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A Review on Cytogenetically Studied Species of Family Coenagrionidae (Odonata: Zygoptera)

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Cytotaxonomy is useful for separating sister and cryptic species as well as for figuring out the evolutionary relationship between taxa. Family Coenagrionidae is considered as one of the largest zygopteran families under order Odonata. Globally, a lot of investigation has been undertaken on the family Coenagrionidae and significantly contributed by biologists throughout the world. Type number of the family Coenagrionidae is n=14 with XO-XX type of sex determining mechanism. Karyotypic variations within and between species are observed due to chromosome breaks and fusions, absence/presence of m chromosomes because of the holokinetic nature of chromosomes. Cytogenetically, 107 coenagrionid species have been studied all over the world which also includes 37 species from India. Among these, most of the species possesses n=14 haploid complement, while variation in chromosome number has been observed in 25% species.

Keywords: Coenagrionidae; Holokinetic chromosomes; m chromosome; Recombination index; Sex determining mechanism.

Insects are one of the prime sources of karyological research. An entomologist tries to study each and every aspect of insects, but the most negligible and critical aspect is the chromosomal studies. Chromosomal analysis provides information about the genetic structure and nature of an organism and displays a wide range of variations. Cytological studies contribute in three ways: (1) to design natural and phylogenetic relationship among the various groups (2) to understand various cytogenetic processes in the evolution of different groups and (3) to solve twitched cases like variation among geographical races, individual abnormalities and polymorphic morphs.

Order Odonata includes three suborders, Zygoptera (damselflies), Anisoptera (dragonflies) and Anisozygoptera. Suborder Zygoptera comprises of 3162 species under 319 genera globally and 211 species under 59 genera and 9 families are present in India. Family Coenagrionidae is considered as one of the largest damselflies family. Taxonomically, 1351 species and 121 genera are present all over the world and 60 species and 12 genera are recorded in India [1]. The first coenagrionid species, *Ceriagrion rubiae* was studied by Asana and Makino [2]. They documented that an unpaired X chromosome migrated to one pole during [3] secondary spermatocyte division in all the species. Size of m chromosomes varies

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from species to species and is closely related to the size of X element. However, in *Ceriagrion rubiae*, size of m chromosome is found to be equal to X chromosome. Kuznetsova and Golub revise the checklist of chromosome numbers for Odonata, which covers 92 species of the family Coenagrionidae. Presently, a review on 107 species of family Coenagrionidae has been catalogued and discussed based on key cytogenetic characteristics of the family (Table I). For this, the following parameters have been undertaken.

Holokinetic Chromosomes

One of the fundamental components of chromosome structure is its kinetic organization. This has always been a disputed topic in the case of odonates. Oksala [4, 5, 6, 7] expresses that odonates possess localized centromere and his view has been shared by Dasgupta [8], Seshachar and Bagga [9] and White [10]. On the other hand, Piza [11, 12] reports dicentric chromosomes in odonates, while Schrader [13], Hughes- Schrader[14] and Lima de Faria[15] agree with the opinion of diffused kinetochores.

In presently studied 21 Indian species it is found that two parallel chromatids without any constriction in chromosomes are seen during the spermatogonial metaphases of *Ceriagrion cerinorubellum, Ceriagrion coromandelianum*, *Ischnura elegans*, *Ischnura senegalensis* and rod shaped chromosomes are present in *Aciagrion hisopa*, *Agriocnemis pygmaea*, *Ischnura aurora*, *Ischnura forcipata*. At the time of late diakinesis, bivalents of holocentric chromosomes appear to be held together by end to end association due to the terminalisation of chiasmata. This is seen in almost all the studied species, while chromatids are seen to separate by parallel disjunction during anaphase- I in *Agriocnemis pygmaea*. The autosomal bivalents appear to be rod shaped in metaphase- I in all the studied species and when it enters in metaphase- II, the size of the chromosomes remain half as seen in *Ischnura aurora, Ischnura forcipata, Pseudagrion laidlawi* and *Pseudagrion rubriceps.* This type of chromosome behaviour also supports the holokinetic chromosomes in Odonata.

