

SYNOPSIS OF THE MAIN CYTOTAXONOMIC DATA IN THE ORDER ODONATA

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So far 371 species and subspecies of 20 families of the three living suborders have been studied cytologically. This figure represents more than 6% of the total number of species described, making dragonflies cytologically by far the best studied order of insects. A review is given of the main data on the chromosomal cytology, viz. haploid chromosome number, general morphology and origin of the karyotype, distinctions, if any, between geographic populations, peculiarities in chromosome behaviour and mode of sex determination of all species and subspecies hitherto studied. In addition, a complete bibliography related to the subject is presented.

INTRODUCTION

Since several years the author is working on a monograph on the cytotaxonomy and cytogenetics of the Order, which will include also a detailed annotated catalogue of the chromosomal cytology of dragonflies. It may take some time before the work will appear in print, therefore it seems useful to give here a synopsis of the main data on the chromosomal cytology of the 371 species and subspecies so far studied and to present a complete bibliography related to the subject.

Because of the limited space available, the information listed had to be restricted to the most essential data, viz. locality, haploid chromosome number, occurrence of *m*-chromosomes, general morphology and origin of the karyotype (if peculiar), distinctions, if any, between geographic populations, peculiarities in chromosome behaviour, mode of sex determination (if other than the usual XO type) and reference to the source publication.

The species are listed under valid taxonomic names, in alphabetic sequence within a genus, regardless of the synonym under which originally cytotaxonomically described.

For the sake of convenience the system followed is that outlined by FRASER (1957, A reclassification of the order Odonata, R. zool. Soc. N.S.W., Sydney), though this does not imply that the author agrees with all of his suggestions. Several of his families and subfamilies are certainly not tenable, e.g. *Macrodiplacidae*, *Sympecmatinae*, subdivision of *Petaluridae* etc. — to mention just some of them.

REPRESENTATIVENESS OF THE CYTOLOGICALLY STUDIED MATERIAL

The available sample covers 20 families of the three living suborders and represents more than 6% of the total number of species described. Though this figure makes dragonflies cytologically by far the best studied insect order, the cytotaxonomic record does not include several phylogenetically important families.

In Figure 1 Fraser's genealogical tree has been used to present graphically the family affiliation of the material hitherto studied (in figure family names framed). At a first glance at least two important lacunae in the cytotaxonomic record are evident:

- (1) The superfamily Hemiphlebioidea, with a single family *Hemiphlebiidae*, containing a monotypic genus *Hemiphlebia* (species *H. mirabilis* Selys, from Gouldburn River, Victoria, Australia) is considered, on the basis of venational characters, as a transitional form between the Coenagrionidea on one hand, and the extinct suborder Protozygoptera on the other. It could, therefore, perhaps furnish some evidence on the cytological conditions during the earliest history of Zygoptera.
- (2) In view of the peculiar cytotaxonomic situation found in the only hitherto studied member of the primitive *Pseudolestidae*, it would be interesting to gather some information on the karyotypic condition in the *Amphipterygidae*, which occupy a key position at the base of the higher Calopterygoidea and in their direct derivatives, viz. *Heliocharitidae* and *Chlorocyphidae*.

Aside from the fact that in several families too little material has been examined to permit any generalisations, we are of the opinion that cytotaxonomic data on the *Hemiphlebiidae* and *Amphipterygidae* are urgently needed before more far reaching cytophylogenetic considerations on the Order can be discussed.

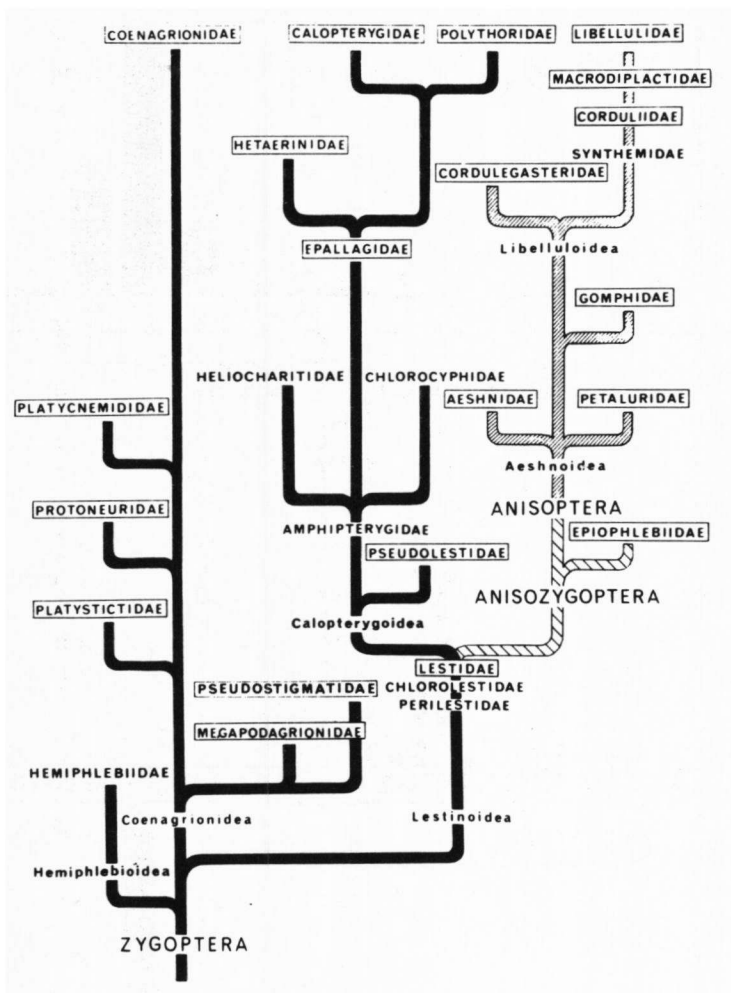


Fig. 1. Cytologically studied (framed) and unknown (unframed) odonate families, placed in Fraser's genealogical tree.

CHROMOSOME NUMBER

The chromosome number has been determined in all species studied; for 20 of these more than one number has been reported. The variation occurs either in different cells of the same specimen or different chromosome numbers are peculiar to different geographic populations. The forms with numeric variation in the complement were omitted from the graphs in Figure 2.

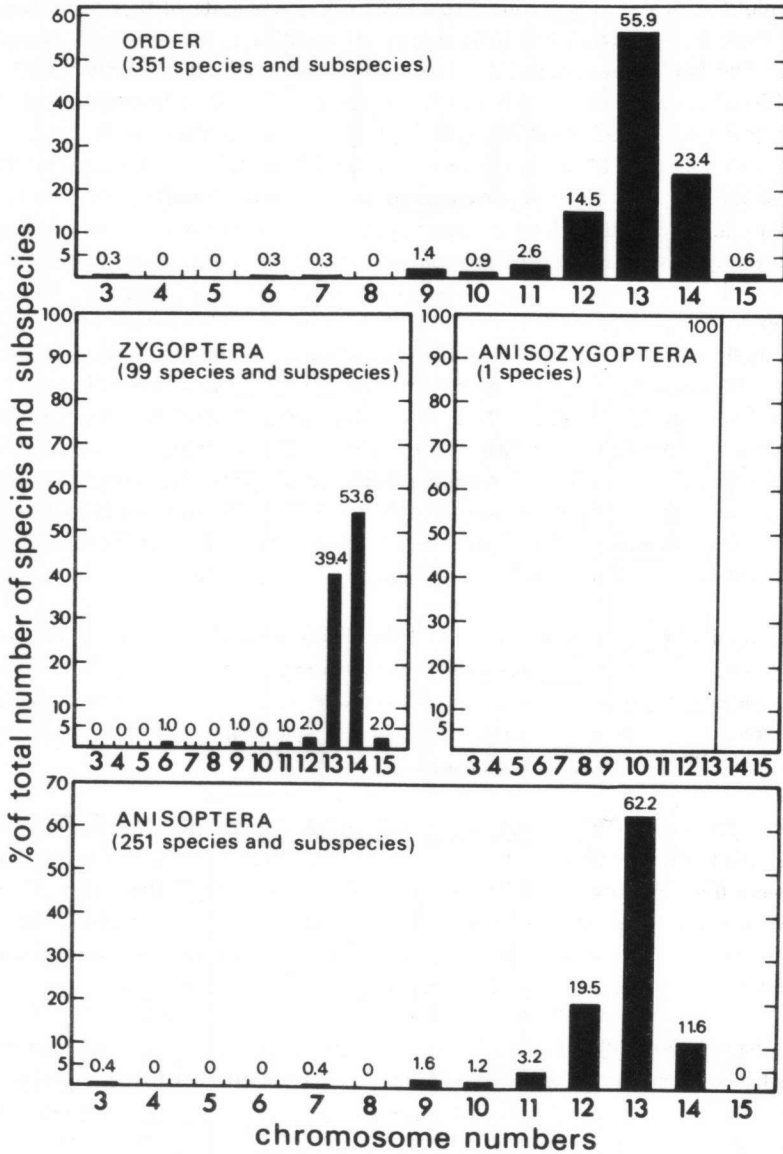


Fig. 2. Histograms of haploid chromosome numbers in the order and in the three living suborders (in % of total number of species studied). The width of columns is proportional to the absolute number of cytotaxonomically examined species within the order and suborders.

