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REVIEW **Open Access**

A review on intraspecific karyomorphological variations of m chromosomes in family Libellulidae (Anisoptera: Odonata)

Gurinder Kaur Walia* and Hardeep Singh

Abstract

Background: Family Libellulidae is one of the largest families of suborder Anisoptera (Odonata) including 1035 species of 144 genera throughout the world. Libellulids are distributed all around the globe, while some are cosmopolitan and some are endemic. Cytogenetic data pertains to 258 libellulid species and chromosome number varies from $2n = 6–47$. Majority of the species possess $2n$ (♂) $= 25$, which is the modal number of the family. The m chromosomes are considered as the fragments of autosomes and are present in 78% of studied libellulid species.

Main body: Presently, 29 libellulid species have been catalogued based on various research articles related to cytogenetic studies regarding intraspecific chromosomal variations especially due to the m chromosomes within the same or different geographical populations of the species.

Conclusions: Odonata possess holokinetic chromosomes and m chromosomes are the fragments of autosome. The break can occur at any time, at any place, which is responsible for variations in the size of m chromosomes. These variations also depend on the geographical distribution of the species which persists over generations by the action of natural selection and also play role in speciation.

Keywords: Dragonfly, Anisoptera, Libellulidae, Chromosomal fusions, Chromosomal fragmentations, Geographical variations, m chromosomes

Background

Family Libellulidae is one of the largest families of suborder Anisoptera (Odonata) which includes 1035 species of 144 genera throughout the world and 91 species of 40 genera are present in India (Subramanian & Babu, 2017). The dragonflies of family are widely distributed from tropical to tempate regions. They commonly fly around lakes and ponds (Jarzembowski & Nel, 1996). Their size, shape and colour differ widely (Fraser, 1936). Most of the libellulids have coloured and patterned wings and anal loop is present on the hind wing. They are able to survive in low oxygen water and some species can also live in brackish water (Mitra, 2005). They act as predator in aquatic and terrestrial life. They feed on small insects like moth, chironomid midges and beetles, which act as pest on various crops. Their larvae feed on the mosquito larvae and also referred as "mosquito hawks" (Kenny & Burne, 2001).They help to control of the diseases like malaria, dengue, chikungunya, etc. Dragonflies can act as good bioindicator as they detect environmental changes and react quickly (McGeoch, 1998).They require specific habitat and their presence indicate the environmental conditions (Simaika & Samways, 2012).

*Correspondence: gurinderkaur_walia@yahoo.co.in

Department of Zoology and Environmental Sciences, Punjabi University, Patiala, Punjab 147002, India

Cytogenetic work plays an important role to describe the evolutionary relationships between different groups of Odonata. Cytogenetically, 258 libellulid species have been described throughout the world which also includes 45 species from India (Dasgupta, 1957; Kuznetsova & Golub, 2020; Walia & Singh, 2021). The chromosome number varies from $2n=6$–47 in the studied species. This wide range in the chromosome number is due to the chromosomal fusion/fragmentation or the presence/absence of m chromosomes in both intra and interspecific populations which is very frequent in odonates because of the holocentric chromosomes (Kuzenstova & Golub, 2020). Kiauta (1967) explained the evolution of the chromosome number in Odonates as the ancestral chromosome number is $n=9$, which increased in stepwise manners as specialization increases in the order and the secondary complements in the order arise due to fusion or fragmentation of the chromosomes in different ways (Fig. 1). In the family libellulidae, 78% species possess possess $2n$ (♂) = 25, which is the modal number of the family, while 22% species show variations in the chromosome number (Kuzenstova & Golub, 2020, Walia & Singh, 2021). The most common sex determination mechanism in libellulid is XX (♂)/X0(♀) which is derived from primitive XX (♂)/XY (♀) sex determining mechanism in animals (Asana & Makino, 1935; Das, 1956; Oguma, 1915, 1917; Smith, 1916; White, 1954). X chromosomes shows postreductional behaviour during the meiosis and its size varies in different species. In addition to this, Neo-XY (Fig. 2) and $X_1X_1X_2X_2/X_1X_2Y$ (Fig. 3) are also present in various libellulid species which are originated by the fusion of X chromosome with autosomes (Kiauta, 1968d, 1969a; Mola et al., 1999; Omura, 1955; Ray Chaudhuri & Dasgupta, 1949; Sandhu & Walia, 1994; Walia & Sandhu, 1998).