Evolution of chromosome number

Kiauta[16, 17, 18] finds haploid number 12, 13 and 14 to be present in more than 90% of Odonata. He considers n=13 to be the type number of the order, which has been cytologically reported in 58% of studied species. Numerical variation in Odonata karyotype due to occurrence of breaks (leading to haploid numbers 10-15) and fusions (leading to haploid complements 3-7) has been explained graphically by him (Fig. 1). He combines genealogical observations of Fraser[19] with cytological findings and concluded that family Coenagrionidae, Aeshnidae and Libellulidae are the most advanced and dominant families, which are of independent origin and are more ancient than present day dragonflies. He also considers greater chromosome numbers as an indication of advancement of families. Further, Kiauta [20] refers that in suborder Zygoptera only 39.4% possess n=13 and 53.6% show n=14. However, n=14 is peculiar only to the families Coenagrionidae and Protoneuridae. So, he considers n=13 as the type number of suborder Zygoptera. In the family Coenagrionidae, majority of the species possess type number n=14m, while variations (25% of species) in chromosome complement due to fusions (in 10% of species) and fragmentations (in 13 % of species) have been also reported (Table-1).

Fragmentations have been found in *Argia apicalis* [21] and *Argia tibialis* [22] (n=19); in *Ceriagrion cerinorubellum* [23], *Enallagma cyathigerum* [24], *Ischnura inarmata* [25], *Ischnura pumilio* [25] and *Leptagrion macrurum* [26] (n=15m); in *Ceriagrion coromandelianum* [27] (n=21/23) and in *Pyrrhosoma nymphula* [5] (n=28). Sandhu and Walia [28], Walia and Sandhu [29] and Walia [30] report aberrant autosomal fragmentations in some species and conclude that aberrant fragmentations occur due to the effect of pollutants to increase the recombination index, which favour the flexibility of the genotype for adaptation of the species in the polluted water [*Ceriagrion coromandelianum* (2nB&=27/41/45), *Coenagrion dyeri* (2n@& =28, 36, 56, 58), *Pseudagrion rubriceps* (2nB&,@&= 27, 37, 43, 45), *Pseudagrion decorum* (2nB&= 27, 34, 42, 52, 56, 58) and *Agriocnemis obscura* (2n@&= 28, 36, 44, 52, 56)].

Autosomal fusions in the family Coenagrionidae have been reported in *Mecistogaster* sp. [31] 2 (n=6) in *Agriocnemis pygmaea* [32] (n=12); in *Coenagrion mercuriale mercurial* [33, 34] and *Pseudagrion whellan* [35] (n=13). Reduction in chromosome number (n=13) due to the absence of m chromosomes has been found in *Ischnura aurora* [27, 37] and *Ischnura forcipata* [38].

Table 1. Worldwide List of Cytogentically Studied Species of the Family Coenagrionidae

S. No.	Name of the Species	Locality	Haploid (1n) number / m-chromosomes	References
1	*Acanthagrion ascendens* Calvert, 1909	Bolivia	14m	Cumming [31]
2	*Acanthagrion chacoense* Calvert, 1909	Bolivia	14m	Cumming [31]
3	*Acanthagrion gracile* (Rambur, 1842)	Brazil		Kiauta [25] [as *Acanthagrion gracile minarum* Selys, 1876]
		Surinam	14	Ferreira [52] [as *Acanthagrion gracile minarum* Selys, 1876]
4	*Aciagrion hisopa* (Selys, 1876)	India	14m	Sandhu and Walia [53], Walia [38], Present study
		India	14m	
5	*Aciagrion pallidum* Selys, 1891	India	14m	Present study
6	*Aciagrion tilliyardi* Laidlaw, 1919	India	14m	Sandhu and Walia [53], Walia [38], Walia and Sandhu [27]
7	*Aeolagrion inca* Selys, 1876	Bolivia	14m	Cumming [31] [as *Aeolagrion foliaceum* (Sjöstedt, 1918)]
8	*Agriocnemis clauseni* (Fraser, 1922)	India	14m	Tyagi [54, 55], Sandhu and Walia [53], Walia [38], Walia and Sandhu [27], Present study
		India	14m	
9	*Agriocnemis femina* (Brauer, 1868)	Thailand	14	Kiauta and Kiauta [56]
		India	14m	Walia and Hallan [57]
10	*Agriocnemis lacteola* Selys, 1877	India	13m	Sandhu and Walia [53]; Walia [38]; Walia and Sandhu [27]
11	*Agriocnemis obscura* (Fraser, 1933)	India	(@&) 14, 18, 22, 26, 28	Walia [38]; Sandhu and Walia [46], Walia and Sandhu [27]; Walia [58]
		India	14	Tyagi [55]
12	*Agriocnemis pygmaea* (Rambur, 1842)	India	12(neo- XY)	Handa and Kochhar [32]
		Thailand	14m	Kiauta and Kiauta [56]