Haploid numbers range from 3 to 15 (cf. Fig. 2). In spite of this rather broad range there is, in general, but little numerical variation in the dragonfly complements. The haploid numbers 12, 13 and 14 are represented in nearly 93.8% of the Odonata examined; $n = 13$ can be considered as the type number of the Order. It is found in 55.9% of the species studied cytologically.

On the suborder level the pattern is essentially similar in Anisoptera. The haploid number, $n = 13$, is represented in 62.2% of the sample. The same type number can be assumed also for Anisozygoptera, since it was found in the single cytologically studied representative of the suborder, that consists of two living species only. The situation seems more complicated in Zygoptera. The haploid number, $n = 13$, was found only in 39.4% of cases studied, whereas 14 elements occur in the haploid sets of 53.6% of them. It would appear, from this evidence, that $n = 14$ should be regarded as the type number of the suborder, if it were not for the fact that 14 elements are peculiar only to the families *Protoneuridae* and *Coenagrionidae* and that the latter covers more than 51.5% of the total number of the representatives of the suborder hitherto examined cytologically. This being so, it is clear that the studied sample is not representative for the suborder and that for the Zygoptera too, the haploid number, $n = 13$, can more safely be assumed as the true type number.

The family type numbers are as follows: $n = 9$ (*Pseudolestidae* [?], *Petaluridae*), $n = 12$ (*Polythoridae*, *Gomphidae*), $n = 13$ (*Platystictidae* [?], *Platycnemididae*, *Megapodagrionidae*, *Lestidae*, *Epallagidae*, *Hetaerinae*, *Calopterygidae*, *Epiophlebiidae*, *Cordulegasteridae*, *Corduliidae*, *Macrodiplactidae*, *Libellulidae*), and $n = 14$ (*Protoneuridae*, *Coenagrionidae*, *Aeshnidae*).

Some genera deviate distinctly from the prevailing chromosome number pattern of the families they belong to, notably *Leptagrion* ($n = 15$) in *Coenagrionidae*, *Mecistogaster* ($n = 3$ and 15) in *Pseudostigmatidae*, *Trigomphus* ($n = 10$ and 12) in *Gomphidae*, *Tetragoneuria* ($n = 11$ and 14) in *Corduliidae* and *Orthemis* ($n = 12$) in *Libellulidae*. Some of these complements, however, are of secondary origin and only point to the genetic instability of the genera involved.

In the cytologically studied material with uniform chromosome numbers throughout the species range 79.8% of the taxa have a number that is equal to or higher than the type number of the Order. If the distribution is analyzed from the point of view of the geological age of the families concerned, a significant shift can be observed. A tendency towards lower chromosome numbers is clearly apparent in the geologically old families, whereas in the younger groups numerically higher complements prevail. Thus, *Epallagidae*, *Gomphidae*, *Petaluridae*, *Aeshnidae* and *Cordulegasteridae* are the only families of our sample the representatives of which are known already from the Mesozoic beds. In these only

some 10.5% of species studied possess chromosome numbers equal to or higher than the present type number of the Order.

Summarizing the above information, it can be concluded that the chromosome numbers do reflect, to some extent, the taxonomic affinities and phylogenetic character of some superspecific taxa in dragonflies.

PRIMARY AND SECONDARY COMPLEMENTS

Karyotypes of dragonflies can be divided roughly in two groups: (1) the "normal", high-n complements ($n = 9$ to 14), and (2) the low-n complements ($n = 3$ to 8). Chromosome size in the high-n species is approximately half that in the low-n forms.

In the high-n species a parallel is apparent between the increase in specialization and advancement on one hand, and the increase of the chromosome number on the other. The low-n species can be found in any systematic group, of any type number. It has been demonstrated in numerous cases, that the low-n complement arises by fusion of some or all elements of the original complement, hence the nomenclature "primary" and "secondary" complements.

Aside from fusions, in several species fragmentation of one or more elements of the original set has taken place, resulting in an increase of the chromosome number. These complements too, are called "secondary" and may occur in single species of any taxonomic group.

THE *m*-CHROMOSOMES

The *m*-chromosomes (= micro-chromosomes) represent a peculiar feature of dragonfly cytotaxonomy. They can be found in any species of any family, though in some groups they appear to be scarcer than in others. Thus, they are lacking in all species of the genera *Argia* and *Ophiogomphus*, in all primary complements of *Enallagma* and *Megapodagrion* and in most representatives of the subfamilies *Coenagrioninae*, *Ischnurinae* and *Gomphoidinae*, whereas in many genera they were found in all species studied.

Contrary to the chromosome numbers, the distribution of *m*-chromosomes does not reflect any taxonomic affinities, save perhaps for a few cases in the above mentioned taxa.

On the geographic population level, on the other hand, the *m*-chromosomes may represent a peculiar feature: they may be present in one population and

lacking in the other. This condition has been observed in the following species: *Lestes dryas*, *Gomphus exilis*, *Anax junius*, *Cordulegaster boltoni*, *Macromia magnifica*, *Pachydiplax longipennis*, *Leucorrhinia hudsonica*, *L. intacta* and *Brechmorhoga mendax*. Also the relative size of the *m*-elements may be different in different populations or in different infraspecific forms of the same species, e.g. in *Calopteryx virgo*, *Libellula quadrimaculata* etc.

SEX CHROMOSOMES AND SEX DETERMINATION

The original mode of sex determination in dragonflies is XO/XX, the male being the heterogametic sex. It is observed in all primary complements, regardless of the chromosome number viz. the degree of advancement and specialization achieved by the taxa concerned.

In secondary complements a neo XY-sex determination occurs in those cases where the original X was involved in a fusion with an autosome. Its occurrence is related neither to any taxonomic groups nor to phylogeny, though in some families (e.g. *Aeshnidae*) it is found more frequently than in others.

The original sex chromosome is usually one of the smallest elements of the karyotype, in some cases it is medium-sized, while it is the largest in a few species other than *Gomphidae*. It has been argued that the present type number of the latter family is of secondary rather than of primary origin and that the large X-es met with in many gomphidan dragonflies arose in complicated fusions with autosomes (cf. KIAUTA, 1969 a), but the suggestion should be understood as a working hypothesis only.

It is a matter of course that the neo-X element is at least medium sized, if it is not the largest of the complement. The unfused homologue of the autosomal part of the neo-sex element is usually small, it has the function of a neo-Y and is confined to the male line.

REVIEW OF THE MAIN CYTOTAXONOMIC DATA IN THE ORDER

The following explanations on the tabulation of the data are considered useful:

- (1) As a rule the male haploid numbers are indicated. If a number was derived from a mitotic figure, it is given in brackets. Where only female complements were described, the sex is indicated in brackets, preceding the number. If for a species several numbers are listed, those connected by "+" appear in one and the same specimen, while those separated by ";" were reported for different specimens or populations.

- (2) The presence of *m*-chromosomes is indicated in brackets behind the chromosome number. In the latter, however, the *m*-chromosomes are also included.
- (3) The remarks are derived both from the text and from the illustrations of the score publication.
- (4) If the name of an author appears in brackets behind the synonym as listed under "Remarks" and is printed in *italics*, it refers to the author of the cytological publication where the synonym was used, and not to the author of the synonym.

SYNOPSIS

FAMILY Subfamily <i>Genus, Species, Subspecies</i>	Locality	δn (and presence of <i>m</i>)	Remarks	References
PLATYSTICTIDAE				
Palaemnematinae				
<i>Palaemnema paulina</i> (Drury, 1773)	Costa Rica	13 (<i>m</i>)		CUMMING, 1964a
PROTONEURIDAE				
Protoneurinae				
<i>Epipleoneura</i> sp.	Bolivia	14		CUMMING, 1964a
<i>Neoneura rubriventris</i> (Selys, 1860)	Bolivia	14 (<i>m</i>)		CUMMING, 1964a
PLATYCNEMIDIDAE				
Platycnemidinae				
<i>Copera annulata</i> (Selys, 1863)	Japan, India	13 (<i>m</i>)	sub <i>Platycnemis</i>	KICHIJO, 1941, 1942a, 1942c; DASGUPTA, 1957
<i>Platycnemis pennipes</i> (Pallas, 1771)	Finland, Italy	13	in δ occasionally two chiasmata in one of the longer bivalents	OKSALA, 1945; KIAUTA, 1971b
COENAGRIONIDAE				
Amphicneminae				
<i>Diceratobasis macrogaster</i> (Selys, 1875)	Jamaica	14 (<i>m</i>)		CUMMING, 1964a
Pseudagrioninae				
<i>Ceragrion cerinorubellum</i> (Brauer, 1866)	India	14 (<i>m</i>)		DASGUPTA, 1957
<i>C. coromandelianum</i> (Fabricius, 1798)	India	14 (<i>m</i>)		RAY CHAUDHURI & DAS GUPTA, 1949; SRIVASTAVA & DAS, 1953; DAS, 1956
<i>C. fallax</i> Ris, 1914	Bangla Deah	14 (<i>m</i>)		DASGUPTA, 1957
<i>C. rubiae</i> Laidlaw, 1916	India	14 (<i>m</i>)		ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942e
<i>C. tenellum tenellum</i> (Villers, 1789)	Italy	14 (<i>m</i>)		KIAUTA, 1971b
<i>Megalagrion oahuense</i> (Blackburn, 1884)	Hawaii	14 (<i>m</i>)		KIAUTA, 1969d
<i>Pseudagrion australasiae</i> Selys, 1876	India	14 (<i>m</i>)	sub <i>P. bengalense</i> Laidlaw	DASGUPTA, 1957