m chromosomes and their role in phylogenetic assessment of Odonata: m chromosomes are small chromosomes which possess particular meiotic behaviour as compared to both autosomes and sex chromosomes (Wilson, 1905). They were noticed for the first time in the dragonfly, *Anax junius* (Lefevre & McGill, 1908). They are small in size, shows negative heteropycnosis and their size varies in different species. These are smaller than or equal to half the size of immediately large chromosomes (Mola, 1992). According to Oguma (1930), m chromosomes are normal autosomes which undergo gradual diminution in volume until they eventually disappeared. This view has been accepted by Dagupta (1957) and Cumming (1964). However, Kiauta (1968a) discarded the "m chromosome theory" and described m chromsomes as the fragments of autosomes. The breaks can occur at any time, at any place in the holokinetic chromosomes which are responsible for variations in the size of m chromosomes in different and in the same specimen. These variations also depend on the geographical distribution of the species which persists over generations through the action of natural selection and also play role in speciation (Souza Bueno, 1982).

The presence/absence of m chromosomes in the species is also helpful in determining the phylogenetic relationship of species. Genus *Libellula L.* is mainly holoarctic in distribution and found in the temperate zones of the northern hemisphere, while it developed some species also in the transitional and subtropical zones (Kaiuta, 1968c). However, it is thought to be originated from the Eastern Hemisphere based on the penile characters. The dominancy of this genus is shifted from Eurasia in past to North America, and various centres of specialization were form during migration (Kennedy, 1922a, 1922b). Cytogenetically, same frequencies of two chromosome complements $n=12$and $n=13$ were found in specimens of *Libellula depressa* from Austria. There were total four kinds of karyotypes found in specimens—(a) complement without m chromosome, (b) cells having one bivalent had a subterminal constriction, (c) the m chromosome is clearly separated from the original bivalent, but is found lying in the prolonged longitudinal axis close to the latter and (d) complement in which the m chromosome occupies a random positions among other elements (Kiauta, 1968c). The fragmentation of the autosome in this species is important as this species is most specialized and probably represents European offshoot of the American *Plathemis* stock. It must have migrated to Eurasia before *L. quadrimaculata* entered into America. The difference between *L. quadrimaculata* and *Platethemis* is great, suggesting that it branched off much earlier (Kennedy, 1922b). Similarly, infraspeciation and radiation of *Erythemis connata fusca* stock is described. It is based on the distributional patterns, structural characters and the cytological evidences. The *Erythemis connata fusca* is supposed to be the oldest forn of *connata*" Artnkresis" and present in the centre of species range in the Atlantic drainage of South America, Central America and Mexico and without m chromosomes, while *Erythemis connata* and *Erythemis minuscula* present in the periphery and contain m chromosomes and thought to be originated from the central species (Kiauta & Boyes, 1972). m chromosomes are present in 78% of studied libellulid species and show variations in different pouplations of the species. Presently, intraspecific chromosomal variations based on m chromosomes in 29 libellulid species have been enlisted (Tables 1, 2 and 3).

