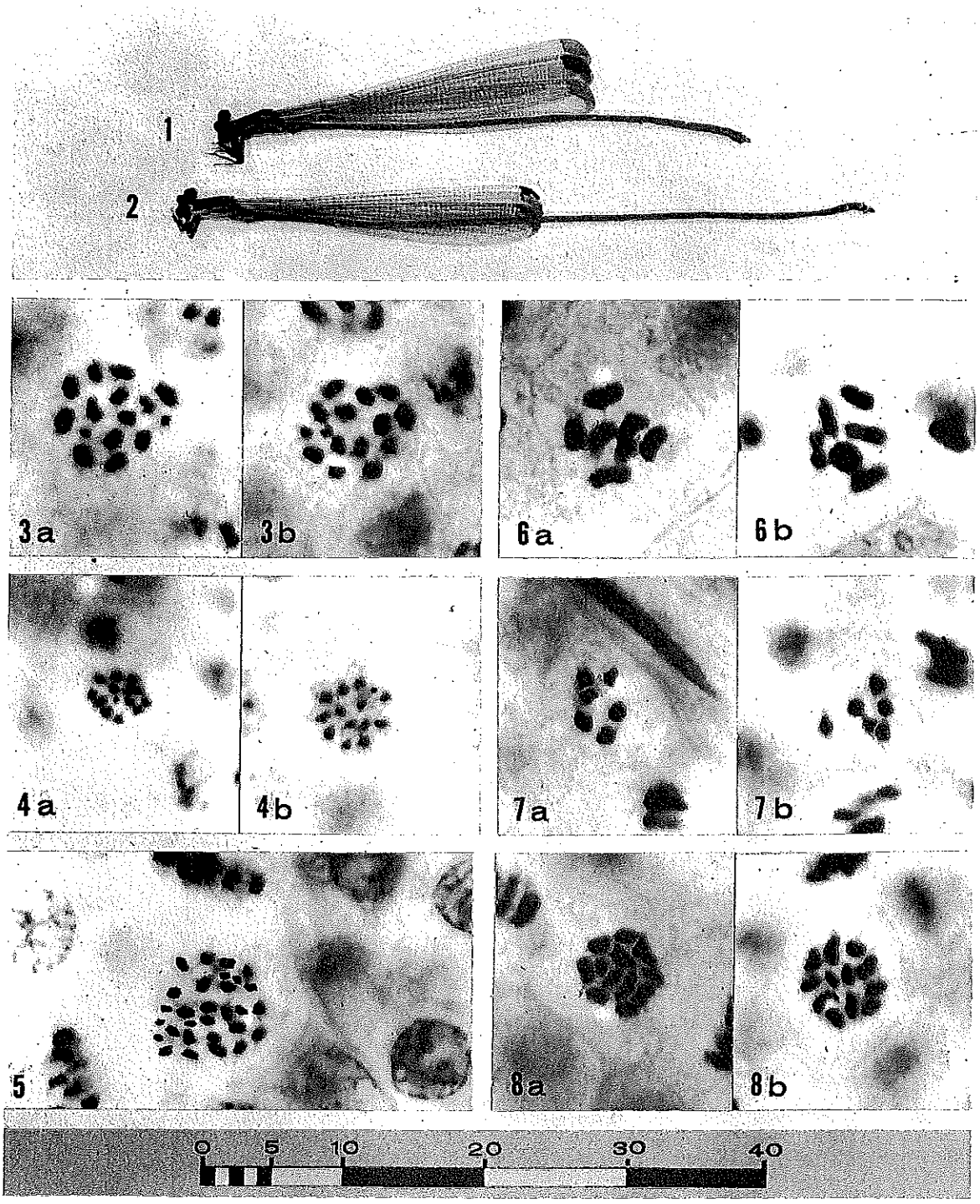


PLATE II

Chromosomes of some Orthemis

Figures 9 through 12 are Orthemis biolleyi Calvert.

Figures 13 through 16 are Orthemis ferruginea (Fabricius).

Figures 10 and 14 metaphase I, polar view.

Figures 11 and 15 metaphase II, polar view.

Figures 12 and 16 metaphase II, lateral view.

Figures 9 and 13 are actual size. The scale is in microns and is for all other figures on this plate. The arrows in Figures 14, 15, and 16 indicate the structures referred to in the text. The arrows in Figure 12 indicate the X-chromosome.