FAMILY Subfamily Genus, Species, Subspecies	Locality	♂ n (and presence of m)	Remarks	References
<i>P. decorum</i> (Rambur, 1842)	India	14 (m)		DASGUPTA, 1957
<i>P. microcephalum</i> (Rambur, 1842)	India	14 (m)		DASGUPTA, 1957
<i>P. rubriceps</i> Selys, 1876	India	14 (m)		DASGUPTA, 1957
<i>P. spencei</i> Fraser, 1922	India	14 (m)		DASGUPTA, 1957
Coenagrioninae				
<i>Cercion lindeni</i> (Selys, 1840)	Italy	14 (m)		KIAUTA, 1971b
<i>Chromagrion conditum</i> (Hagen, 1876)	U.S.A.	14		CRUDEN, 1968
<i>Coenagrion armatum</i> (Charpentier, 1840)	Finland, U.S.S.R.	14	sub <i>Agriion</i>	OKSALA, 1939a; MAKALOWSKAJA, 1940
<i>C. hastulatum</i> (Charpentier, 1825)	U.S.S.R.	14	sub <i>Agriion</i>	MAKALOWSKAJA, 1940
<i>C. hieroglyphicum</i> (Brauer, 1865)	Japan	14 (m)	sub <i>Agriion</i>	KICHIO, 1941, 1942a, 1942c
<i>C. pulchellum</i> (Vander Linden, 1823)	U.S.S.R., Netherlands	14	sub <i>Agriion</i> (<i>Makalowskaja</i>)	MAKALOWSKAJA, 1940; KIAUTA, 1969a
<i>C. resolutum</i> (Hagen, 1876)	U.S.A.	14		CRUDEN, 1968
<i>Coenagrion</i> sp.	Japan	14 (m)	sub <i>Agriion</i>	KICHIO, 1941, 1942a, 1942c
<i>Erythromma najas</i> (Hansemann, 1823)	Finland, U.S.S.R., Netherlands	14		OKSALA, 1939a; MAKALOWSKAJA, 1940; KIAUTA, 1969a
<i>Nehalennia irene</i> (Hagen, 1861)	U.S.A.	14		CRUDEN, 1968)
<i>N. speciosa</i> (Charpentier, 1840)	Finland	(♀) 14 (m ?)		OKSALA, 1945
<i>Pyrhosoma nymphula</i> (Sulzer, 1776)	Finland	(♀) 14		OKSALA, 1945
Ischnurinae				
<i>Acanthagrion ascendens</i> Calvert, 1909	Bolivia	14 (m)		CUMMING, 1964a
<i>A. chacoense</i> Calvert, 1909	Bolivia	14 (m)		CUMMING, 1964a
<i>Aeolagrion foliaceum</i> (Sjöstedt, 1918)	Bolivia	14		CUMMING, 1964a
<i>Amphiagrion abbreviatum</i> (Selys, 1876)	U.S.A.	14		CRUDEN, 1968
<i>Enallagma aspersum</i> (Hagen, 1861)	U.S.A.	14		CRUDEN, 1968
<i>E. boreale</i> Selys, 1875	U.S.A.	14		CRUDEN, 1968
<i>E. carunculatum</i> Morse, 1895	U.S.A.	14		CRUDEN, 1968
<i>E. civile</i> (Hagen, 1861)	U.S.A.	14		CRUDEN, 1968
<i>E. cyathigerum</i> (Charpentier, 1840)	Finland, U.S.S.R., Netherlands, U.S.A.	14; 14+15 (m); 15 (m)+14; 15 (m)	fragmentation of one of the smaller bivalents in some or in all cells of some populations (Netherlands, U.S.A.)	OKSALA, 1939a, 1945; MAKALOWSKAJA, 1940; VAN BRINK & KIAUTA, 1964; CRUDEN, 1968; KIAUTA, 1969a, 1969b

FAMILY Subfamily Genus, Species, Subspecies	Locality	♂n (and presence of m)	Remarks	References
<i>E. ebrium</i> (Hagen, 1861)	U.S.A.	14		CRUDEN, 1968
<i>E. procerum</i> (Hagen, 1861)	U.S.A.	14		CRUDEN, 1968
<i>Ischnura cervula</i> Selys, 1876	U.S.A.	14		CRUDEN, 1968
<i>I. denticollis</i> (Burmeister, 1839)	U.S.A.	14		CRUDEN, 1968
<i>I. elegans</i> (Vander Linden, 1823)	Finland, Netherlands	14	at ♂ diakinesis X occasionally negatively allocyclic (<i>Kiauta</i>)	OKSALA, 1939a, 1945 KIAUTA, 1969a
<i>I. fluviatilis</i> Selys, 1876	Bolivia	14		CUMMING, 1964a
<i>I. perparva</i> Selys, 1876	U.S.A.	14		CRUDEN, 1968
<i>I. senegalensis</i> (Rambur, 1842)	Japan, India, Ethiopia	14 (m)		KICHIJO, 1941, 1942a, 1942c; DASGUPTA, 1957; KIAUTA, 1969c
<i>I. verticalis</i> (Say, 1839)	U.S.A.	14		CRUDEN, 1968
<i>I. cf. ultima</i> Ris, 1908	Bolivia	14		CUMMING, 1964a
<i>Leptagrion macrurum</i> (Burmeister, 1839)	Brazil	(15)	neo-XY	KIAUTA, 1971c, 1972
<i>Tigriagrion aurantinigrum</i> Calvert, 1909	Bolivia	14		CUMMING, 1964a
<i>Zoniagrion exclamationis</i> (Selys, 1876)	U.S.A.	14		CRUDEN, 1968
Agriocneminae <i>Ceratura capreola</i> (Hagen, 1861)	Bolivia	14		CUMMING, 1964a
<i>Mortonagrion selenion</i> (Ris, 1916)	Japan	14 (m)	sub <i>Agriocnemis</i>	KICHIJO, 1941, 1942a, 1942c, 1942e
Arginae <i>Argia funebris</i> (Hagen, 1861)	Mexico	(♀) (14)		KIAUTA, unpublished
<i>A. sedula</i> (Hagen, 1861)	U.S.A.	14		CUMMING, 1964a
<i>A. violacea</i> (Hagen, 1861)	U.S.A.	14		CRUDEN, 1968
<i>A. virida</i> Hagen, 1865	U.S.A.	14		CRUDEN, 1968
PSEUDOSTIGMATIDAE Pseudostigmatinae <i>Mecistogaster</i> sp. 1	Bolivia	15 (m)	XO; fragmentation of two bivalents	CUMMING, 1964a; KIAUTA, 1969a
<i>Mecistogaster</i> sp.2	Bolivia	6	neo-XY (?); fusion of all elements	CUMMING, 1964a; KIAUTA, 1969a
MEGAPODAGRIONIDAE Megapodagrioninae <i>Megapodagrion contortum</i> (Selys, 1862)	Brazil	13(m); 13(m) +14 (m)	fragmentation of a bivalent in some figures	KIAUTA, unpublished

FAMILY Subfamily Genus, Species, Subspecies	Locality	♂n (and presence of <i>m</i>)	Remarks	References
<i>M. macropus</i> (Selys, 1862)	Bolivia	13	X largest of the set a ♂ metaphase I	CUMMING, 1964a
<i>M. setigerum</i> Selys, 1886	Bolivia	13		CUMMING, 1964a
Argiolestinae <i>Heteragrion flavidorum</i> Calvert, 1909	Bolivia	13		CUMMING, 1964a
<i>H. inca</i> Calvert, 1909	Bolivia	13(<i>m</i>)		CUMMING, 1964a
<i>Philogenia carrilica</i> Calvert, 1907	Costa Rica	13(<i>m</i>)		CUMMING, 1964a
LESTIDAE Sympecmatinae <i>Sympecma fusca</i> (Vander Linden, 1823)	Japan	13(<i>m</i>)	sub <i>Sympycna</i> ; one bivalent extra large	KICHIJO, 1941, 1942a, 1942c
Lestinae <i>Chalcolestes viridis</i> (Vander Linden, 1825)	Netherlands	13(<i>m</i>)		KIAUTA, 1969a
<i>Lestes congener</i> Hagen, 1861	U.S.A.	13(<i>m</i>)	one bivalent extra large; X minute	CRUDEN, 1968
<i>L. disjunctus</i> Selys, 1862	U.S.A.	13	one bivalent extra large	CRUDEN, 1968
<i>L. dryas</i> Kirby, 1890	U.S.A.	13; 13(<i>m</i>)	<i>m</i> present in some populations; one bivalent extra large	CRUDEN, 1968
<i>L. forcipatus</i> Rambur, 1842	U.S.A.	11	two extra large bivalents, probably due to fusion; XO	CRUDEN, 1968
<i>L. forcifcula</i> Rambur, 1842	Jamaica	13(<i>m</i>)		CUMMING, 1964a
<i>L. rectangularis</i> Say, 1839	U.S.A.	13(<i>m</i>)	one bivalent extra large	CRUDEN, 1968
<i>L. simulatrix</i> McLachlan, 1895	Madagascar	13(<i>m</i>)	bivalents of gradually decreasing magnitude	KIAUTA, 1968f; 1969c
<i>L. sponsa</i> (Hansemann, 1823)	U.S.S.R., Japan	13; 13(<i>m</i>)	in Japanese material one extra large bivalent and <i>m</i> , both absent in the Russian population	MAKALOWSKAJA, 1940; KICHIJO, 1941, 1942a, 1942c, 1942e
<i>L. stultus</i> Hagen, 1861	U.S.A.	13(<i>m</i>)	one bivalent extra large	CRUDEN, 1968
<i>L. vidua</i> Hagen, 1861	U.S.A.	13(<i>m</i>)		CUMMING, 1964a
<i>L. virens vestalis</i> Rambur, 1842	Netherlands	13(<i>m</i>)		KIAUTA, 1969a
PSEUDOLESTIDAE Pseudolestinae <i>Hypolestes clara</i> (Calvert, 1891)	Jamaica	9		CUMMING, 1964a
POLYTHORIDAE Polythorinae <i>Cora irene</i> Ris, 1918	Bolivia	12(<i>m</i>)		CUMMING, 1964a
<i>Polythore boliviana</i> (McLachlan, 1878)	Bolivia	12(<i>m</i>)		CUMMING, 1964a