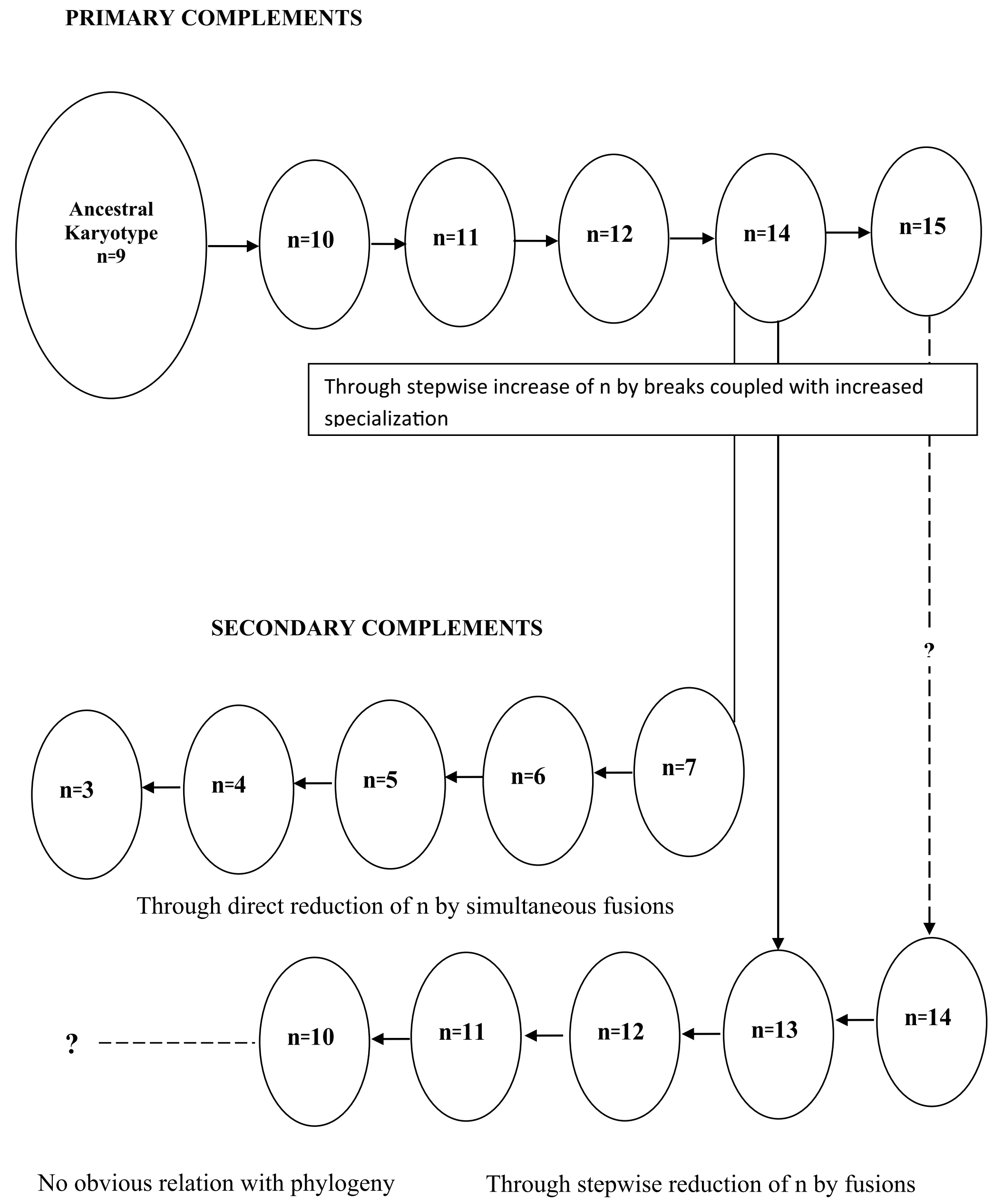

Fig. 1 Diagrammatic representation of the karyotypic evolution of chromosome number in Odonata (Kiauta, 1967)

Main text

Cytogenetically, 258 libellulid species has been studied worldwide and m chromosomes are present in 78% of libellulid species (Kuznetsova & Golub, 2020; Walia & Singh, 2021). Intraspecific karyomorphological variations in the chromosome complement due to m chromosomes have been recorded in 29 species and divided as:

A) Fusion of m chromosome with an autosome pair or X chromosome (Table 1):
B) Presence/absence of m chromosomes in different geographical populations of the species (Table 2):
C) Two chromosome complements (with/without m chromosomes) in the same specimen of the species (Table 3):