PLATE II

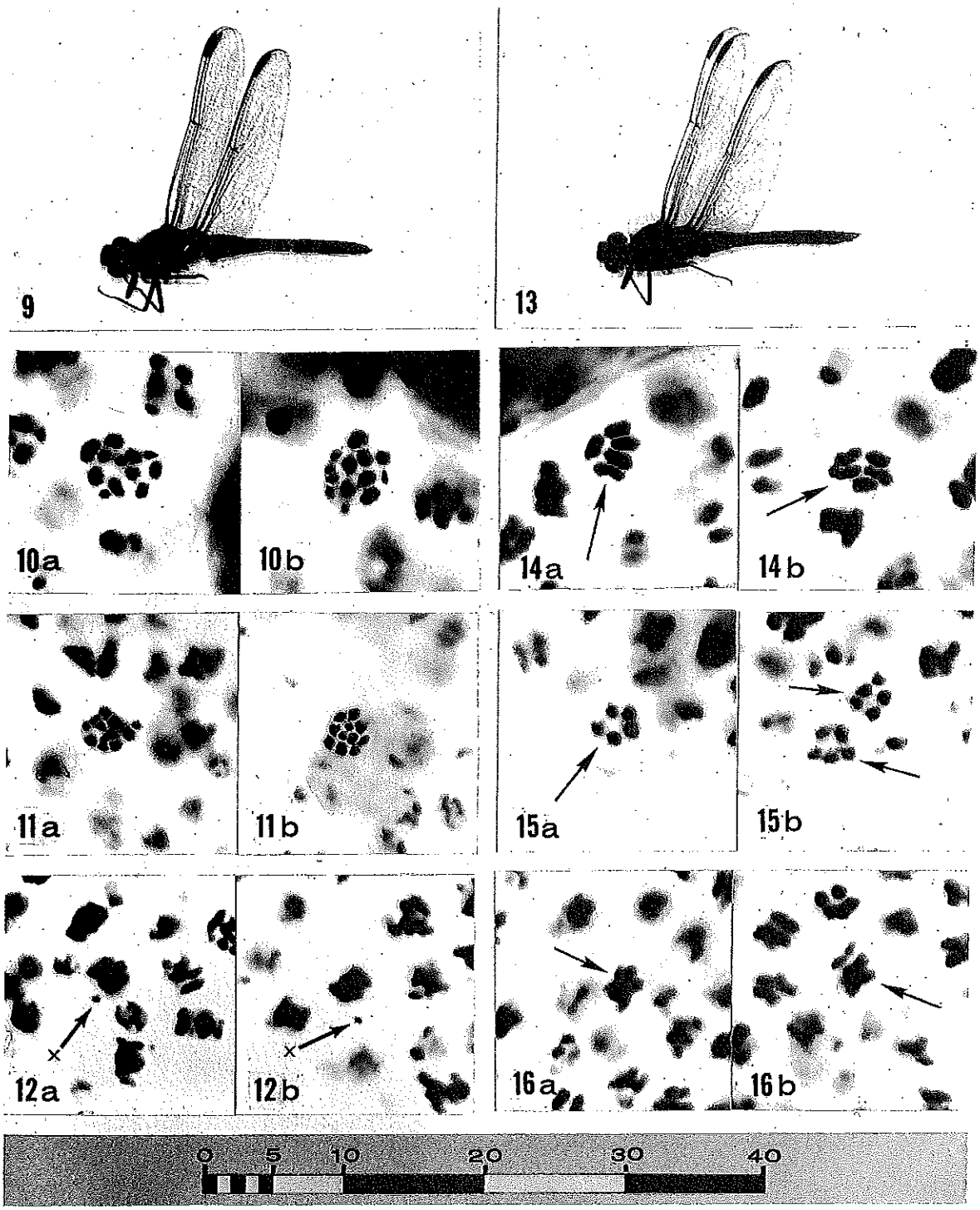


PLATE III

Chromosomes of some *Orthemis*

Figures 17 through 20 are *Orthemis levis* Calvert.

Figures 21 through 24 are *Orthemis cultriformis* Calvert.

Figures 18 and 22 metaphase I, polar view.

Figures 19 and 23 metaphase II, polar view.

Figures 20 and 24 metaphase II, lateral view.

Figures 17 and 21 are actual size. The scale is in microns and is for all other figures on this plate. The arrows in Figures 18, 19, and 20 indicate the structures referred to in the text. The arrows in Figure 24 indicate the X-chromosome.