		India	14m	Walia [38]; Walia and Sandhu [27]; Walia and Hallan [57]
13	*Amphiagrion abbreviatum* (Selys, 1876)	U.S.A.	14	Cruden [24]
14	*Amphiallagma parvum* (Selys, 1876)	India	14m	Handa and Kochhar [41]; Walia [38]; Walia and Sandhu [27] [as *Enallagma parvum* Selys, 1876]
			14	Present study
15	*Argia apicalis* (Say, 1839)	USA	19	Kiauta and Kiauta [21]
		Florida	14	Kiauta and Van Brink [59] [as *Argia fumipennis fumipennis* (Burmeister, 1839)]
		U.S.A.	14	Kiauta and Kiauta [22]
16	Argia fumipennis (Burmeister, 1839)			[as *Argia fumipennis atra* Gloyd, 1968]
		U.S.A.	14	Kiauta and Kiauta [21] [as *Argia fumipennis fumipennis* (Burmeister, 1839)]
		Canada	14m	Kiauta and Kiauta [22] [as *Argia fumipennis violacea* (Hagen, 1861)]
17	*Argia funebris* (Hagen, 1861)	U.S.A.	14	Kiauta [20]
		Mexico	14(@&)	Kiauta and Kiauta [22]
18	*Argia immunda* (Hagen, 1861)	U.S.A.	14	Kiauta and Kiauta [22]
19	*Argia moesta* (Hagen, 1861)	Canada		Kiauta [68]
		U.S.A.	13	Kiauta and Kiauta [22]
20	*Argia nahuana* Calvert, 1902	U.S.A.	13	Kiauta and Kiauta [22]
21	*Argia sedula* (Hagen, 1861)	Bolivia		Cumming [31]
		U.S.A.	14	Cruden [24]
		U.S.A.		Kiauta and Kiauta [22]
22	*Argia tibialis* (Rambur, 1842)	U.S.A.	19	Kiauta and Kiauta [22]
23	*Argia translata* Hagen, 1865	U.S.A.	13m	Kiauta and Kiauta [22]
24	*Argia violcea* (Hagen, 1861)	U.S.A.	14	Cruden [24]
25	*Argia vivida* Hagen, 1865	U.S.A.	14	Cruden [24]
26	*Cercion lindani* (Selys, 1840)	Italy	14m	Kiauta [22]
27	*Ceriagrion auranticum*	Thailand	14m	Kiauta and Kiauta [56]

	Fraser, 1922			[as *Ceriagrion latericium* Lieftinck, 1951]
28	*Ceriagrion azureum*	India	14	Das [61]
	(Selys, 1891)			
		Nepal		Kiauta [62, 50]
29	*Ceriagrion cerinomelas*	India	14	Das [61]
	Lieftinck, 1927	Nepal		Kiauta [62, 50]
			14m	Dasgupta [8]
			14m	Prasad and Thomas [63]
			13m,14m,15m	Tyagi [54];
30	*Ceriagrion*	India		Sandhu and Walia [23]
	cerinorubellum (Brauer,		14m	Walia [38]; Walia and Sandhu [27]; Walia and Kaur [37]; Walia and Hallan [57]
	1865)			
				Ray Chaudhuri and Dasgupta [39]
				Srivastava and Das [64]
		India		Das [61]
			14m	Handa and Kochhar [32]
31	*Ceriagrion*			Goni and Abenanta [65]
	coromandelianum	Nepal		Sandhu *et al.* [66]
	(Fabricius,1798)			
				Walia [38]
		India	14m/21/23	Walia and Sandhu [27]
			14m	Walia and Hallan [57]
32	*Ceriagrion fallax*	India	14m	Dasgupta [8]; Walia [38];
	Ris, 1914			Walia and Sandhu [27];
				Present study
		India	14m	
33	*Ceriagrion glabrum*	Swaziland	14	Boyes *et al.* [67]
	(Burmeister, 1839)	(South Africa)		
34	*Ceriagrion lieftincki*	Philippines	14	Kiauta and Kiauta [56]
	Asahina, 1967			
35	*Ceriagrion rubiae*	India	14m	Asana and Makino[2]; Makino [68]; Kichijo [69]
	Laidlaw, 1916			
36	*Ceriagrion tenellum*	Italy	14m	Kiauta [70]
	(Villers, 1789)			
37	*Chromagrion conditum*	U.S.A.	14	Cruden [24]
	(Hagen, 1876)			
38	*Coenagrion armatum*	Finland,	14	Oksala [36]
	(Charpentier, 1840)	U.S.S.R.		Makalowskaja [33]