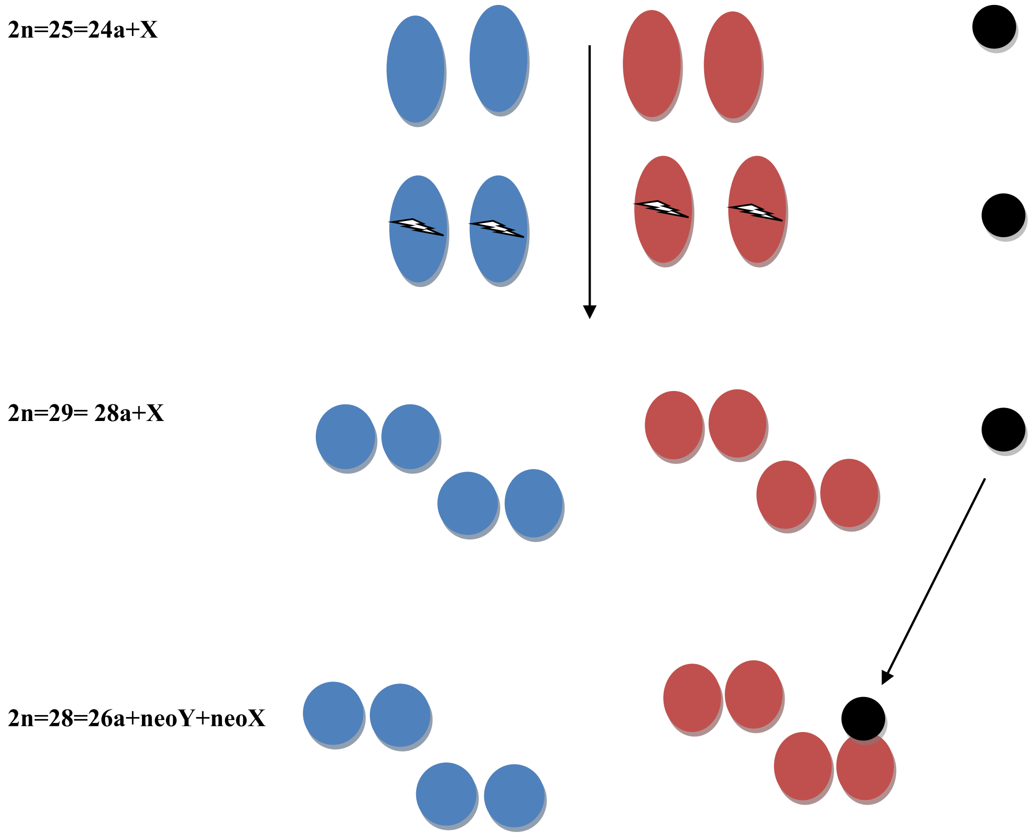

Fig. 2 Evolution of sex determination and numeric increase of the chromosome complement in *Neurothemis tullia tullia* (Kiauta, 1968a, 1968b, 1968c, 1968d)

A) Fusion of m chromosome with autosome pair or X chromosome: In Odonata, fusions and fragmentations play an important role in karyotypic evolution due to holokinetic nature of chromosomes and are responsible for the increase/decrease in the chromosome number in species (Kiauta, 1968a). In the family Libellulidae, the fusion of m chromosomes with autosomal pair leads to decrease in the chromosome number from $n = 13$ m to $n = 12$ and the complement of the species is characterized by the presence of one large autosomal bivalent in *Acisoma panporides*, *Elasmothemis cannacrioides*, *Erythrodiplax paraguayensis*, *Libellula depressa*, *Micrathyria hypodydima*, *Orthetrum brachiale*, *Orthetrum luzonicum* (Ferreira et al., 1979; Kaur, 2016; Kiauta, 1969b, 1969c; Souza Bueno, 1982; Walia & Sandhu; 2002). Fusion of m chromosomes with X chromosome resulted in large X chromosome present in the complement with intermediate neo-XY stage in *Crocothemis servilia*, *Orthetrum japonicum*, *Pontamarcha congener*, *Tholymis tillarga* and *Trithemis festiva* (Higashi et al., 2001; Kaur, 2016; Omura, 1955; Sandhu & Walia, 1995a, 1995b; Walia & Sandhu, 2002).

B) Presence/absence of m chromosomes in different geographical populations of the species: m chromosomes are present in one population and are absent in other populations of different geographical areas in *Brachydiplax farniosa*, *Brechmorhoga mendax*, *Erythemis attala*, *Brachydiplax vesiculosa*, *Erythrodiplax basalis*, *Erythrodiplax fusca*, *Leucorrhinia hudsonica*, *Leucorrhinia intact*, *Orthemis ferruginea*, *Pachydiplax longipennis*, *Perithemis mooma*, *Tramea binotata*, *Trithemis annulata* and *Uracis ovipotrix* (Agopian & Mola, 1988; Boyes et al., 1980; Cruden, 1968; Cumming, 1964; Dasgupta, 1957; Ferreira et al., 1979; Kaiuta and Boyes, 1972; Kiauta, 1979; Kiauta & Kiauta, 1983; Mola, 1996; Souza Bueno, 1982; Wasscher, 1985). Moreover, in *Erythrodiplax fusca*, size of m chromosomes varies in comparison to X chromosome as it is of the same size of X chromosome in Brazalian population (Ferreira et al., 1979), larger than X chromosome in Chile and Brazalian population (Kaiuta and Boyes, 1972; Souza Bueno, 1982)