PLATE III

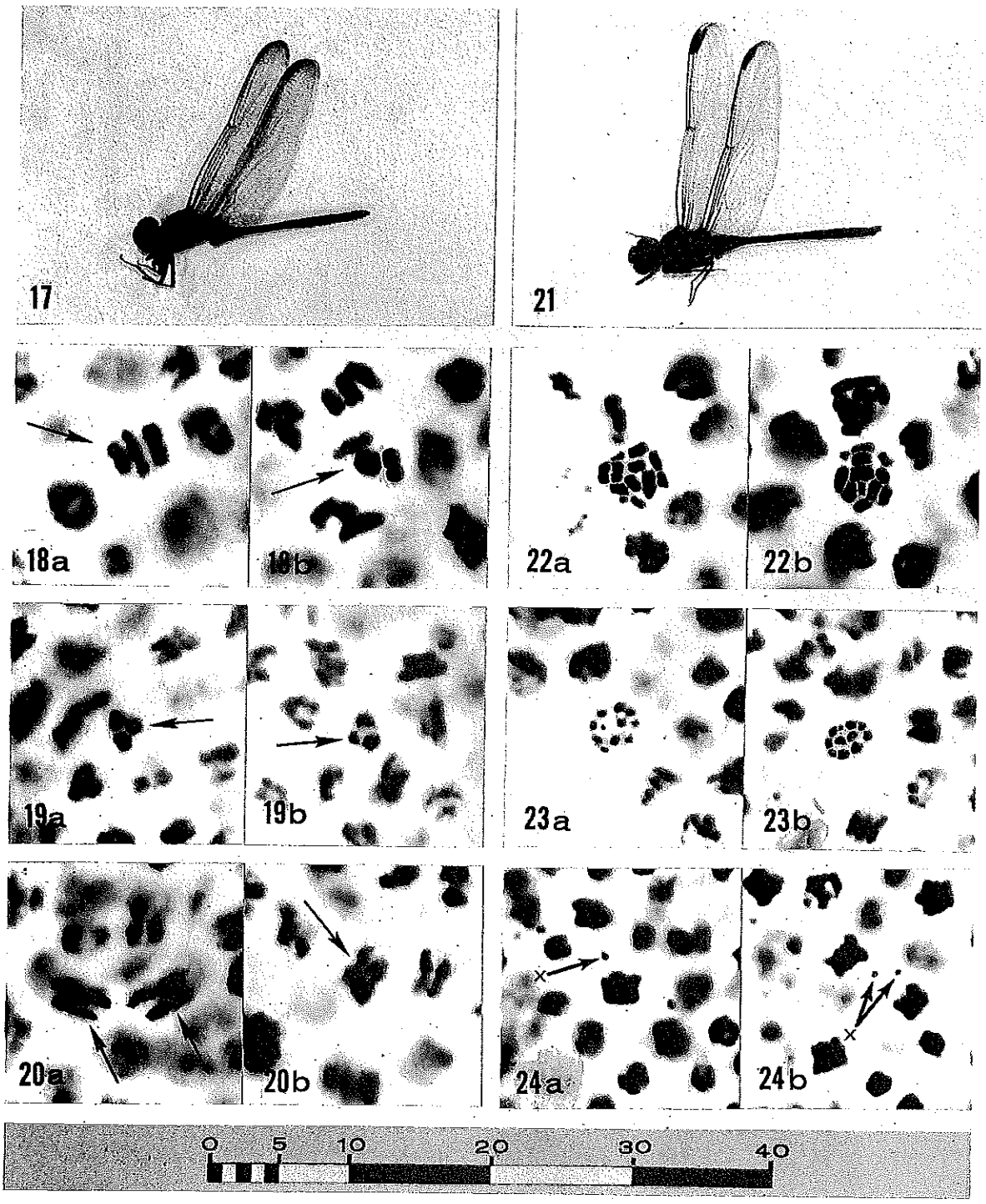

17
21
18a
18b
22a
22b
19a
19b
23a
23b
20a
20b
24a
24b
0
5
10
20
30
40

PLATE IV

Chromosomes of some Macrothemis

Figures 25 through 28 are Macrothemis musiva (Hagen).

Figures 29 through 32 are Macrothemis hemichlora (Burmeister).

Figures 33 through 36 are Macrothemis mortoni Ris.

Figures 26, 30, and 34 metaphase I, polar view.

Figures 27, 31, and 35 metaphase II, polar view.

Figures 28, 32, and 36 metaphase II, lateral view.

Figures 25, 29, and 33 are actual size. The scale is in microns and is for all other figures on this plate. The arrows in Figures 27, 31, and 32 indicate structures referred to in the text. The arrows in Figures 28 and 36 indicate the X-chromosome.

PLATE IV

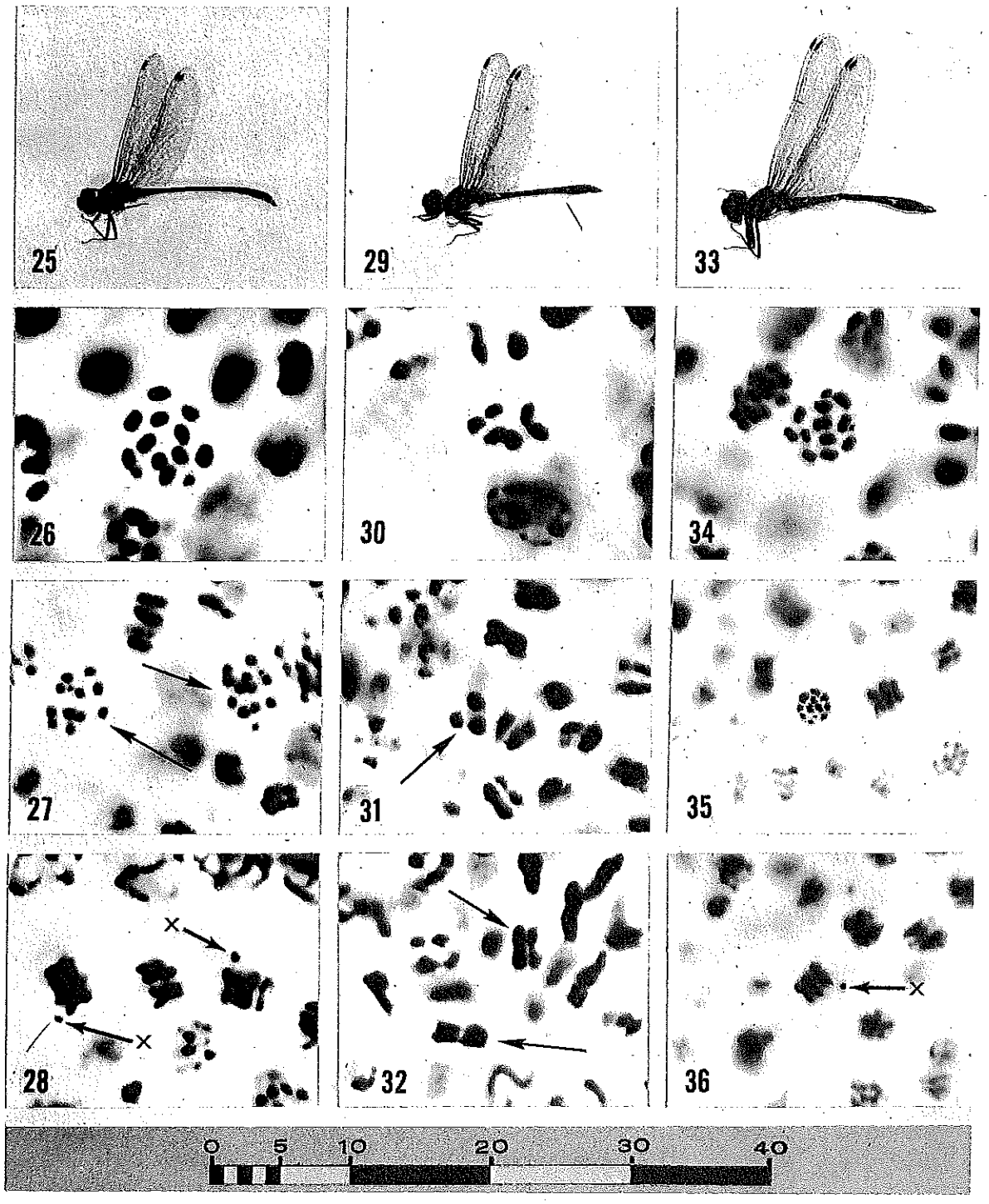


PLATE V

Chromosomes of some Aeshnidae

Figures 37 through 39 are Coryphaeshna adnexa (Hagen).