39	*Coenagrion dyeri* (Fraser, 1924)		(@&) 14	Walia [38]
			18	Sandhu and Walia [46]
			28	Walia and Sandhu [27]
		India	29	Walia [58]
			14	Makalowskaja [33]
40	*Coenagrion hastulatum* (Charpentier, 1825)	U.S.S.R	14m	Kichijo [71, 72, 69]
			14	Makalowskaja [33]
		Russia	14	Perepelov and Bugrov [73]
41	*Coenagrion hylas* (Trybom, 1889)	Austria	14	Kiauta and Kiauta [74] [as *Coenagrion hylas freyi* (Bilek, 1954)]
42	*Coenagrion lunulatum* (Charpentier, 1840)	Russia	14m	Perepelov and Bugrov [73]
43	*Coenagrion mercuriale* (Charpentier, 1840)	Liechtenstein	14	Makalowskaja [33]; Kiauta [34]
		U.S.S.R., Netherlands	14	Cruden [24]
44	*Coenagrion pulchellum* (Vander Linden, 1823)	Former USSR Netherlands		Makalowskaja [33] Kiauta [34]
		Russia	14m	Kuznetsova *et al.* [75]
45	*Coenagrion puella* (Linnaeus, 1758)	Russia	14m	Kuznetsova *et al.* [75]
46	*Coenagrion resolatum* (Hagen, 1876)	U.S.A.	14	Cruden [24]
			14m	Kichijo [71], 1942a,c
47	*Coenagrion* sp.	Japan	14m	Cumming [31]
				Kichijo [71, 72]
48	*Diceratobasis macrogaster* (Selys, 1875)	Jamaica	14m	Cumming [31]
		Bolivia	14	Cruden [24]
49	*Enallagma aspersum* (Hagen, 1861)	U.S.A.	14	Cruden [24]
50	*Enallagma boreale* Selys, 1875	U.S.A.	14	Cruden [24]
51	*Enallagma carunculatum* Morse, 1895	U.S.A.	14	Cruden [24]
52	*Enallagma circulatum* Selys, 1883	Russia	14m	Perepelov and Bugrov [73]

53	*Enallagma civile* (Hagen, 1861)	U.S.A.	14	Cruden [24]
		Finland	14	Oksala [5]
		Former USSR	14	Makalowskaja [33]
54	*Enallagma cyathigerum* (Charpentier, 1840)		USA	14 Cruden [24]
			15	
		Netherlands	14m	Kiauta [42, 34]
			15m	
55	*Enallagma eprium* (Hagen, 1861)	U.S.A.	14	Cruden [24]
56	*Enallagma praevarum*	U.S.A.	14	Cruden [24]
	(Hagen, 1861)	India	13m	Sandhu and Walia [53]; Walia [38]; Walia and Sandhu [27]
57	*Enallagama malayanum* Selys, 1876	India	14	Oksala [36];
				Makalowskaja [33]
				Kiauta [34]
			13m	Sandhu and Walia [53]; Walia [38]; Walia and Sandhu [27]
58	*Erythromma lindeni* (Selys, 1840)	Italy	14m	Kiauta, 1971
		Finland	14	Oksala [36]
		Former USSR	14	Makalowskaja [33]
		Netherlands	14	Kiauta [42]
59	*Erythroma najas*	Russia	14	Perepelov and Bugrov [73]
	(Hansemann, 1823)	Russia	14m	Kuznetsova *et al.* [75]
		India	13m/ 13	Walia [38];Walia and Sandhu [47];
			14m	Walia and Kaur [37]; Walia and Hallan [57]
60	*Homeoura chelifera* (Selys, 1876)	Brazil	14m	Ferreira [52]
		Nepal	14	Kiauta [62, 50]
		India	14	Handa and Kochhar [41]
61	*Ischnura aurora*		14	Walia [38]
	(Brauer, 1865)		13m/ 13	Walia and Sandhu [47, 27]
			13	Walia and Kaur [37]
			14m	Walia and Hallan [57]
62	*Ischnura capreola*	Bolivia	14	Cumming [31]
	(Hagen, 1861)			[as *Ceratura capreola* (Hagen, 1861)]