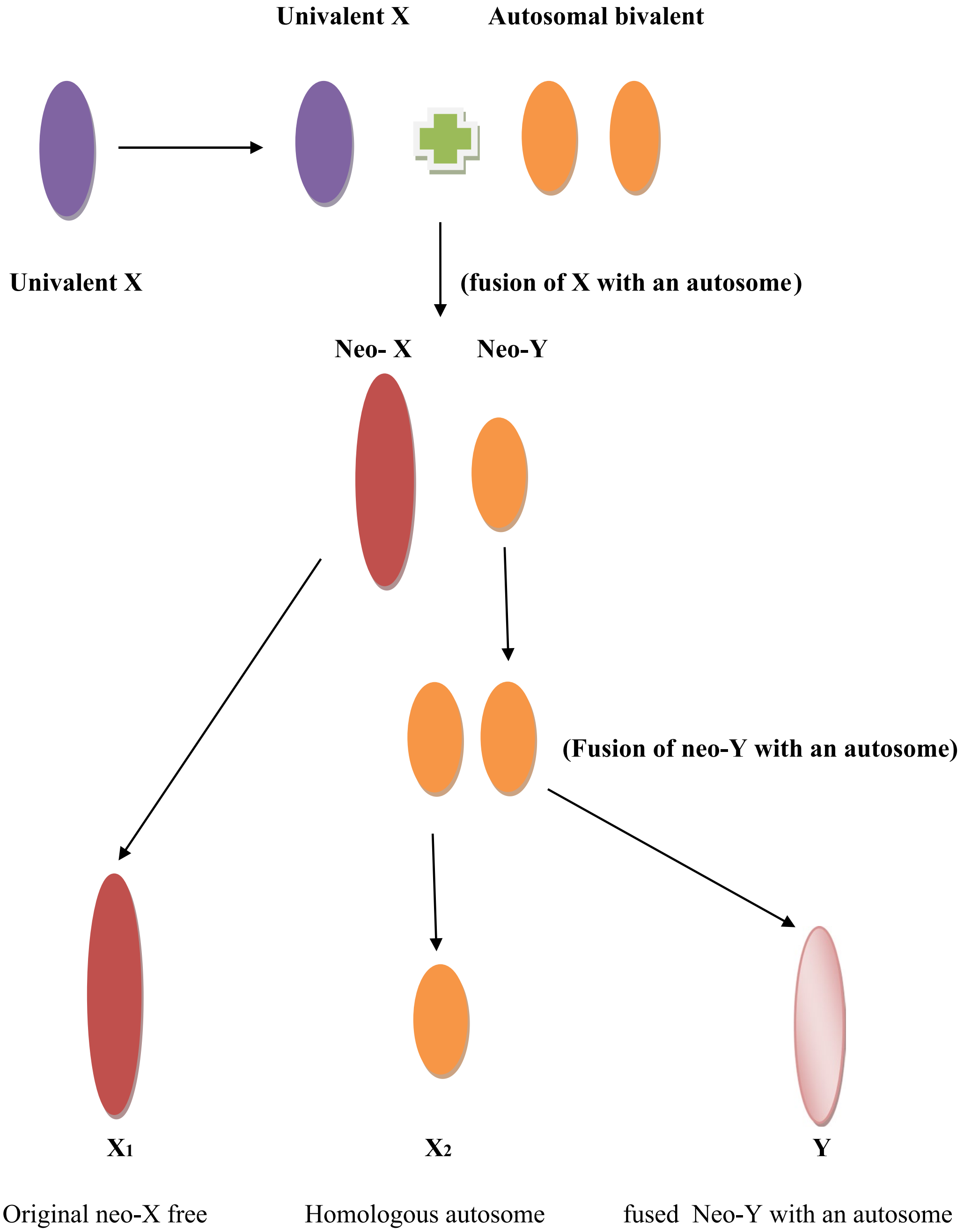

Fig. 3 Representation of X1X2Y sex determining mechanism in *Micrathyria ungulata* given by Mola et al. (1999)