FAMILY Subfamily Genus, Species, Subspecies	Locality	♂n (and presence of m)	Remarks	References
EPALLAGIDAE Epallaginae <i>Epallage fatime</i> (Charpentier, 1840)	Greece	13		KIAUTA, 1970b
HETAERINIDAE Hetaeriniinae <i>Hetaerina americana</i> (Fabricius, 1798)	U.S.A.	13(m)	in a published figure two bivalents extremely minute (<i>Cruden</i>)	CUMMING, 1964a; CRUDEN, 1968
<i>H. charca</i> Calvert, 1909	Bolivia	13(m)		CUMMING, 1964a
<i>H. rosea</i> Selys, 1853	Bolivia	14(m)	the increase in n probably due to fragmentation	CUMMING, 1964a; KIAUTA, 1969b
<i>H. sanguinea</i> Selys, 1853	Bolivia	13		CUMMING, 1964a
<i>H. titia</i> (Drury, 1773)	Bolivia	13(m)		CUMMING, 1964a
<i>H. tricolor</i> (Burmeister, 1839)	Mexico	13(m)		KIAUTA, 1970c
<i>H. vulnerata</i> (Selys, 1853)	Mexico	(♀) (13) (m?)		KIAUTA, 1970c
CALOPTERYGIDAE Calopteryginae <i>Anaciagrion cornelia</i> (Selys, 1853)	Japan	13(m)	sub <i>Calopteryx</i>	OGUMA, 1930; KICHIJO, 1942e
<i>Calopteryx aequabile</i> Say, 1839	U.S.A.	13(m)	sub <i>Aggrion</i>	CRUDEN, 1968
<i>C. atrata</i> Selys, 1853	Japan	13(m)		OGUMA, 1930; KICHIJO, 1942e; OMURA, 1957
<i>C. maculata</i> (Beauvois, 1805)	U.S.A.	13(m)	sub <i>Aggrion maculatum</i> (<i>Cruden</i>)	CUMMING, 1964a; CRUDEN, 1968
<i>C. splendens caprai</i> Conci, 1956	Italy	13(m)	at ♂ diplotene at least four bivalents with two chiasmata; high re- combination index is in accordance with high morphological variability	KIAUTA, 1971b
<i>C. splendens splendens</i> (Harris, 1782)	U.S.S.R., Finland, Germany	13		MAKALOWSKAJA, 1940; OKSALA, 1945; KIAUTA, 1969a, 1971b
<i>C. virgo japonica</i> Selys, 1869	Japan	13(m)	m minute	KICHIJO, 1942e; HIRAI, 1956; OMURA, 1957; KIAUTA, 1968b, 1968c
<i>C. virgo meridionalis</i> Selys, 1873	Spain	13(m); 13(m) +14(m)	fragmentation of a bivalent in some figures; often precocious segregation of several bivalents	KIAUTA, 1971a
<i>C. virgo padana</i> Conci, 1956	Slovenia (Yugo- slavia), Austria	13(m)	sub <i>C. virgo</i> (1967a)	KIAUTA, 1967a, 1968b, 1968c
<i>C. virgo virgo</i> (Linnaeus, 1758)	Belgium, Finland, U.S.S.R., Germany Luxembourg, Netherlands	13; 13(m)	occasionally precocious segregation of some biva- lents (<i>Makalowskaja</i>)	CARNOY, 1885 (of historic value only); OKSALA, 1939a; MAKALOWSKAJA, 1940; KIAUTA, 1968b, 1968c, unpublished
<i>Matrona basilaris</i> Selys, 1853	Taiwan	13		KIAUTA, 1968f

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<i>Mnais costalis</i> Selys, 1869	Japan	13(m)	absolute magnitude of all elements and relative size of m smaller than in <i>M. strigata</i>	OGUMA, 1930; KICHIJO, 1942e
<i>M. strigata</i> Selys, 1853	Japan	13(m)	absolute magnitude of all elements and relative size of m bigger than in <i>M. costalis</i>	OGUMA, 1930; KICHIJO, 1942e; OMURA, 1957
EPIOPHLEBIIDAE				
Epiophlebiinae				
<i>Epiophlebia superstes</i> Selys, 1889	Japan	13		OGUMA, 1951
GOMPHIDAE				
Gomphinae				
<i>Anisogomphus bivittatus</i> (Selys, 1854)	India	12(m)	X medium sized at metaphase I	DAS, 1956
<i>Davidius nanus</i> (Selys, 1869)	Japan	12	sub <i>Gomphus hakiensis</i> ; no extra large element; X smallest at metaphase I	KICHIJO, 1939, 1942e
<i>Dromogomphus spinosus</i> (Selys, 1854)	U.S.A.	12(m)		CRUDEN, 1968
<i>D. spoliatus</i> (Hagen, 1857)	U.S.A.	12(m)	no extra large element	CRUDEN, 1968
<i>Erpetogomphus designatus</i> Hagen, 1857	U.S.A.	12(m)		CUMMING, 1964a
<i>E. diadophis</i> Calvert, 1905	U.S.A.	12		CUMMING, 1964a
<i>E. ophiobolus</i> Calvert, 1905	Mexico	12(m)	X most voluminous at metaphase I	KIAUTA, 1970c
<i>Gomphus confraternus</i> Selys, 1873	U.S.A.	12(m)	no extra large element	CRUDEN, 1968
<i>G. exilis</i> Selys, 1854	U.S.A., Canada	12(m); 12	m present in one of the two U.S.A. populations; in some oogonial figures of Canadian material two smaller elements attached to two longest chromosomes (<i>Kiauta</i>)	CRUDEN, 1968; KIAUTA, 1969a
<i>G. graslini</i> Rambur, 1842	France	12(m)	X largest at all stages; neo-X/neo-neo-Y (?)	KIAUTA, 1968d, 1969a
<i>G. lentulus</i> Needham, 1902	U.S.A.	12		CRUDEN, 1968
<i>G. lividus</i> Selys, 1854	U.S.A.	12(m)	no extra large element	CRUDEN, 1968
<i>G. melaenops</i> Selys, 1854	Japan	12(m)	for identity of the species listed by Toyoshima & Hirai and Hirai cf. CRUDEN, 1968 and KIAUTA, 1969a	TOYOSHIMA & HIRAI, 1953; HIRAI, 1956; OMURA, 1957
<i>G. militaris</i> Hagen, 1857	U.S.A.	12		CRUDEN, 1968
<i>G. pallidus</i> Rambur, 1842	U.S.A.	12		CUMMING, 1964a
<i>G. plagiatus</i> Selys, 1854	U.S.A.	12(m)		CRUDEN, 1968
<i>G. postocularis</i> Selys, 1869	Japan	12(m?)		OMURA, 1957
<i>G. scudderii</i> Selys, 1873	U.S.A.	12		CRUDEN, 1968

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<i>G. spicatus</i> Selys, 1854	U.S.A.	12(m)		CRUDEN, 1968
<i>G. submedianus</i> Williamson, 1914	U.S.A.	12		CRUDEN, 1968
<i>Nihonogomphus viridis</i> Oguma, 1926	Japan	12(m?)		OMURA, 1957
<i>Octogomphus specularis</i> (Hagen, 1859)	U.S.A.	12	no extra large element	CRUDEN, 1968
<i>Onychogomphus forcipatus</i> (Linnaeus, 1758)	Finland, Austria	12+13	in Austrian material in the same specimen two different complements; XO in n = 13; neo-XY in n = 12; neo-X longest; X smallest; kinetic behaviour of neo-X normal	OKSALA, 1945; KIAUTA, 1969a
<i>Ophiogomphus bison</i> Selys, 1873	U.S.A.	12+13; 13+12	one element extra large in n = 13; variation in n due to fragmentation	CRUDEN, 1968
<i>O. colubrinus</i> Selys, 1854	U.S.A.	12	no extra large element	CRUDEN, 1968
<i>O. occidentalis</i> Hagen, 1882	U.S.A.	12	no extra large element	CRUDEN, 1968
<i>O. rupinsulensis</i> (Walsh, 1862)	U.S.A.	12	one extra large element	CRUDEN, 1968
<i>O. serpentinus</i> (Charpentier, 1825)	Finland	(♀) 12	X largest	OKSALA, 1945
<i>Stylogomphus suzukii</i> (Matsumura, 1926)	Japan	12(m)	sub <i>Gomphus</i> ; no extra large element; X second smallest at metaphase I	OGUMA, 1930; KICHIJO, 1942c
<i>Trigomphus citinus tabei</i> Asahina, 1949	Japan	11(m)	sub <i>Gomphus</i> ; one element extra large; X marked in figure as one of smallest elements at metaphase I	TOYOSHIMA & HIRAI, 1953; HIRAI, 1956
<i>T. interruptus</i> (Selys, 1854)	Japan	10(m)	sub <i>Gomphus melampus</i> (<i>Oguma</i>) and <i>G. melampus</i> <i>bifasciatus</i> (other authors); for the identity of the species listed by <i>Toyoshima</i> & <i>Hirai</i> and <i>Hirai</i> cf. CRUDEN, 1968 and KIAUTA, 1969a	OGUMA, 1930; TOYOSHIMA & HIRAI, 1953; HIRAI, 1956; OMURA, 1957
<i>T. "unifasciatus"</i> (Oguma, 1926)	Japan	11	sub <i>Gomphus</i> ; the "species" is in fact composed of three species	OGUMA, 1930, 1942
Epigomphinae <i>Epigomphus llama</i> Calvert, 1903	Bolivia	12		CUMMING, 1964a
Ictinogomphinae <i>Ictinogomphus rapax</i> (Rambur, 1942)	India	12(m)	sub <i>Ictinus</i> ; X largest at all stages	ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942e; OMURA, 1949, 1952, 1953; DASGUPTA, 1957
Gomphoidinae <i>Aphylla edentata</i> Selys, 1869	Bolivia	12		CUMMING, 1964a
<i>A. producta</i> Selys, 1854	Bolivia	12		CUMMING, 1964a
<i>Gomphoides</i> sp.	Bolivia	12		CUMMING, 1964a