63	*Ischnura cervula* Selys, 1876	U.S.A	14	Cruden [24]
64	*Ischnura delicate* (Hagen, 1854)	India	14	Handa and Kochhar [32, 76]
65	*Ischnura denticollis* (Burmeister, 1839)	U.S.A	14	Oksala [5]; Cruden [24]; Kiauta [42]
66	*Ischnura elegans* (Vander Linden, 1820)	Finland;	14	Oksala [36, 5]
		Netherlands		Kiauta [42]
		Russia		Perepelov [77]
		India	14m	Present study
		Bolivia	14	Cumming [31]
67	*Ischnura fluviatilis*		14	Walia [38];
	Selys,1876	India	13	Sandhu and Walia [78]
			13m/ 13	Walia and Sandhu [27]
			14m	Walia [38]; Walia and Sandhu [27]
68	*Ischnura forcipata* Morton, 1907	India	14	Cruden [24]
		Nepal		Kiauta [50]
		India	13	Walia [38]
		India	14m	Present study
69	*Ischnura inarmata* Calvert, 1898	U.S.A.	15	Kiauta [25]
		India	14m	Walia [38]; Walia and Sandhu [27, 47]
70	*Ischnura* nursei (Morton, 1907)	India	13m	Tyagi [55];
		India	13m	Present study [as *Rhodischnura nursei* (Morton, 1907)]
		India	14m	Present study [as *Rhodischnura nursei* (Morton, 1907)]
71	*Ischnura perparva* Selys,1876	U.S.A.	14	Cruden [24]
		Netherlands	14m	Kiauta and Van Brink [59]
72	*Ischnura pumilio* (Charpentier, 1825)	Netherlands	15	Kiauta [25]
		Florida	14	Kiauta [50];
		India		Sandhu and Walia [53]
			14m	Walia [38],
			14	Walia and Sandhu [47, 27]
73	*Ishnura ramburi* (Selys, 1850)	USA	14m	Kiauta and Brink [79]

74	*Ischnura rufostigma annandalei* Laidlaw,1919	Nepal	14	Kiauta [62, 50] [as *Ischnura rufostigma annandalei* Laidlaw, 1919]
		India	14m	Sandhu and Walia [53]
		India	14	Walia [38], Walia and Sandhu [47, 27]
			14	Present study
		Japan	14m	Kichijo [71, 72, 80]
		India	14m	Dasgupta [8]
		Bolivia	14	Cruden [24]
		Ethiopia	14m	Kiauta [34]
75	*Ischnura senegalensis* (Rambur, 1842)	Philippines	14m	Kiauta and Kiauta [22]
		Thailand	14	Kiauta and Kiauta [56]
			14m	Prasad and Thomas [63]
			14	Sandhu and Walia [23]
		India	14	Walia [38]
			14m	Walia and Sandhu [47, 27] Walia and Hallan [57]
76	*Ischnura ultima* Ris, 1908	Bolivia	14	Cumming [31]
77	*Ischnura verticalis* (Say,1839)	USA	14	Cruden [24]
78	*Leptagrion macrurum* (Burmeister, 1839)	Brazil	15+neo- XY	Kiauta [26]
79	*Mecistogaster* sp. 1	Bolivia	15m	Cumming [31]
80	*Mecistogaster* sp. 2	Bolivia	6+neo-XY	Cumming [31]
81	*Megalagrion oahuense* (Blackburn,1884)	Hawaii	14	Kiauta [49]
82	*Mortnagrion selenion* (Ris, 1916)	Japan	14m	Kichijo [71, 72, 80]
83	*Nehalennia irene* (Hagen, 1861)	USA	14	Cruden [24]
84	*Nehalennia spectosa* (Charpentier, 1840)	Finland	14	Oksala [5]
85	*Oxyagrion hempeli* Calvert, 1909	Brazil	14	Souza Bueno [81]
86	*Oxyagrion terminale*	Surinam	14	Kiauta [25]