Figures 40 through 42 are Aeshna peralta Ris.

Figures 43 through 45 are Aeshna sp. nr. unicolor Martin.

Figures 46 through 48 are Aeshna d. diffinis Rambur.

Figures 49 through 51 are Aeshna intricata Martin.

Figures 37, 40, 43, 46, and 49 metaphase I, polar view.

Figures 38, 41, 44, 47, and 50 metaphase II, polar view.

Figures 39, 42, 45, 48, and 51 metaphase II, lateral view.

The scale is in microns and is for all figures. The arrows indicate X-chromosomes.

PLATE V

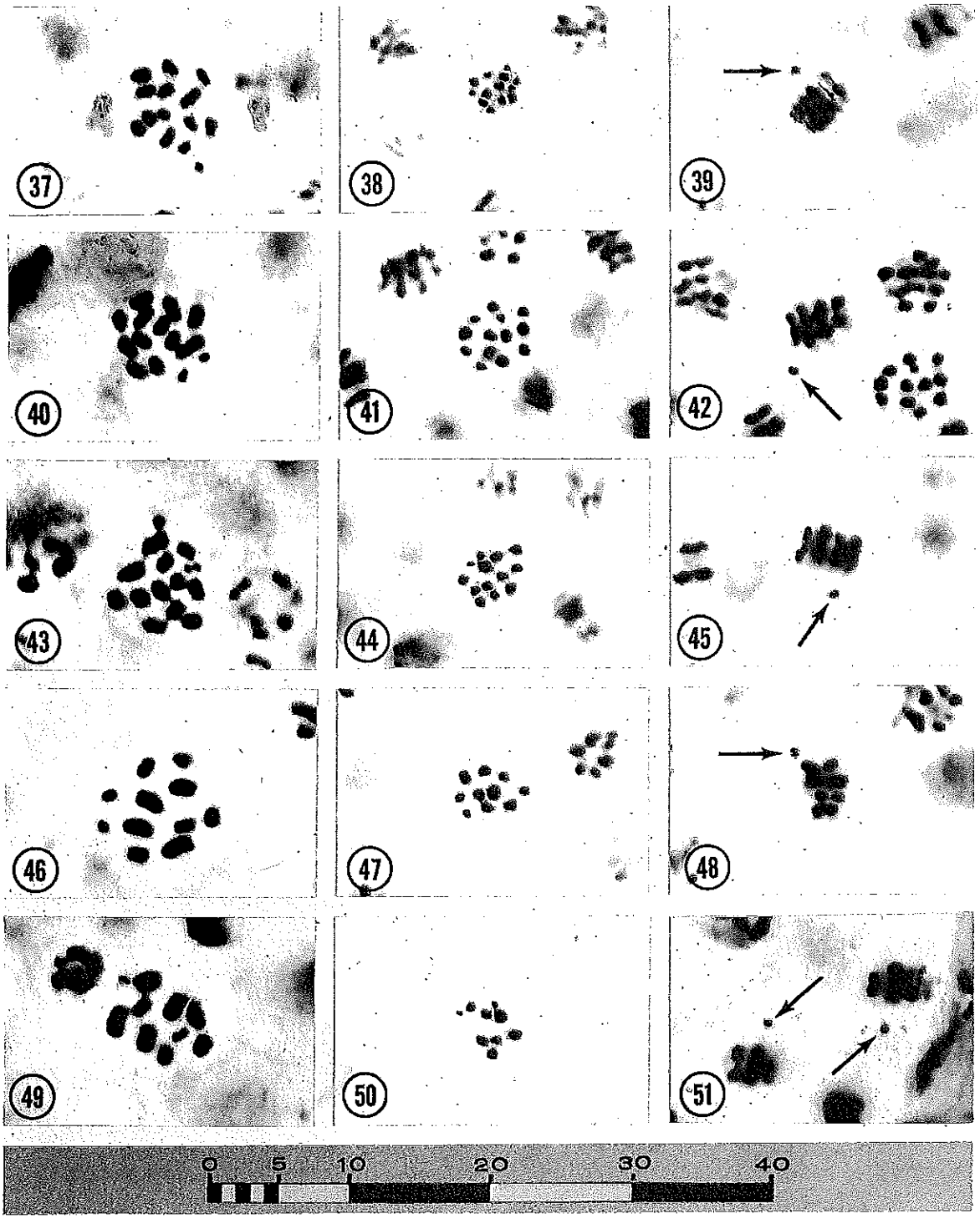


PLATE VI

Chromosomes of some *Perithemis*

Figures 52 through 54 are *Perithemis mooma* Kirby.

Figures 55 through 57 are *Perithemis* sp. #2.

Figures 58 through 60 are *Perithemis cornelia* Ris.

Figures 61 through 63 are *Perithemis electra* Ris.

Figures 64 through 66 are *Perithemis lais* (Perty).

Figures 52, 55, 58, 61, and 64 metaphase I, polar view.

Figures 53, 56, 59, 62, and 65 metaphase II, polar view.

Figures 54, 57, 60, 63, and 66 metaphase II, lateral view.

The scale is in microns and is for all figures. The arrows indicate X-chromosomes.