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<i>Phyllocycla</i> sp.	Bolivia	12		CUMMING, 1964a
<i>Progomphus borealis</i> McLachlan, 1873	U.S.A.	12		CRUDEN, 1968
<i>P. intricatus</i> (Hagen, 1857)	Bolivia	12		CUMMING, 1964a
<i>P. obscurus</i> (Rambur, 1842)	U.S.A.	12		CRUDEN, 1968
<i>P. phyllochromus</i> Ris, 1918	Bolivia	12(m)		CUMMING, 1964a
Hageninae <i>Sieboldius albardae</i> Selys, 1886	Japan	12(m)	X largest	OMURA, 1957
PETALURIDAE				
Petalurinae <i>Tachopteryx thoreyi</i> (Hagen, 1857)	U.S.A.	10(m)	at ♂ diplotene multiple chiasmata	CUMMING, 1964a
<i>Uropetala carovei</i> (White, 1846)	New Zealand	9(m)	X medium-sized	WOLFE, 1953
Tanypterictinae <i>Tanypteryx hagani</i> (Selys, 1879)	U.S.A.	9(m)		CRUDEN, 1968
<i>T. pryzeri</i> (Selys, 1889)	Japan	9(m)	m minute; X second smallest at all stages	KICHIO, 1939, 1942c
AESHNIDAE				
Gomphaeschninae <i>Basiaeschna janata</i> (Say, 1839)	U.S.A.	13		CRUDEN, 1968
<i>Oplonaeschna armata</i> (Hagen, 1861)	Mexico	14(m)	X and m nearly equal in size and extremely minute at metaphase I	KIAUTA, 1970c
Brachytrinae <i>Acanthaeschna anacantha</i> (Tillyard, 1908)	Australia	14(m)	X smallest at metaphase I	KIAUTA, 1968f
<i>A. multipunctata</i> (Martin, 1901)	Australia	14(m)		KIAUTA, 1968f
<i>Boyeria maclachlani</i> (Selys, 1883)	Japan	14(m)	X second smallest, the m's occasionally unpaired at metaphase I	OMURA, 1957
<i>B. vinosa</i> (Say, 1839)	U.S.A.	14		CRUDEN, 1968
<i>Planaeschna milnei</i> (Selys, 1883)	Japan	14(m)		KIAUTA, 1968f, 1969a
Aeshninae <i>Aeshna canadensis</i> Walker, 1908	U.S.A.	14		CRUDEN, 1968
<i>A. clepsydra</i> Say, 1839	U.S.A.	14(m)		HUNG, 1971
<i>A. coerulea</i> (Ström, 1783)	Finland	12	original m fused with the original relatively small X; neo-XY; no heterokinesis of neo-X at anaphase II	OKSALA, 1943a
<i>A. crenata</i> Hagen, 1856	Finland	14(m)	in one figure the m's unpaired at metaphase I	OKSALA, 1939a, 1943a, 1944a, 1952

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<i>A. cyanea</i> (Mueller, 1764)	Finland, Netherlands	14(m)	m minute	OKSALA, 1943a; KIAUTA, 1969a
<i>A. diffinis diffinis</i> Rambur, 1842	Bolivia	11(m)	decrease in n due to fusion of autosomes; four extra large bivalents; XO	CUMMING, 1964a
<i>A. grandis</i> (Linnaeus, 1758)	U.S.S.R., Finland, Netherlands	13(m)+14(m), 14(m)+13(m), 13(m)	decrease in n due to fusion of X with an autosome (usu- ally both kinds of comple- ments in the same specimen); neo-XY in fused comple- ments; neo-X largest	FUCHSÓWNA & SAWCZYŃSKA, 1928; OKSALA, 1939a, 1943a, 1944a, 1945; MAKALOWSKAJA, 1940; KIAUTA, 1967b, 1967c, 1967d, 1967e, 1968a, 1968d, 1969a
<i>A. intricata</i> Martin, 1908	Bolivia	10(m)	decrease in n due to fusion of autosomes; five extra large bivalents; XO; X smallest at metaphase I	CUMMING, 1964a
<i>A. juncea</i> (Linnaeus, 1758)	Finland, U.S.S.R., Italy	13(m), 13(m) +14(m)	decrease in n due to fusion of X with an autosome, pri- mary complements in a few cells; neo-XY in secondary complements, no heterokinesis of neo-X at anaphase II	OKSALA, 1939a, 1943a, 1944a, MAKALOWSKAJA, 1940; KIAUTA, 1971b
<i>A. mixta</i> Latreille, 1805	Netherlands	14(m)		KIAUTA, 1969a
<i>A. palmata</i> Hagen, 1856	U.S.A.	14(m)	X minute	CRUDEN, 1968
<i>A. peralta</i> Ris, 1918	Bolivia	14(m)		CUMMING, 1964a
<i>A. serrata fennica</i> Valle, 1938	Finland	13(m)	sub <i>A. osliensis fennica</i> ; one element extra large; neo-XY	OKSALA, 1943a
<i>A. subarctica elisabethae</i> Djakonov, 1922	Finland	14(m)	X smallest at metaphase I	OKSALA, 1939a, 1943a, 1952
<i>A. umbrosa occidentalis</i> Walker, 1912	U.S.A.	14(m)	absolute size of all elements smaller than in nominate form	CRUDEN, 1968
<i>A. umbrosa umbrosa</i> Walker, 1908	U.S.A.	14	absolute size of all elements larger than in <i>A. umbrosa</i> <i>occidentalis</i>	CRUDEN, 1968
<i>A. verticalis</i> Hagen, 1861	U.S.A.	14(m)	m hardly recognizable at diakinesis	HUNG, 1971
<i>A. viridis</i> Eversman, 1836	Finland	13(m)	decrease in n due to fusion of X with an autosome; neo-XY	OKSALA, 1943a
<i>A. walkeri</i> Kennedy, 1917	U.S.A.	14(m)		CRUDEN, 1968
<i>A. cf. unicolor</i> Martin, 1908	Bolivia	14(m)		CUMMING, 1964a
<i>Castoraeschna castor</i> (Brauer, 1865)	Brasil	14(m)		KIAUTA, unpublished
<i>Coryphaeschna adnexa</i> (Hagen, 1861)	Bolivia	14		CUMMING, 1964a
Anactinae <i>Anax imperator</i> Leach, 1815	France	14(m)		KIAUTA, 1965, 1969a