	Selys, 1876	Brazil		Ferreira, *et al*. [52]
87	*Paracercion hieroglyphicum* (Brauer, 1865)		Japan	14m Kichijo [71, 72, 80] [as *Coenagrion hieroglyphicum* (Brauer, 1865)]
88	*Paracercion malayanum* (Selys, 1876)	Nepal	14m	Kiauta [50]
89	*Proischnura subfurcata* (Selys, 1876)	Kenya	14	Wasscher [82] [as *Enallagma subfurcatum* Selys, 1876]
90	*Pseudagrion acacia* (Foerst, 1906)	Republic of South Africa		14m Boyes *et al.* [67]
91	*Pseudagrion australasiae*	India	14m	Dasgupta [8];
	Selys, 1876	India	14m	Present study
92	*Pseudagrion bengalense* Laidlaw, 1919	India	14m	Dasgupta [8]; Walia [38]; Walia and Sandhu [27]
			14m	Dasgupta [8]
			>14m	Walia [38]; Sandhu and Walia [28]
93	*Pseudagrion decorum*		14m, 30, 38(B&)	Walia and Sandhu [27]
	(Rambur, 1842)	India	15, 17, 21, 26, 28, 29	Walia [30]
			14m	Walia and Hallan [57]
94	*Pseudagrion hypermelas* Selys, 1876	India	14m	Sandhu and Walia [53]; Walia [38]; Walia and Sandhu [27]
95	*Pseudagrion kersteni* (Gerstacker, 1869)	Kingdom of Eswatini (Former Swaziland)	14	Boyes *et al.* [67]
96	*Pseudagrion laidlawi* Fraser, 1922	India	14m	Sandhu and Walia [23]; Walia [38]; Walia and Sandhu [27]; Present study
		India	14m	
97	*Pseudagrion microcephalum* (Rambur, 1842)		India	14m Dasgupta [8];
			14m	Present study
		Philippines		Kiauta and Kiauta [22]
98	*Pseudagrion pruinosum* (Burmeister, 1839)		Thailand	14m Kiauta and Kiauta [56]
		India	14m	Dasgupta [8]
99	*Pseudagrion rubriceps*	Philippines	14m	Kiauta and Kiauta [22]
	Selys,1876	Thailand	14m	Kiauta and Kiauta [56]
				Sandhu and Walia 1999
		India	37, 43, 45, 14m	Walia and Sandhu [27]; Walia [30]
				Walia and Hallan [57]
100	*Pseudagrion saliburyense*	Kingdom of Eswatini (Former Swaziland)		14m Boyes *et al.* [67]

	Ris, 1921			
101	*Pseudagrion spencei* Fraser,1922	India	14m	Dasgupta [8]; Walia [38]; Sandhu and Walia [28]; Walia and Sandhu [27]; Walia and Hallan [57]
102	*Pseudagrion whellani* Pinhey, 1956	Burkina Faso (Former Voltiac Republic)	13m	Kiauta and Ochssée [35]
103	*Pyrrhosoma nymphula* (Sulzer,1876)	Finland	28	Oksala [5]
104	*Telebasis carmesina* Calvert, 1909	Surinam	14	Kiauta [25]
		Brazil	14	Ferreira *et al.* [52]
105	*Tigriagrion aurantingrum* Calvert, 1909	Bolivia	14	Cumming [31]
106	*Xanthocnemis zealandica* (mclachlan, 1873)	New Zealand	14	Jensen [83] [as *Xanthocnemis zelandica* (mclachlan, 1873)]
107	*Zoniagrion exclamtionis* (Selys, 1876)	USA	14	Cruden [24]

m chromosomes

m chromosomes have been used as a standard in comparative karyotypic studies of dragonflies for the first time by Ray Chaudhuri and Dasgupta [39]. Kiauta [40] considers m chromosomes as fragments of normal autosomes, which occur by the fragmentations in normal chromosomes. Out of total 107 cytogenetically studied coenagrionid species, m chromosomes are found to be present in 35 species, absent in 50 species, while in 22 species m chromosomes show variations (means absent and present) (Table I). Absence or presence of m chromosome in the species might be due to the geographical isolated populations of the species. In present study, species n=14 (without m chromosomes) has been reported in *Amphiallagma parvum* (Himachal Pradesh, India), while n=14m observed in the same species (as named- *Enallagma parvum*) by Handa and Kochhar [41]; Walia [38]; Walia and Sandhu [27] (Punjab, India).

Recombination Index

Recombination index is the sum of number of bivalents and average number of chiasmata per nucleus can be considered key character of genetic system of a species (Darlington, 1939). Chiasma frequency is fixed in the order Odonata and change in chromosome number is the only way of changing the recombination index. Chromosomal fusions and fragmentations play a major role in the evolution and phylogeny of the order [42, 25, 35, 43, 44, 45, 28, 46, 47, 29, 48].