PLATE VI

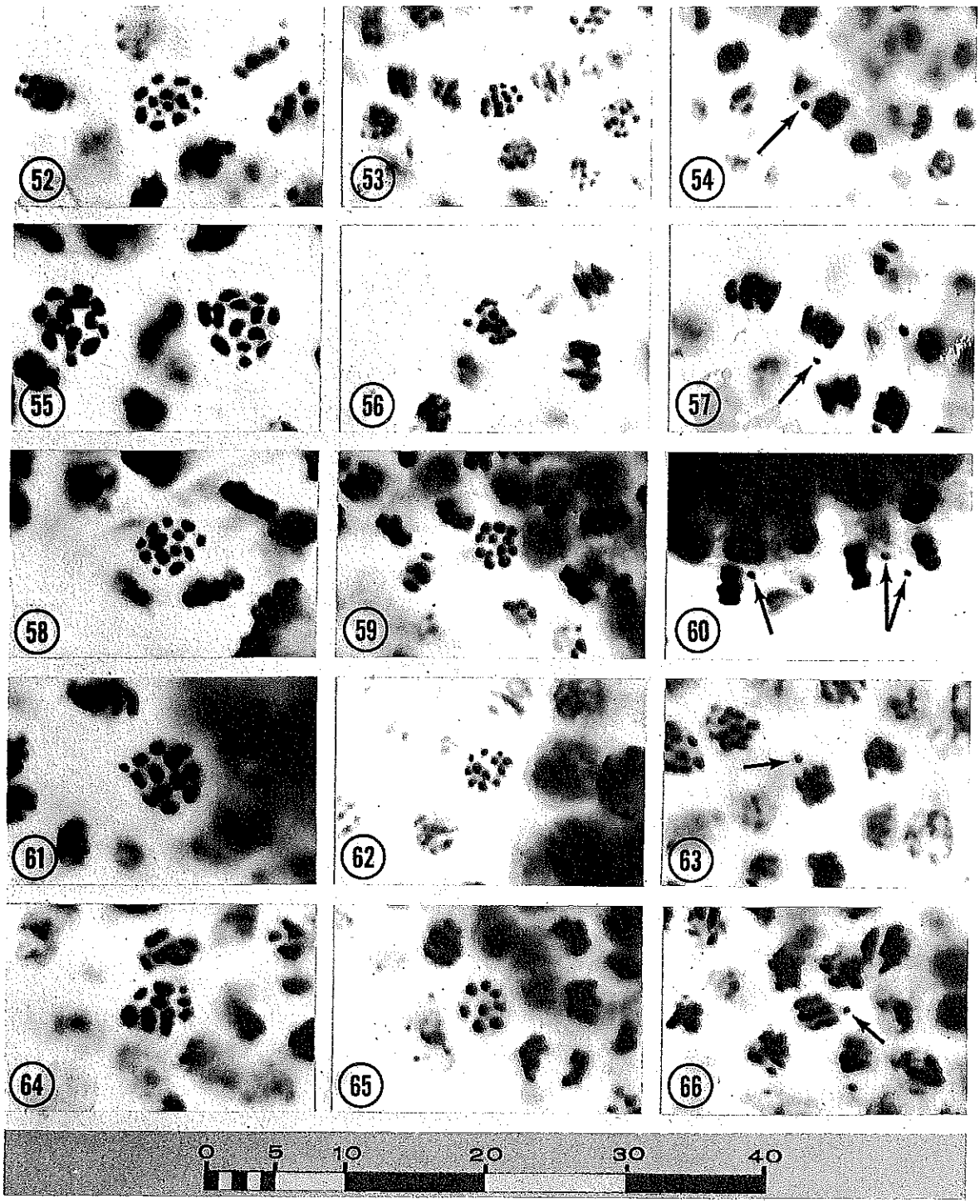


PLATE VII

Figure 67 — Macrothemis hemichlora (Burmeister). Spermatogonial metaphase, polar view (upper left figure) and anaphase lateral view (lower right figure). Feulgen section, bright field, 3000 X.

Figure 68 — Hetaerina titia (Drury). Spermatogonial metaphase, lateral view. Feulgen squash, phase contrast, 3000 X.

Figure 69 — Hetaerina titia (Drury). Metaphase II, lateral view, showing double spindle fibers. Feulgen squash, phase contrast, 3000 X.

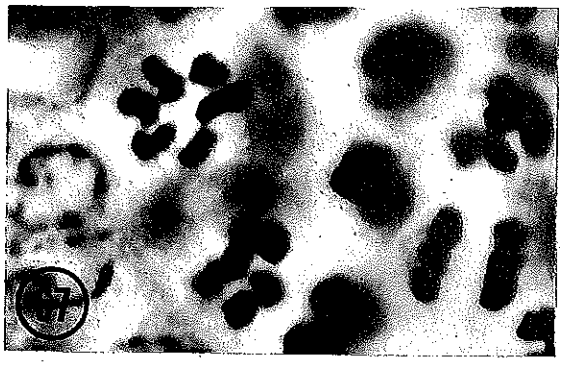
Figure 70 — Hetaerina titia (Drury). Metaphase II, lateral view. Figures 69 and 70 are of the same cell at different focus. Feulgen squash, phase contrast, 3000 X.

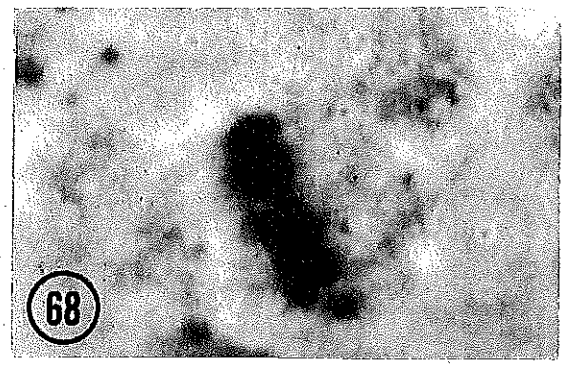
Figure 71 — Tachopteryx thoreyi (Hagen). Diplotene showing apparent multiple chiasmata. Feulgen squash, phase contrast, 3000 X.