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<i>A. junus</i> (Drury, 1773)	U.S.A.	14(m); 14	<i>m</i> lacking in one of the two populations studied by Cruden	McGILL, 1904, 1907; LEFEVRE & McGILL, 1908; KICHJO, 1942c; CRUDEN, 1968
<i>A. longipes</i> Hagen, 1861	U.S.A.	14(m)		CRUDEN, 1968
<i>A. parthenope julius</i> Brauer, 1865	Japan	14(m)		OMURA, 1957
<i>Hemianax ephippiger</i> (Burmeister, 1839)	India	7(m)	decrease in n due to fusion; probably neo-XY (<i>Kiauta</i>); <i>m</i> extremely minute	SESHACHAR & BAGGA, 1962; KIAUTA, 1969a
<i>H. papuensis</i> (Burmeister, 1839)	Australia	14(m)		KIAUTA, 1968f, 1969a
Gynacanthaginae <i>Gynacantha japonica</i> Bartenev, 1909	Japan	14(m)		OMURA, 1957
CORDULEGASTERIDAE				
Cordulegasterinae <i>Anotogaster sieboldii</i> (Selys, 1854)	Japan	13(m)		OGUMA, 1930; KICHJO, 1942c; KIAUTA, 1969a
<i>Cordulegaster boltoni</i> (Donovan, 1807)	Finland, Austria, Sweden	13(m); 13	sub <i>C. annulatus</i> (Oksala, <i>Kichijo</i>); <i>m</i> present in Fennoscandian populations but lacking in Austrian material; X occasionally negatively heterocyclic at diakinesis	OKSALA, 1939a, 1939b; KICHJO, 1942c; KIAUTA, 1968c, 1968e, 1969a
<i>C. deserticola</i> Cruden, 1969	U.S.A.	13(m?)		CRUDEN, 1969
<i>C. diastatops</i> (Selys, 1854)	U.S.A.	13(m)		CRUDEN, 1968
<i>C. dorsalis</i> Hagen, 1857	U.S.A.	13(m)		CRUDEN, 1968
<i>C. maculatus</i> Selys, 1854	U.S.A.	13(m)		CRUDEN, 1968
CORDULIIDAE				
Corduliinae <i>Cordulia aenea</i> (Linnaeus, 1758)	Finland, U.S.S.R., Netherlands	13		OKSALA, 1939a; MAKALOWSKAJA, 1940; KIAUTA, 1968d, 1969a
<i>C. shurtleffi</i> Scudder, 1866	U.S.A.	13		CRUDEN, 1968
<i>Dorocordulia libera</i> (Selys, 1871)	U.S.A.	6+7; 7	decrease in n due to fusion; the two different complements in two different geographic populations; all elements extra large; neo-XY in n = 7 assumed (<i>Kiauta</i>)	CRUDEN, 1968; KIAUTA, 1969a
<i>Epicordulia princeps</i> (Hagen, 1861)	U.S.A.	13(m)		HUNG, 1971
<i>Epitheca canis</i> McLachlan, 1886	U.S.A.	13(m)		CRUDEN, 1968
<i>E. cynosura</i> (Say, 1839)	U.S.A.	10+11; 11	decrease in n due to fusion; the two different complements in different geographic populations; in n = 10 one element extra large; mode of sex determination uncertain	CRUDEN, 1968; KIAUTA, 1969a
<i>E. semiaquea</i> (Burmeister, 1839)	U.S.A.	13		CRUDEN, 1968

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<i>E. spinigera</i> (Selys, 1871)	U.S.A.	13(m)		CRUDEN, 1968
<i>Somatochlora flavomaculata</i> (Vander Linden, 1825)	U.S.S.R.	13		MAKALOWSKAJA, 1940
<i>S. metallica</i> (Vander Linden, 1825)	Finland	(♀) 13		OKSALA, 1945
<i>S. semicircularis</i> (Selys, 1871)	U.S.A.	13		CRUDEN, 1968
<i>S. uchidai</i> Foerster, 1909	Japan	13(m)	<i>m</i> minute and occasionally unpaired at diakinesis	OGUMA, 1915, 1930; KICHIJO, 1942d
<i>S. viridiaenea</i> (Uhler, 1858)	Japan	13		OGUMA, 1915, 1930; KICHIJO, 1942d
<i>Tetragoneuria petechialis</i> Muttkowski, 1911	U.S.A.	11		CUMMING, 1964a
<i>T. spinigera</i> (Selys, 1871)	U.S.A.	14		HUNG, 1971
Epophthalmiinae <i>Didymops transversa</i> (Say, 1839)	U.S.A.	13(m)		CRUDEN, 1968
<i>Epophthalmia frontalis frontalis</i> Selys, 1871	India	13(m)		DASGUPTA, 1957
<i>Macromia magnifica</i> (McLachlan, 1874)	U.S.A.	13(m); 13	<i>m</i> present in one of the two geographic populations studied	CRUDEN, 1968
MACRODIPLACTIDAE				
Macrodiplactinae				
<i>Aethriamanta brevipennis</i> (Rambur, 1842)	India	13(m)		DASGUPTA, 1957
<i>Urothemis signata signata</i> (Rambur, 1842)	India	13(m)		DAS, 1956; DASGUPTA, 1957
LIBELLULIDAE				
Tetratheminae				
<i>Nannothemis bella</i> (Uhler, 1857)	U.S.A.	13(m)		CRUDEN, 1968
Libellulinae				
<i>Cannaphila vibex</i> (Hagen, 1861)	Bolivia	13(m)		CUMMING, 1964a
<i>Dasythemis esmeralda</i> Ris, 1910	Bolivia	13(m)		CUMMING, 1964a
<i>D. venosa</i> (Burmeister, 1839)	Brasil	13(m)		KIAUTA, unpublished
<i>Ladona julia</i> (Uhler, 1857)	U.S.A.	13(m)		CRUDEN, 1968
<i>Lathrecista asiatica</i> (Fabricius, 1798)	India	13(m)		DASGUPTA, 1957
<i>Libellula angelina</i> Selys, 1883	Japan	13(m)		OGUMA, 1915, 1930; KICHIJO, 1942e
<i>L. axilena</i> Westwood, 1837	U.S.A.	12		CUMMING, 1964a
<i>L. composita</i> (Hagen, 1873)	U.S.A.	13(m)		CRUDEN, 1968
<i>L. croceipennis</i> Selys, 1868	U.S.A.	13(m)		CRUDEN, 1968
<i>L. cyanea</i> Fabricius, 1775	U.S.A.	13		CRUDEN, 1968

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<i>L. depressa</i> Linnaeus, 1758	Belgium, England Austria	12; 12+13(m)	increase in n due to fragmentation of a bivalent in Austrian material only (<i>Kiauta</i>)	CARNOY, 1885 (of historic value only); HOGBEN, 1921; KIAUTA, 1968c, 1969b
<i>L. flavida</i> Rambur, 1842	U.S.A.	13(m)		CRUDEN, 1968
<i>L. forensis</i> Hagen, 1861	U.S.A.	13(m)	X second smallest at diakinesis	CRUDEN, 1968
<i>L. incesta</i> Hagen, 1861	U.S.A.	13		CUMMING, 1964a; CRUDEN, 1968
<i>L. luctuosa</i> Burmeister, 1839	U.S.A.	13	sub <i>L. basalis</i>	SMITH, 1916
<i>L. pulchella</i> Drury, 1773	U.S.A., Canada	13(m)		CRUDEN, 1968; KIAUTA, 1969a
<i>L. quadrimaculata asahinei</i> Schmidt, 1957	Japan	13(m)	sub <i>L. quadrimaculata</i> (<i>Oguma, Kichijo, Omura</i>)	OGUMA, 1915, 1930; KICHIO, 1942d; OMURA, 1955; KIAUTA, 1968b, 1968c
<i>L. quadrimaculata quadrimaculata</i> Linnaeus, 1758	U.S.S.R., Finland, Netherlands, U.S.A.	13(m)		FUCHSÓWNA & SAWCZYŃSKA, 1928; OKSALA, 1939a, 1939b, 1945; MAKALOWSKAJA, 1940; KIAUTA, 1968b, 1968c; CRUDEN, 1968
<i>L. saturata</i> Uhler, 1857	U.S.A.	13(m)		CRUDEN, 1968
<i>L. semifasciata</i> Burmeister, 1839	U.S.A.	13(m)		CRUDEN, 1968
<i>L. vibrans</i> Fabricius, 1793	U.S.A.	13(m)		CRUDEN, 1968
<i>Lyriothemis pachygastra</i> (Selys, 1878)	Japan	13(m?)		OMURA, 1955
<i>Nesciothemis farinosum</i> (Foerster, 1898)	Kenya	(13) (m?)		KIAUTA, 1969c
<i>Orthemis biolleyi</i> Calvert, 1906	Bolivia	12	XO	CUMMING, 1964a
<i>O. cultiformis</i> Calvert, 1906	Bolivia	12(m)	XO	CUMMING, 1964a
<i>O. ferruginea</i> (Fabricius, 1775)	Bolivia, U.S.A., Guatemala, Domi- nican Republic, Peru	5; 12; 12(m)	decrease in n due to fusion; n = 5 in Bolivia only; neo-XY in n = 5; m in some populations only	CUMMING, 1964a; CRUDEN, 1968; KIAUTA, 1969a, 1971c
<i>O. levis</i> Calvert, 1906	Bolivia	3; 4	decrease in n due to fusion; neo-XY probable (<i>Kiauta</i>)	CUMMING, 1964a, 1964b; KIAUTA, 1969a
<i>Orthetrum albistylum albistylum</i> (Selys, 1848)	Italy	13(m)		KIAUTA, 1971b
<i>O. albistylum speciosum</i> (Uhler, 1858)	Japan	13(m)		OGUMA, 1915, 1917, 1930; KICHIO, 1942d; OMURA, 1955
<i>O. azureum</i> (Rambur, 1842)	Madagascar	13(m)		KIAUTA, 1969b, 1969c
<i>O. brachiale</i> (Beauvois, 1805)	Kenya	11	decrease in n due to fusion of autosomes; one bivalent extra large; in eight or nine bivalents at least two chiasmata per bivalent; XO	KIAUTA, 1969b, 1969c