and is half the size of X chromosome in Argentina population (Mola, 1996). The variations in the size of m chromosomes are because of the site of breakage in the holokinetic chromosomes. Chromosomal breaks and fusions can occur at any times in the holokinetic chromosomes and are retained because of their abilities to attach the spindle apparatus during divison. The kinetic activity of holokinetic chromsomes do not depends on specific nucleotide sequences while it is epigentically controlled (Guerra et al., 2010).

Environment plays an important role for the survival of species in the particular area. Geographical populations are related to the surrounding environment conditions which act as the stimulant for the chromosomal rearrangements. In *Erythrodiplax berenice,* shows the venational "anomalies" as increase in the number of marginal cells in the Northern populations

Table 1 Fusion of m chromosome with autosome pair or X chromosome

S. No	Taxa	Origin	Haploid complement (*n*)	References	Remarks
1	*Acisoma panorpoides* Rambur, 1842	Nepal	13 m	Kiauta (1975)	
		Bangladesh	13 m	Dasgupta (1957)	
		Thailand	13 m	Kiauta and Kiauta (1983)	
		India	13 m	Dasgupta (1957); Handa and Batra (1980); Tyagi (1982); Handa et al. (1984); Walia and Sandhu (1998); Walia (2008)	
			12	Kaur (2016)	Presence of one extra large autosomal bivalent
2	*Crocothemis servilia* (Drury, 1773)	Japan	13 m	Katatani (1987); Higashi and Kayano (1993); Higashi et al. (2001)	
		Nepal	13 m	Kiauta (1975); Kiauta and Kiauta (1982)	
		Philippines	13 m	Kiauta and Kiauta (1980)	
		Thailand	13 m	Kiauta and Kiauta (1983)	
		Taiwan	13 m	Higashi et al (2001)	
		India	13 m	Asana and Makino (1935); Makino (1935); Kichijo (1942); Ray Chaudhuri and Dasgupta (1949); Yadav (1979); Walia and Sandhu (1998); Walia (2008); Walia et al. (2010)	
		Japan	12	Omura (1955)	Neo-XY
			12	Kiauta (1983) Higashi et al. (2001)	Neo-XY
3	*Elasmothemis cannacrioides* (Calvert, 1906)	Bolivia	12 m	Cumming (1964) as *Dythemis cannacriodes* Calvert, 1906	
		Brazil	11	Ferreira et al. (1979)	Presence of one extra large autosomal bivalent and large X chromsome
4	*Erythrodiplax paraguayensis* (Förster, 1905)	Surinam	13 m	Kiauta (1979)	
		Bolivia	12	Cumming (1964)	
5	*Libellula depressa* Linnaeus, 1758	France	13 m	Kiauta (1973)	
		Croatia	13 m	Francovic and Jurecic (1986, 1989)	
		Russia	13 m	Perepelov et al. (1998) Kuzenstova et al. (2018)	
		Belgium	12	Carnoy (1885)	
		England	12	Hogben (1921)	
		Ausria	12	Kiauta (1969b)	
			12, 13 m	Kiauta (1968b)	
6	*Micrathyria hypodydima* Calvert, 1906	Argentina	13 m	Agopian and Mola (1988)	
		Brazil	12	Souza Bueno (1982)	Presence of one large autosomal bivalent
7	*Orthetrum brachiale* (Palisot de Beauvois, 1805)	Burkina Faso (Former Voltiac Republic)	13 m	Kiauta and Ochssee (1979)	
		Kenya	11	Kiauta (1969b, 1969c)	Presence of one large autosomal bivalent

Table 1 (continued)