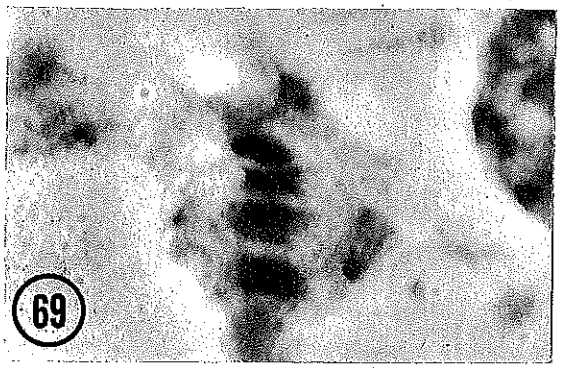
Figure 72 — Tachopteryx thoreyi (Hagen). Diplotene showing apparent multiple chiasmata. Feulgen squash, phase contrast, 3000 X.

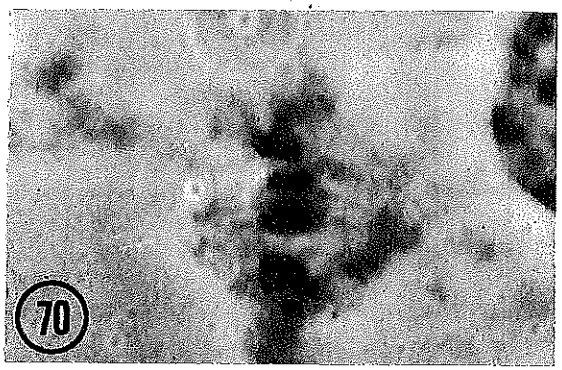
Figure 73 — Macrothemis hemichlora (Burmeister). Metaphase I, polar view, showing terminalized chiasmata. Feulgen section, bright field, 3000 X.

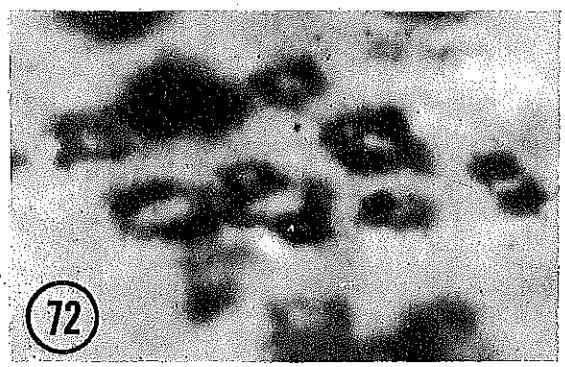
PLATE VII











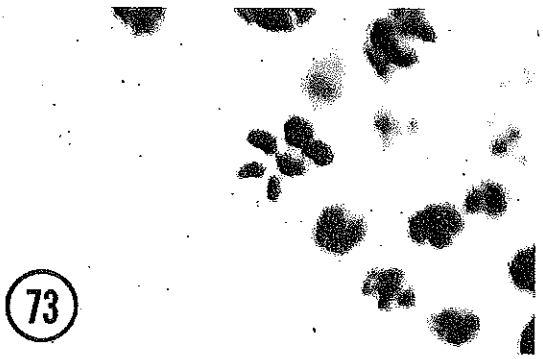


PLATE VIII

Figure 74 Diagram of orientation at metaphase I of the type of bivalent proposed by Resende (1953) for holokinetic chromosomes.

Figure 75 Diagram of the structure actually seen at metaphase I in the holokinetic bivalents of Odonata. The single chiasma may or may not be completely terminalized. The force of terminalization acts in the plane of the equatorial plate.

Figure 76 Two lateral view of metaphase I showing that the initial movement toward the poles is in the center of the bivalent and not at the ends. Figure 76a, Macrothemis hemichlora (Burmeister), n = 3. Figure 76b, Macrothemis musiva (Hagen), n = 13. The structure of bivalents of low n species is essentially the same as those of species with normal karyotypes. 3000 X.

Figure 77 Mecistogaster sp. #2. Spermatogonial division, early and late anaphase. The center of the chromosomes initiate movement toward the poles. Feulgen section, bright field, 3000 X.

PLATE VIII

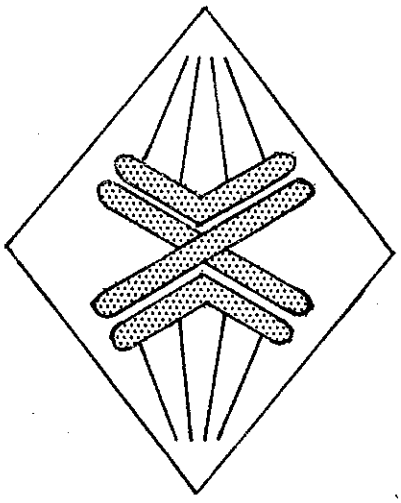


Figure 74 Resende's hypothesis for holokinetic bivalents.

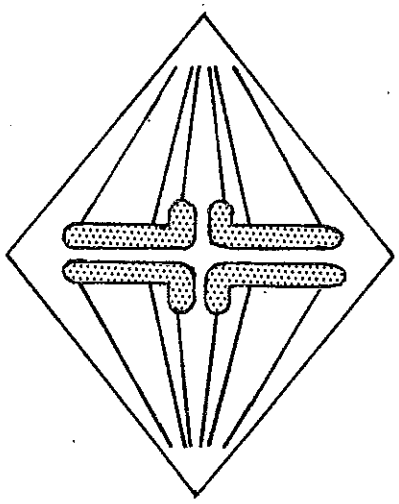
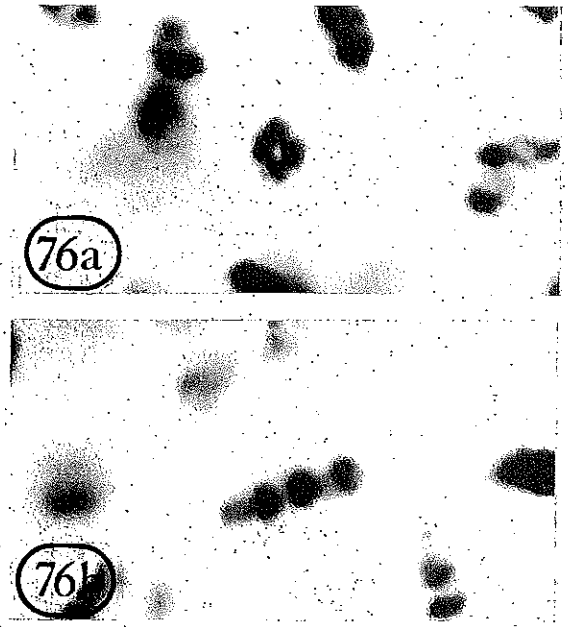


Figure 75 Orientation of odonate bivalents.