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<i>O. brunneum</i> (Fonscolombe, 1837)	Italy	13(m)		KIAUTA, 1971b
<i>O. cancellatum</i> (Linnaeus, 1758)	Finland, India, Netherlands	13(m)		OKSALA, 1939a; DASGUPTA, 1957; KIAUTA, 1969a, 1969b
<i>O. coerulescens</i> (Fabricius, 1798)	Austria, Italy	13(m); 12+13(m); 13(m)+14(m)	increase in n due to fragmentation of autosomes; different complements in the same specimen; m occasi- onally unpaired at metaphase I	KIAUTA, 1969b, 1971b
<i>O. glaucum</i> (Brauer, 1865)	India	13(m)		DASGUPTA, 1957
<i>O. japonicum</i> (Uhler, 1858)	Japan	13(m)		OGUMA, 1917, 1930; KICHIJO, 1942d; OMURA, 1955
<i>O. pruinosum neglectum</i> (Rambur, 1842)	India, Taiwan	13(m)		DASGUPTA, 1957; KIAUTA, 1969a, 1969b
<i>O. sabina</i> (Drury, 1773)	India	13(m)		ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942d; RAY CHAUDHURI & DASGUPTA, 1949
<i>O. taeniolatum</i> (Schneider, 1845)	Greece	13(m)		KIAUTA, unpublished
<i>O. triangulare melania</i> (Selys, 1883)	Japan	13(m)	sub <i>O. triangulare</i> (<i>Oguma</i>)	OGUMA, 1917; OMURA, 1955
<i>O. triangulare triangulare</i> (Selys, 1878)	Taiwan	13(m)		KIAUTA, 1969a, 1969b
<i>Platthemis lydia</i> (Drury, 1773)	U.S.A.	13 (m)		McGILL, 1907; CRUDEN, 1968
<i>Potamarcha obscura</i> (Rambur, 1842)	India	13(m)		ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942d; DASGUPTA, 1957
Diastatopodinae <i>Diastatops intensa</i> Montgomery, 1940	Bolivia	13(m)	sub <i>D. intensa</i> Ris	CUMMING, 1964a
<i>D. obscura</i> (Fabricius, 1775)	Bolivia	13(m)		CUMMING, 1964a
<i>Perithemis cornelia</i> Ris, 1910	Bolivia	13		CUMMING, 1964a
<i>P. domitia</i> (Drury, 1773)	Jamaica	13(m)		CUMMING, 1964a
<i>P. electra</i> Ris, 1928	Bolivia	13		CUMMING, 1964a
<i>P. lais</i> (Perty, 1834)	Bolivia	9	decrease in n due to fusion of autosomes; five extra large bivalents; XO	CUMMING, 1964a
<i>P. moorei</i> Kirby, 1889	Bolivia	13(m)		CUMMING, 1964a
<i>P. seminole</i> Calvert, 1907	U.S.A.	13(m)		CUMMING, 1964a
<i>Perithemis</i> sp.	Bolivia	13		CUMMING, 1964a
<i>Zenithoptera viola</i> Ris, 1910	Bolivia	13(m)		CUMMING, 1964a

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Brachydiplactinae <i>Brachydiplax chalybea</i> Brauer, 1868	India	13(m)		DASGUPTA, 1957
<i>B. farinosa</i> Krueger, 1902	India	13(m)	X occasionally fused with a dividing autosome, giving rise to neo-XY	DASGUPTA, 1957
<i>B. sobrina</i> (Rambur, 1842)	India	13(m)		RAY CHAUDHURI & DASGUPTA, 1949
<i>Micrathyria atra</i> (Martin, 1897)	Bolivia	13(m)		CUMMING, 1964a
<i>M. didyma</i> (Selys, 1857)	Jamaica	13(m)		CUMMING, 1964a
<i>M. hageni</i> Kirby, 1890	Jamaica	13(m)		CUMMING, 1964a
<i>M. itheringi</i> Dos Santos, 1946	Bolivia	12(m)		CUMMING, 1964a
<i>M. laevigata</i> Calvert, 1909	Bolivia	13(m)		CUMMING, 1964a
<i>M. ocellata dentiens</i> Calvert, 1909	Bolivia	13(m)		CUMMING, 1964a
<i>M. spuria</i> (Selys, 1900)	Bolivia	13(m)		CUMMING, 1964a
<i>M. cf. eximia</i> Kirby, 1897	Bolivia	11		CUMMING, 1964a
<i>Micrathyria</i> sp. (<i>ungulata</i> Foerster, 1907-group)	Bolivia	12		CUMMING, 1964a
Sympetrinae <i>Acisoma panorpoides panorpoides</i> Rambur, 1842	Bangla Desh, India	13(m)		DASGUPTA, 1957
<i>Brachythemis contaminata</i> (Fabricius, 1793)	India	13(m)		ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942d; DASGUPTA, 1957
<i>Bradynopyga geminata</i> (Rambur, 1842)	India	13(m)		DASGUPTA, 1957
<i>Crocothemis erythraea</i> (Brullé, 1832)	India, Kenya, Italy	13(m)	two chiasmata in a medium-sized pair occasionally in Italian material; two Italian populations cytotaxonomically identical, in Indian material a larger X and slightly higher chiasma frequency	DASGUPTA, 1957; KIAUTA, 1969c, 1971b
<i>C. servilla</i> (Drury, 1773)	India, Japan	13(m); 12(m?)	in Japanese material (<i>Omura</i>) permanent fusion of X with an autosome (save in a single cell), therefore neo-XY	ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942d; RAY CHAUDHURI & DASGUPTA, 1949; OMURA, 1955
<i>Diplacodes bipunctata</i> (Brauer, 1866)	Australia	13(m)+15(m)	increase in n due to fragmentation of a bivalent	KIAUTA, 1969b
<i>D. haematodes</i> (Burmeister, 1839)	Australia	13(m)+12	increase in n due to fragmentation of a bivalent	KIAUTA, 1969b
<i>D. lefebvrei</i> (Rambur, 1842)	Madagascar	13(m)		KIAUTA, 1968f, 1969c
<i>D. nebulosa</i> (Fabricius, 1793)	India	13(m)		DASGUPTA, 1957

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<i>D. trivialis</i> (Rambur, 1842)	India, Australia	13(m)		ASANA & MAKINO, 1935; MAKINO, 1935; DASGUPTA, 1957; KIAUTA, 1969b
<i>Erythemis atala</i> (Selys, 1857)	Bolivia	13		CUMMING, 1964a
<i>E. collocata</i> (Hagen, 1861)	U.S.A.	13(m)		CRUDEN, 1968
<i>E. plebeja</i> (Burmeister, 1839)	Bolivia	13		CUMMING, 1964a
<i>E. simplicicollis</i> (Say, 1839)	U.S.A.	13(m)		CRUDEN, 1968
<i>Erythrodiplax basalis basalis</i> (Kirby, 1897)	Bolivia	13		CUMMING, 1964a
<i>E. berenice</i> (Drury, 1770)	U.S.A.	13; 13+14(m)		CRUDEN, 1968; HUNG, 1971
<i>E. castanea</i> (Burmeister, 1839)	Bolivia	12(?), 13(?)	probably due to printer's error different numbers are given on different pages	CUMMING, 1964a
<i>E. connata connata</i> (Burmeister, 1839)	Chile	13(m)		KIAUTA, unpublished
<i>E. connata fusca</i> (Rambur, 1842)	Bolivia, Guatemala	13		CUMMING, 1964a; CRUDEN, 1968
<i>E. fervida</i> (Erichson, 1848)	Jamaica	13(m)		CUMMING, 1964a
<i>E. justiniana</i> (Selys, 1857)	Jamaica	13(m)		CUMMING, 1964a
<i>E. media</i> Borror, 1942	Bolivia	11(m)		CUMMING, 1964a
<i>E. melanorubra</i> Borror, 1942	Bolivia	13(m)		CUMMING, 1964a
<i>E. paraguayensis</i> (Foerster, 1904)	Bolivia	12(m)		CUMMING, 1964a
<i>E. umbrata</i> (Linnaeus, 1758)	Bolivia, Domi- nican Republic	13(m)		CUMMING, 1964a; CRUDEN, 1968
<i>E. unimaculata</i> (De Geer, 1773)	Bolivia	13(m)		CUMMING, 1964a
<i>Lepthemis vesiculosa</i> (Fabricius, 1775)	Bolivia	13		CUMMING, 1964a
<i>Nesogonia blackburni</i> (McLachlan, 1883)	Hawaii	13(m)		KIAUTA, 1969d
<i>Neurothemis tullia tullia</i> (Drury, 1773)	India	14(m)	increase in n due to fragmentation of two autosomal pairs and subsequent fusion of the original X with a fragment; neo-XY (<i>Kiauta</i>); delayed pairing of neo-sex elements in primary spermatocytes	RAY CHAUDHURI & DASGUPTA, 1949; KIAUTA, 1969a
<i>Pachydiplax longipennis</i> (Burmeister, 1839)	U.S.A.	13(m); 13	<i>m</i> present in three Californian populations but lacking in Florida and W. Virginia material	CUMMING, 1964a; CRUDEN, 1968
<i>Rhodopygia cardinalis</i> (Erichson, 1848)	Bolivia	13(m)		CUMMING, 1964a
<i>Sympetrum costiferum</i> (Hagen, 1861)	U.S.A.	13(m)		CRUDEN, 1968