S. No	Taxa	Origin	Haploid complement (*n*)	References	Remarks
8	*Orthetrum luzonicum* (Brauer, 1868)	Nepal	13 m	Kiauta (1975)	
		India	13 m	Thomas and Prasad (1981)	
		India	13 m	Kiauta and Kiauta (1982, 1983)	
		India	13 m	Prasad and Thomas (1992)	
		India	12	Walia and Sandhu (2002)	Presence of one large autosomal bivalent
9	*Orthetrum japnicum* (Uhler, 1858)	Nepal	13 m	Kiauta (1975) as *Orthetrum japonicum internum* McLachlan, 1894	
		Japan	13 m	Omura (1955) *Orthetrum Japonicum internum* McLachlan, 1894	
		India	12	Walia and Sandhu (2002) as *Orthetrum japonicum internum* McLachlan, 1894	Presence of largest X chromosome
10	*Potamarcha congener* (Rambur, 1842)	India	13 m	Tyagi (1982)	
		India	13 m	Prasad and Thomas (1992)	
		India	12	Sandhu and Walia (1995a, 1995b)	Presence of largest X –chromosome
11	*Tholymis tillarga* (Fabricius, 1798)	Nepal	13 m	Kiauta and Kiauta (1982)	
		Thailand	13 m	Kiauta and Kiauta (1983)	
		India	13 m	Prasad and Thomas (1992)	
		India	12	Walia and Sandhu (2002)	Presence of largest X chromosome
		India	12, 13 m	Kaur (2016)	Size of m chromosome is minute
12	*Trithemis festiva* (Rambur, 1842)	Nepal	13 m	Kiauta (1975)	
		India	13 m	Prasad and Thomas (1992)	
		India	12	Walia and Sandhu (2002); Kaur (2016)	Presence of largest X chromosome

(Shortness, 1930). Two populations of species have been studied from North Carolina, USA and North Dakota, USA. The chromosome number was 13 and 14 m (Cruden, 1968; Hung, 1971). The populations close to the northernmost limit of species increase the recombination index by increase in the chromosome number, thus promoting the ability of species to vary and adapt to changing environmental conditions, morphologically and genetically (Kiauta & Boyes, 1972). Similarly, *Erythrodiplax basalis*, geographical variation in the male addominal and wing colouration is resulted due to the change in chromosome complement of Brazil, Bolivia and Surinam populations (Cumming, 1964; Ferriera et al.1979; Kiauta, 1979).

C) Two chromosome complement (with/without m chromosomes) in the same speciemen of species: The numerical variations in the chromosome complement (with m/without m chromosomes) have been observed in the cells of same individual of *Diplocodes haematodes*, *Elasmothemis williamsoni*, *Erythrodiplax berenice*, *Leucorrhinia frigida*, *Ologoclada laetitia*, *Orthetrum coerulescens* and *Tholymis tillarga* (Cruden, 1968; Hung, 1971; Kaur, 2016; Kiauta, 1969b, 1971, 1979; Souza Bueno, 1982). The presence of two complements indicates the new adaptive level of the recombinations by the species which suits their evolutionary requirements. It is not a sudden event, the successful arrangement becomes stable in a population and others are eliminated (Kiauta, 1983). As in case of *Crocothemis servilia*, a large autosomal bivalent originated due to fusion of m chromosome with autosome pair is present only in the population of Japan and is absent in the other populations of species from China, Philippines, Taiwan and India. It represents the retention of suitable rearrangements in the population. Kiauta (1983) erected new genus *Crocothemis servilia marrinae* based on this cytological character as these rearrangements have been occurring from the generations to generation and play an important role in speciations.

Table 2 Presence/absence of m chromosomes in different geographical populations of the species