In the family Coenagrionidae, most of the male damselflies possess single chiasma per bivalent which indicates that the species are well adapted to its habitat. Increase in recombination index by autosomal fragmentation has been reported in *Enallagma cyathigerum* (n= 15m) [24, 49], *Ceriagrion cerinorubellum* (n= 15m) [50], *Ischnura pumilio* (2n=29) [51], and *Ceriagrion coromandelianum* (n=14m/21/23) [27]. Moreover, aberrant fragmentations due to the effect of pollutants have been found in *Ceriagrion coromandelianum* (2nB&==27, 37, 45), *Coenagrion dyeri* (2n@&=28, 36, 56, 58), *Pseudagrion rubriceps* (2nB&=27, 37, 43, 45 and 2n@&= 28, 41, 45), *Pseudagrion decorum* (2n=27, 34, 42, 52, 54) and *Agriocnemis obscura* (2n@&=28, 36, 44, 52, 56) [28, 46, 29, 27, 30].

Autosomal fusions decrease the chromosome number as well as recombination

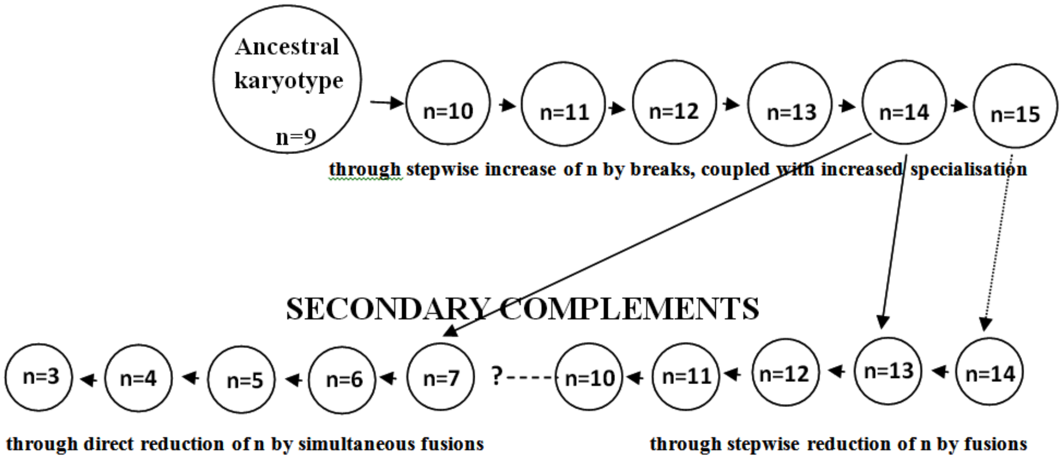

Fig. 1. Proposed hypothesis of karyotypic evolution in Odonata by Kiauta (1967c)