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<i>S. danae</i> (Sulzer, 1776)	U.S.S.R., Finland, U.S.A.	13(m)	sub <i>S. scoticum</i> (<i>Makalowskaja</i>)	MAKALOWSKAJA, 1940; OKSALA 1945; CRUDEN, 1968
<i>S. eroticum eroticum</i> (Selys, 1883)	Japan	11	one pair (bivalent) extra large; XO; at least three bivalents multiple chiasmata	KICHIIJO, 1942b, 1942d; HIRAI, 1956; KIAUTA, 1969b
<i>S. flaveolum</i> (Linnaeus, 1758)	U.S.S.R.	13(m)		MAKALOWSKAJA, 1940
<i>S. frequens frequens</i> (Selys, 1883)	Japan	12	no element extra large	OGUMA, 1917, 1930; KICHIIJO, 1942d, 1942e; KIAUTA, 1969b
<i>S. madidum</i> (Hagen, 1861)	U.S.A.	13(m)		CRUDEN, 1968
<i>S. meridionale</i> (Selys, 1841)	Switzerland	13(m)		KIAUTA, unpublished
<i>S. obtrusum</i> (Hagen, 1867)	U.S.A.	13(m)		CRUDEN, 1968
<i>S. parvulum</i> Bartenev, 1912	Japan	13(m)		KIAUTA, 1968f
<i>S. pedemontanum elatum</i> (Selys, 1872)	Japan	13(m)	sub <i>S. pedemontanum</i> ; <i>m</i> extremely minute at metaphase I	OGUMA, 1917, 1930; KICHIIJO, 1942d
<i>S. rubicundulum</i> (Say, 1839)	U.S.A.	13(m)		CRUDEN, 1968
<i>S. sanguineum</i> (Mueller, 1764)	Italy	13(m)	in ♂ often two chiasmata at least in one of the small bivalents	KIAUTA, 1971b
<i>S. semicinctum</i> (Say, 1839)	U.S.A.	13(m)		SMITH, 1916; CRUDEN, 1968
<i>S. striolatum</i> (Charpentier, 1840)	Luxembourg	13		KIAUTA, 1966, 1969a, 1969b
<i>S. vicinum</i> (Hagen, 1861)	U.S.A.	13(m)		CRUDEN, 1968
<i>S. vulgatum</i> (Linnaeus, 1758)	Netherlands	13(m)		KIAUTA, unpublished
<i>Tarnetrum corruptum</i> (Hagen, 1861)	U.S.A.	13(m)		CRUDEN, 1968; KIAUTA, 1969a, 1969b
<i>T. illotum</i> (Hagen, 1861)	Jamaica U.S.A.	13(m)		CUMMING, 1964a; CRUDEN, 1968
Leucorrhiniinae <i>Cannacia gravida</i> (Calvert, 1890)	U.S.A.	13(m)		CRUDEN, 1968
<i>C. herbida</i> (Gundlach, 1889)	Jamaica	13(m)		CUMMING, 1964a)
<i>Celithemis elisa</i> (Hagen, 1861)	U.S.A.	13(m)		CRUDEN, 1968
<i>C. fasciata</i> Kirby, 1889	U.S.A.	13(m)		CRUDEN, 1968
<i>Leucorrhinia albifrons</i> (Burmeister, 1839)	U.S.S.R.	13(m)		MAKALOWSKAJA, 1940
<i>L. dubia</i> (Vander Linden, 1825)	Finland	♀ 13		OKSALA, 1939a, 1945
<i>L. frigida</i> Hagen, 1890	U.S.A.	11+12(m)	decrease in n due to fusion of autosomes; both complements in the same specimen; one extra large bivalent in n = 12; XO	CRUDEN, 1968

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<i>L. glacialis</i> Hagen, 1890	U.S.A.	13(<i>m</i>)		CRUDEN, 1968
<i>L. hudsonica</i> (Selys, 1850)	U.S.A.	13(<i>m</i>); 13	<i>m</i> present in Californian and Oregon populations, but lacking in Wisconsin material	CRUDEN, 1968
<i>L. intacta</i> (Hagen, 1861)	U.S.A.	13(<i>m</i>); 13	<i>m</i> present in Californian and Wisconsin populations, but lacking in Ohio material	CRUDEN, 1968
<i>L. pectoralis</i> (Charpentier, 1825)	Finland	(♀) 13(<i>m</i> ?)		OKSALA, 1945
<i>L. proxima</i> Calvert, 1890	U.S.A.	13(<i>m</i>)		CRUDEN, 1968
<i>L. rubicunda</i> (Linnaeus, 1758)	Finland, U.S.S.R.	13		OKSALA, 1939a; MAKALOWSKAJA, 1940
<i>Planiplax sanguiniventris</i> (Calvert, 1907)	Guatemala	13(<i>m</i>)		CRUDEN, 1968
Tritheminae				
<i>Pseudothemis zonata</i> (Burmeister, 1839)	Japan	12	X end-to-end attached to an autosome; neo-XY; neo-X largest	OMURA, 1955
<i>Trithemis aurora</i> (Burmeister, 1839)	India	13(<i>m</i>)		OGUMA & ASANA, 1932
<i>T. pallidineris</i> (Kirby, 1889)	India	13(<i>m</i>)		ASANA & MAKINO, 1935; MAKINO, 1935; KICHIJO, 1942d; DASGUPTA, 1957
Dytheminae				
<i>Brechmorhoga mendax</i> (Hagen, 1861)	U.S.A.	13(<i>m</i>); 13	of the two Californian populations studied <i>m</i> present in material from Nevada, but lacking in that of Humboldt Co.	CRUDEN, 1968
<i>B. nubecula</i> (Rambur, 1842)	Bolivia	13(<i>m</i>)		CUMMING, 1964a
<i>B. pertinax peruviana</i> Ris, 1913	Bolivia	13		CUMMING, 1964a
<i>Dythemis cannaeoides</i> Calvert, 1906	Bolivia	12(<i>m</i>)		CUMMING, 1964a
<i>D. fugax</i> Hagen, 1861	U.S.A.	13(<i>m</i>)		CRUDEN, 1968
<i>D. rufineris</i> (Burmeister, 1839)	Jamaica	13(<i>m</i>)		CUMMING, 1964a
<i>D. velox</i> Hagen, 1861	Bolivia	13(<i>m</i>)	sub <i>D. multipunctata</i>	CUMMING, 1964a
<i>Macrothemis declivata</i> Calvert, 1909	Brasil	12(<i>m</i>)	decrease in n due to fusion of two autosomes; one bivalent extra large; XO	KIAUTA, unpublished
<i>M. hemichlora</i> (Burmeister, 1839)	Bolivia	3	decrease in n due to fusion; two extra large and one smaller bivalent; one of these two chiasmata; no sex-element recognizable at any stage; neo-XY probable	CUMMING, 1964a
<i>M. imitans imitans</i> Karsch, 1890	Brasil	13(<i>m</i>)	<i>m</i> extremely minute at metaphase I	KIAUTA, unpublished

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<i>M. mortoni</i> Ris, 1913	Bolivia	13(m)		CUMMING, 1964a
<i>M. musiva</i> , Calvert, 1898	Bolivia	13(m)		CUMMING, 1964a
<i>Scapanea frontalis</i> (Burmeister, 1861)	Jamaica	13(m)		CUMMING, 1964a
Rhyotheminae <i>Rhyothemis fuliginosa</i> Selys, 1883	Japan	12(m); 13(m)	sub <i>Sympetrum</i> (<i>Toyoshima</i> & <i>Hirai, Hirai</i>); decrease in n due to fusion; one extra large bivalent in n = 12; different n in two different geographic populations; mode of sex determination unclear	TOYOSHIMA & HIRAI, 1953; OMURA, 1955; HIRAI, 1956; KIAUTA, 1969
<i>R. variegata</i> (Linnaeus & Johansson, 1763)	India	13(m)		RAY CHAUDHURI & DASGUPTA, 1949
Pantaliinae <i>Miathyria marcella</i> (Selys, 1857)	Bolivia	13(m)		CUMMING, 1964a
<i>Pantala flavescens</i> (Fabricius, 1798)	India, Bolivia, Madagascar; Hawaii	13(m)		ASANA & MAKINO, 1935; MAKINO, 1935; KICHIO, 1942d; DASGUPTA, 1957; SESHACHAR & BAGGA, 1963; CUMMING, 1964a; KIAUTA, 1969c
<i>P. hymenaea</i> (Say, 1836)	Bolivia, U.S.A.	13(m)		CUMMING, 1964a; CRUDEN, 1968
<i>Tauriphila australis</i> (Hagen, 1867)	Bolivia	13(m)		CUMMING, 1964a
<i>T. azteca</i> Calvert, 1906	Mexico	13(m)		CRUDEN, 1968
<i>Trapezostigma abdominalis</i> (Rambur, 1842)	Bolivia	13	sub <i>Tramea</i>	CUMMING, 1964a
<i>T. basilaris burmeisteri</i> (Kirby, 1889)	India	13(m)	sub <i>Tramea basilaris</i>	DAS, 1956; DASGUPTA, 1957
<i>T. carolina</i> (Linnaeus & Johansson, 1763)	U.S.A.	13	sub <i>Tramea</i>	CUMMING, 1964a; CRUDEN, 1968
<i>T. cophysa</i> (Hagen, 1867)	Bolivia	13(m)	sub <i>Tramea</i>	CUMMING, 1964a
<i>T. lacerata</i> (Hagen, 1861)	U.S.A.	13	sub <i>Tramea</i>	CRUDEN, 1968
<i>T. limbata</i> (Desjardins, 1832)	India	13(m)	sub <i>Tramea</i>	ASANA & MAKINO, 1935; MAKINO, 1935; KICHIO, 1942d
<i>T. virginia</i> (Rambur, 1842)	India	13(m)	sub <i>Tramea chinensis</i> (<i>Oguma & Asana,</i> <i>Kichijo</i>)	OGUMA & ASANA, 1932; KICHIO, 1942d; DASGUPTA, 1957

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