S.No	Taxa	Origin	Haploid chromosome complement (*n*)	References	Remarks
1	*Brachydiplax farinosa* Kruger, 1902	India	13 m	Dasgupta (1957)	
		Thailand	13	Kiauta and Kiauta (1983)	
2	*Brechmorhoga mendax* (Hagen, 1861)	Nevadaco (U.S.A)	13 m	Cruden (1968)	
		Humboldt County (U.S.A)	13		
3	*Erythemis attala* (Selys, 1857)	Argentina	13 m	Agopian and Mola (1988)	
		Bolivia	13	Cumming (1964)	
4	*Erythrodiplax basalis* (Kirby, 1897)	Brazil	13 m	Ferreira et al. (1979)	X and m chromsomes have approximately the same size
		Bolivia	13	Cummnig (1964)	
		Surninam	13	Kiauta (1979)	Responsible for the geographical variation in the male abdominal and wing coloration
5	*Erythrodiplax berenice* (Drury, 1773)	North Carolina, USA	13	Cruden (1968)	
		North Dakota, USA	14 m	Hung (1971)	
6	*Erythrodiplax fusca* (Rambur, 1842)	Surinam	13 m	Kiauta (1979)	m bivalent is a little larger than the X chromosome
		Brazil	13 m	Souza Bueno (1982)	m bivalent is a little larger than the X chromosome
		Brazil	13 m	Ferreira et al. (1979)	X and m chromsomes have approximately the same size
		Argentina	13 m	Mola (1996)	The m bivalent has only half the size of the X chromosome
		Chile	12 m	Kiauta and Boyes (1972)	m bivalent is a little larger than the X chromosome
		Bolivia	13	Cumming (1964)	
		Guatemala	13	Cruden (1968)	
7	*Leucorrhinia hudsonica* (Selys, 1850)	California (U.S.A)	13 m	Cruden (1968)	
		Oregon (U.S.A)			
		Wisconsin (U.S.A)	13		
8	*Leucorrhinia intacta* (Hagen, 1861)	California (U.S.A)	13 m	Cruden (1968)	
		Wisconsin (U.S.A)			
		Ohio (U.S.A)	13		
9	*Orthemis ferruginea* (Fabricius, 1775)	Guatemala	12 m	Cruden (1968)	
		Dominica	12 m	Cruden (1968)	
		Peru	12 m	Kiauta and Boyes (1972)	Presence of one large autosomal bivalent
		Surinam	12 m	Kiauta (1979)	
		Brazil	12 m	Ferreira et al. (1979)	Presence of one large autosomal bivalent
		Bolivia	12	Cumming (1964)	
		U.S.A	12	Cumming (1964)	
10	*Pachydiplax longipennis* (Burmeister, 1839)	California (U.S.A)	13 m	Cruden (1968)	
		Florida (U.S.A)	13		
		Virginia (U.S.A)			
11	*Trithemis annulata* (Palisot de Beauvoi 1805)	Kenya	13 m	Wasscher (1985)	
		Republic of South Africa	13	Boyes et al. (1980)	

Table 3 Two chromosome complement (with/without m chromosomes) in the same speciemen of species

S.No	Taxa	Origin	Haploid chromosome complement (*n*)	References	Remarks
1.	*Diplocodes haematodes* (Burmeister, 1839)	Australia	12, 13 m	Kiauta (1969b)	Increase in chromosome number is due to fragmentation
2.	*Elasmothemis Williamsoni* Ris, 1919)	Surinam	11, 12 (Occasionally 13 m)	Kiauta (1979) as *Dythemis williamsoni* Ris, 1916	Neo-XY in $n=11$; m chromosomes are minute size in $n=13$
3.	*Erythrodiplax berenice* (Drury, 1773)	U.S.A	13, 14 m	Hung (1971)	
4.	*Leucorrhinia frigida* Hagen, 1890	U.S.A	11, 12 m	Cruden (1968)	Decrease in chromosome number is due to fusion of autosomes
5.	*Ologoclada laetitia* (Ris, 1911)	Brazil	11, 12 m	Souza Bueno (1982)	
6.	*Orthetrum coerulescens* (Fabricius, 1798)	Italy	13 m, 14 m	Kiauta (1971)	increase in chromosome number is due to fragmentation of autosomes
7.	*Tholymis tillarga* (Fabricius, 1798)	India	12, 13 m	Kaur (2016)	m chromosomes are very minute in size

Conclusions

In Odonata, chromosomes are holokinetic in nature and large numbers of genetic rearrangements are possible in these chromosomes. The m chromosomes are the fragments of autosomes and variations in the size of m chromosomes, their presence/absence in the complement, fusion of m chromosome with autosome pair and two different chromosome complement (with/without m chromosome) in the same specimen have been catalogued for 29 libellilid species.

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Author contributions

HS carried out the literature survey and prepared the mensucript. GKW checked and reframed the manuscript for publication. Both authors read and approved the final manuscript.

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Not applicable.

Declarations

Ethics approval and consent to participate

Not Applicable.

Consent for publication

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Competing interests

We have no competing interests.

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