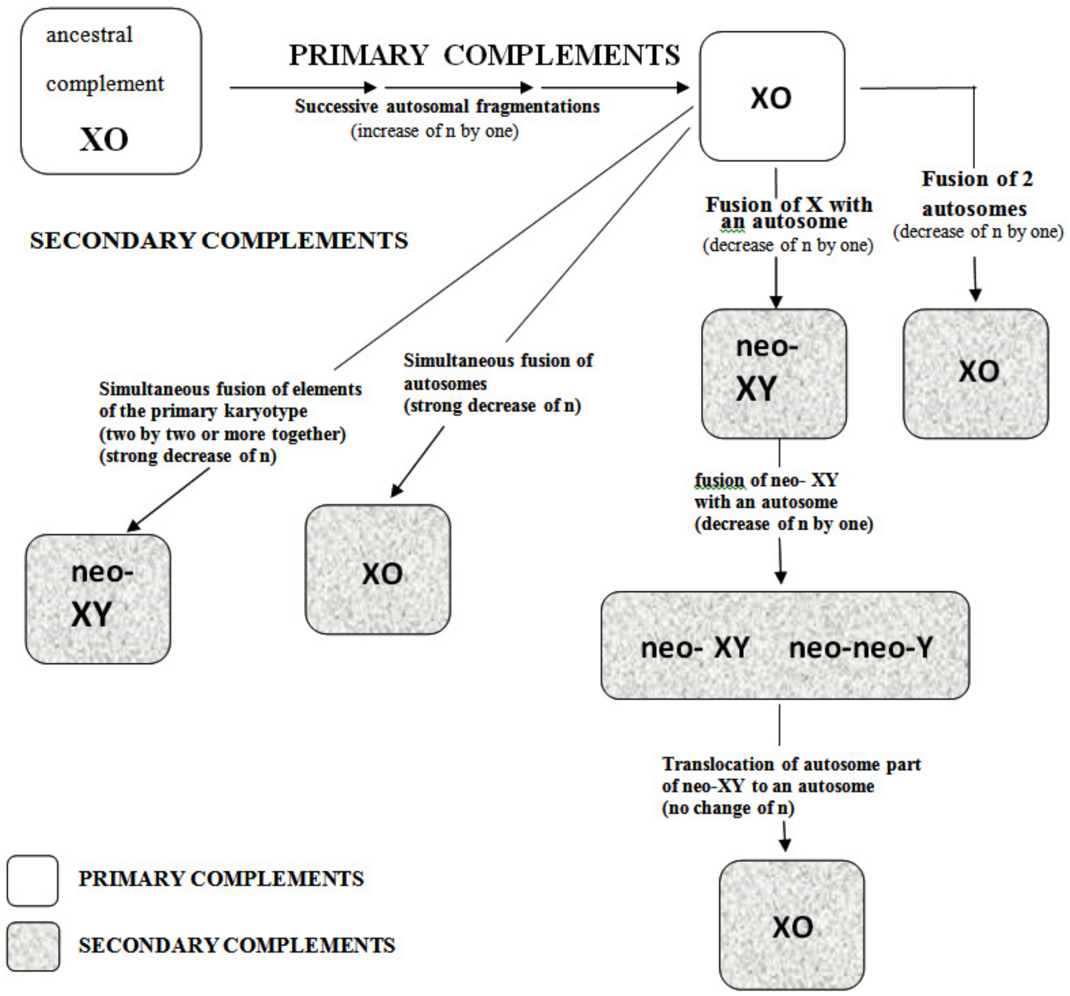

Fig. 2. Evolution of the sex determining mechanisms in the order (Kiauta, 1975)

index, which favour the survival value and reproductive capability of the species to settle over the whole geographical range for ecological adaptation. In the family Coenagrionidae, autosomal fusions have been reported in *Pseudoagrion whellani* (n=13) [25] and *Agriocnemis pygmaea* (n=12) [32] and *Coenagrion mercuriale mercuriale* (n=13) [45].

It has been reported that in the currently studied species, 17 coenagrionid species only have one chiasma per bivalent, while *Agriocnemis femina* and *Ischnura rufostigma* have two large autosomal bivalents, and *Pseudagrion laidlawi*, *Pseudagrion microcephalum* and *Pseudagrion rubriceps* have one large autosomal bivalent that has both interstitial as well as terminal chiasma. Increase in number of chiasmata increases the recombination index of the species, which promote flexibility of the genotype for adaptation and considered as cytological marker of the species.

Sex determining mechanism

All the primitive orders of exopterygote insects seem to have male heterogamety, usually of XO type. Numerous instances are seen in which XO: XX sex chromosomes systems reverted to XY: XX form in case of acrocentric chromosomes. Such a fusion is said to create a neo- X chromosome and when the fusion reaches the fixation in the population, the original acrocentric autosome is confined to the male line and constitutes neo- Y [10]. Kiauta [50] also considers XO: XX sex determining mechanism as the most primitive condition of the odonates and presented the graphical interpretation of the evolution of sex determining mechanisms in dragonflies (Fig. 2). In the family Coenagronidae, majority of the species possess XO-XX type of sex determining mechanism. However, neo- XY mechanism has been reported in *Leptagrion macrurum* [26], in *Agriocnemis pygmaea* [32] and in *Mecistogaster* Sp. 2 [31]. According to reports, the sex chromosome in males is univalent achiasmatic and exhibits bipartite behaviour during meiosis I, supporting the stability of the XO-XX type of sex determination in the Coenagrionidae family.

CONCLUTION

Chromosome number of coenagrionid species varies over a relatively wide range, from n = 6 in *Mecistogaster* sp. 2 [31] to n = 38 in *Pseudagrion decorum* [27], while n=14m is considered as the type number of the family Coenagrionidae. Increase in chromosome number is related to evolutionary advancement of families, Coenagrionidae and Libellulidae, while decreased in number is related to primitive families, Chlorocyphidae and Gomphidae. Decrease in chromosome number also occurs due to the gradual diminution and ultimate disappearance of the m chromosomes. The presence of contaminants in the stagnant water causes an aberration in the chromosomal complement of the species.

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Conflicts of interest

Authors declare no competing interests.

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