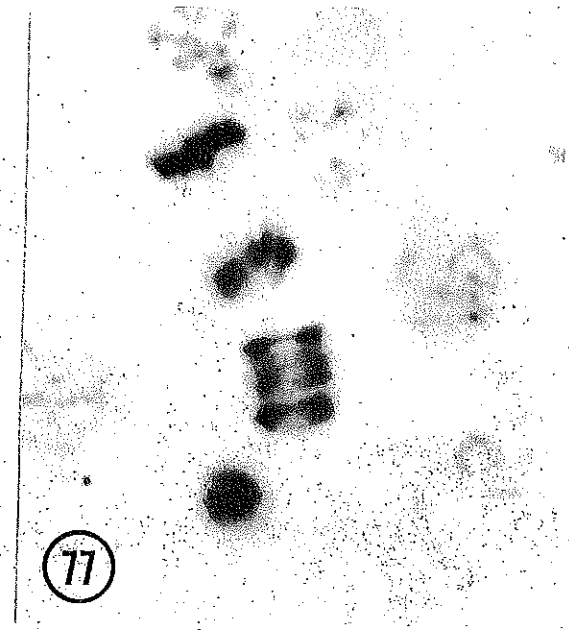


PLATE IX

Figure 78 Auto-orientation may be defined as orientation in which the force of terminalization of chiasmata acts in a direction which is perpendicular to the axis of the spindle at metaphase I.

Figure 79 Co-orientation may be defined as orientation in which the force of terminalization of chiasmata acts in a direction which is parallel to the axis of the spindle at metaphase I.

The above definitions could be applied to either holokinetic chromosomes or those with localized kinetochores.

ax represents the axis of the spindle.

eq represents the equatorial plate.

PLATE IX

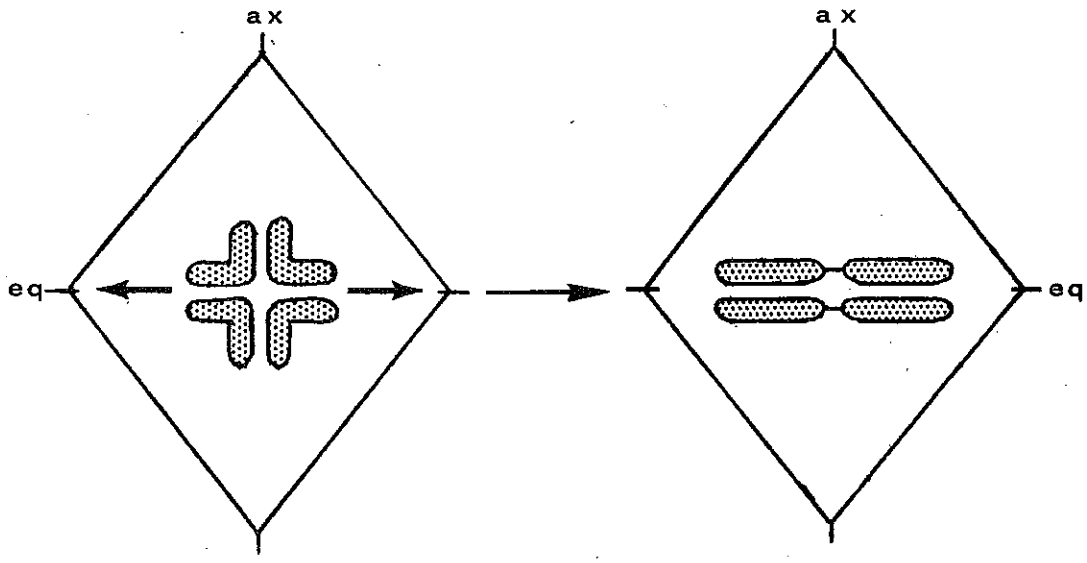


Figure 78 Auto-orientation

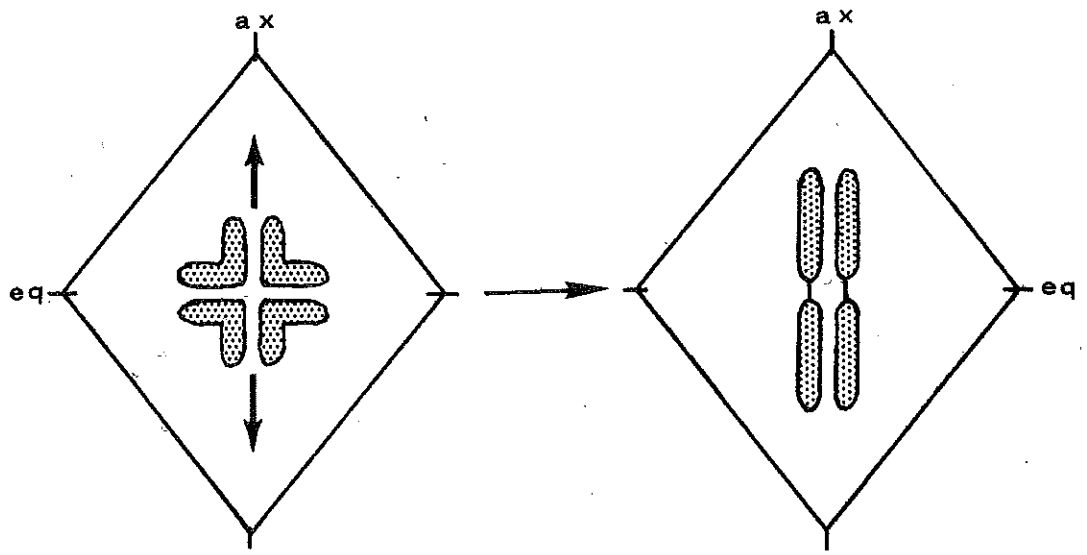


Figure 79 Co-orientation

PLATE X

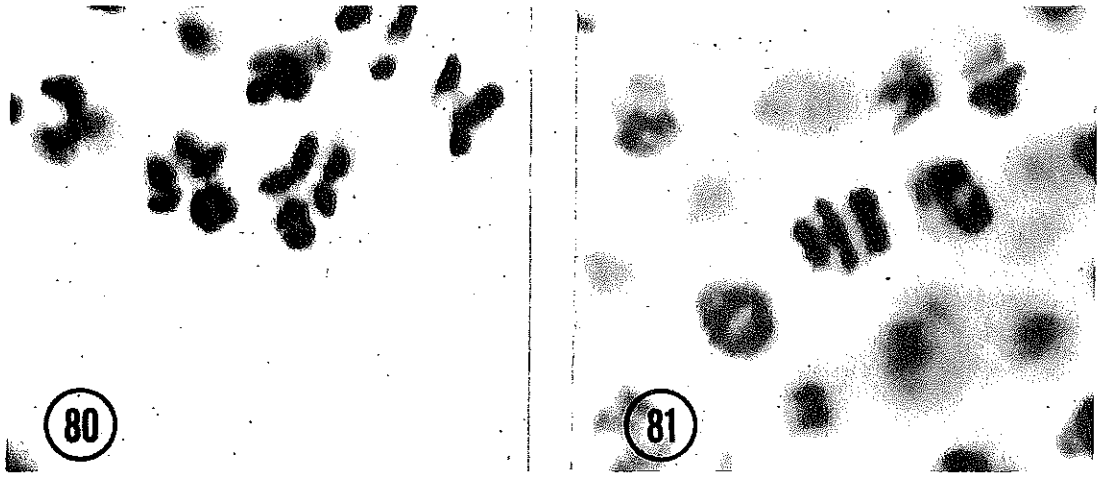
Figure 80 — Macrothemis hemichlora (Burmeister). Metaphase I, polar view, showing one ring bivalent in each of two adjacent cells. Feulgen section, bright field, 3000 X.

Figure 81 — Orthemis levis Calvert. Metaphase I, polar view, showing two chiasmata in the equatorial plate in the tripartite bivalent. Feulgen section, bright field, 3000 X.

Figure 82 — Diagram of the orientation of a double chromatid at metaphase with the half-chiasma in the equatorial plate and the chromatids extended toward the poles.

Figure 83 — Diagram of the orientation of a triple chromatid at metaphase II of a numerical heterozygote. The terminalized half-chiasmata still line up in the equatorial plate. This makes it appear that terminalized half-chiasmata are more important in directing orientation at metaphase II than the kinetic properties of the chromatids.

PLATE X



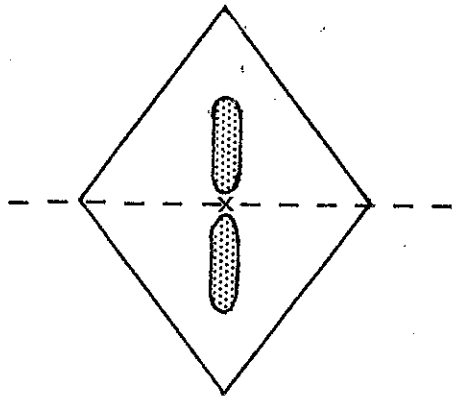


Figure 82

Normal orientation of double chromatid at metaphase II.

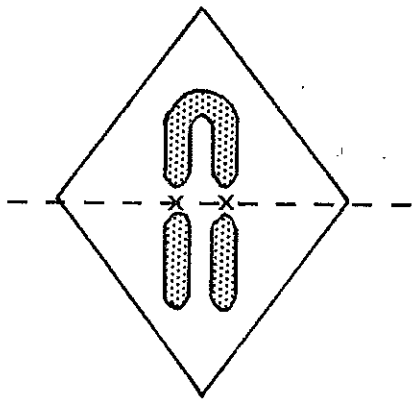


Figure 83

Orientation of triple chromatid at metaphase II of numerical hetero-zygote.

VITA

Robert Bruce Cumming was born in Minneapolis, Minnesota, on October 10, 1928, the son of Virginia Page Cumming and Wallace Chester Cumming. He attended elementary and secondary schools in Omaha, Nebraska, and Jacksonville, Florida. After completing work at Landon High School, Jacksonville, Florida, in 1948, he entered the University of Florida, at Gainesville, Florida. He received the degree of Bachelor of Science with a major in Biology from the University of Florida in June, 1953. He was employed as a biology teacher at Andrew Jackson High School in Jacksonville, Florida, from August, 1954, until June, 1956. He was employed as a junior engineer at the Jet Engine Division of General Electric Corporation in Evendale, Ohio, from July, 1956, to July, 1957. In September, 1957, he entered the Graduate School of the University of Florida and completed work on the degree of Master of Science in June, 1959. From July, 1959, through June, 1960, he was on a collecting trip to Bolivia, Brazil, Peru and Central America. In January, 1960, the degree of Master of Science with a major in Biology and a minor in Geology was awarded to him by the University of Florida. In September, 1960, he was married in San Juan, Puerto Rico, to Carmen Margarita Montes, and the same month he entered the Graduate School of The University of Texas. Since that time he has been employed as a Teaching Assistant or as a Research Scientist in the Department of Zoology.

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