A checklist of chromosome numbers and a review of karyotype variation in Odonata of the world

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Abstract

The ancient insect order Odonata is divided into three suborders: Anisoptera and Zygoptera with approximately 3000 species worldwide each, and Anisozygoptera with only four extant species in the relict family Epiophlebiidae. An updated list of Odonata species studied regarding chromosome number, sex chromosome mechanism and the occurrence of m-chromosomes (= microchromosomes) is given. Karyotypes of 607 species (198 genera, 23 families), covering approximately 10% of described species, are reported: 423 species (125 genera, 8 families) of the Anisoptera, 184 species (72 genera, 14 families) of the Zygoptera, and one species of the Anisozygoptera. Among the Odonata, sex determination mechanisms in males can be of X(0), XY and X₁X₂Y types, and diploid chromosome numbers can vary from 6 to 41, with a clear mode at 2n = 25(60%) and two more local modes at 2n = 27(21%) and 2n = 23(13%). The karyotype 2n = 25(24A + X) is found in each of the three suborders and is the most typical (modal) in many families, including the best-covered Libellulidae, Corduliidae (Anisoptera), Lestidae, Calopterygidae, and Platycnemididae (Zygoptera). This chromosome set is considered ancestral for the Odonata in general. Chromosome rearrangements, among which fusions and fissions most likely

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predominated, led to independent origins of similar karyotypes within different phylogenetic lineages of the order. The karyotype $2n = 27(26A + X)$ prevails in Aeshnidae and Coenagrionidae, whereas the karyotype $2n = 23(22A + X)$ is modal in Gomphidae and Chlorocyphidae, in both pairs of families one being from the Anisoptera while the other from the Zygoptera.

**Keywords**
Chromosome numbers, damseldragons, damselflies, dragonflies, m-chromosomes, sex chromosome mechanisms

**Introduction**

The order Odonata, which comprises slightly more than 6,000 described species worldwide, is one of the most ancient among winged insects (Pterygota), dating from the Permian (Grimaldi and Engel 2005). Extant Odonata include two main suborders with approximately 3,000 species each, the Zygoptera or damselflies with about 308 genera and the Anisoptera or true dragonflies with about 344 genera. Within these suborders, up to 21 and 11 families (and sometimes more), respectively, are currently recognized. The third suborder, the Anisozygoptera or damseldragons, includes only one genus *Epiophlebia* Calvert, 1903 with four extant species in the relict family Epiophlebiidae. A substantial body of evidence indicates that Anisoptera and Zygoptera are each monophyletic, and Zygoptera are sister to *Epiophlebia* plus Anisoptera (Rehn 2003; Kalkman et al. 2008; Dijkstra et al. 2013, 2014; Schorr and Paulson 2020).

The field of Odonata cytogenetics was heavily influenced by Bastiaan Kiauta, who has published dozens of papers and analyzed karyotypes of about 260 species and subspecies of this group (see References and Table 1). During the years that have passed since the publication of chromosome number checklist of Odonata (Kiauta 1972c), approximately 90 chromosome papers have been published. The number of examined species has since increased by more than 2.3 times, and now it seems appropriate to publish an updated list. In this review article, all data available today are presented in two tables and one figure. Table 1 includes all species studied so far cytogenetically and compiles data on their chromosome numbers, sex chromosome mechanisms and the occurrence of the so-called m-chromosomes (= microchromosomes). Table 2 summarizes data presented in Table 1 and shows the family-level variability of the above-mentioned traits (except m-chromosomes, since data on their presence or absence in specific species are often questionable) together with the most characteristic (modal) karyotypes for each of the families explored. On the Fig. 1, the modal karyotypes are mapped onto phylogenetic tree of Odonata families taken from Bybee et al. (2016) who in turn redrawn and synthesized it from Dijkstra et al. (2014) and Carle et al. (2015). In the final section of the review, the main characteristics of Odonata karyotypes are briefly discussed and prospects for future research are outlined.
Table 1. Cytogenetically analyzed species of Odonata and their main karyotype characteristics (chromosome numbers, sex chromosomes, m-chromosomes).

| Taxon                     | Karyotype formula 2n | m-chromosomes | Country | References                     |
|---------------------------|----------------------|---------------|---------|--------------------------------|
| **Anisogryoptera**        |                      |               |         |                                |
| **Ephippiobiidae**        |                      |               |         |                                |
| 1. *Ephippia superbus* Selys, 1889 | 25(24A+X)          | –             | Japan   | Oguma 1951                     |
| **Anisoptera**            |                      |               |         |                                |
| **Aeshnidae**             |                      |               |         |                                |
| 2. *Aeshna caerules* (Ström, 1783) | 24(22A+neo-XY)   | –             | Finland | Cruden 1968                     |
| 3. A. canadiensis Walker, 1908 | 27(26A+X)          | +             | USA     | Hung 1971                       |
| 4. A. clepsydra Say, 1839  | 27(26A+X)           | +             | USA     | Bruun et al. 1980               |
| 5. A. creata Hagen, 1856   | 27(26A+X)           | +             | Finland | Oksala 1939a, 1943, 1944, 1952  |
| 6. A. cyanura (Müller, 1764) | 27(26A+X)          | –             | Finland | Oksala 1943                     |
| 7. A. grandis (Linnaeus, 1758) | 27(26A+X)          | +             | USSR    | Makalowska 1940                 |
| 8. A. isceles (Müller, 1767) | 27(26A+X)          | –             | USA     | Kuznetsova et al. 2002          |
| 9. A. juncea (Linnaeus, 1758) | 25(24A+X)          | –             | USSR    | Makalowska 1940                 |
| 10. A. mixta Latreille, 1805| 27(26A+X)          | +             | India   | Sandhu and Maihotra 1994a       |
| 11. A. nigroflava Martin, 1909| 27(26A+X)          | +             | Japan   | Katsuura 1987                   |
| 12. A. palinata Hagen, 1856| 27(26A+X)          | –             | USA     | Cruden 1968                     |
| 13. A. serrata Hagen, 1856 | 26(24A+neo-XY)      | +             | Finland | Oksala 1943 as *A. s. nana*     |
| 14. A. subarcata Walker, 1908| 27(26A+X)          | +             | USA     | Oksala 1939a, 1943, 1952 as     |
| 15. A. umbrosa Walker, 1908| 27(26A+X)          | +             | USA     | A. s. occidentalis Walker, 1908 |
| Taxon | Karyotype | m-chromosomes | Country | References |
|-------|-----------|---------------|---------|------------|
| 23.  | A. guttatus (Burmeister, 1839) | 15(14A+X) | + | Nepal | Kiauta and Kiauta 1982 |
| 24.  | A. immaculiformis Rambur, 1842 | 27(26A+X) | + | India | Sangal and Tyagi 1982 |
| 25.  | A. imperator Leach, 1815 | 27(26A+X) | + | France | Kiauta 1965, 1969a |
| 26.  | A. junius (Drury, 1773) | 27(26A+X) | + | USA | McGill 1904, 1907 |
| 27.  | A. longipes Hagen, 1861 | 27(26A+X) | + | USA | Cruden 1968 |
| 28.  | A. nigrofasciatus Ogama, 1915 | 27(26A+X) | + | Nepal | Kiauta 1974, 1975 |
| 29.  | A. papuensis (Burmeister, 1839) | 27(26A+X) | + | Australia | Kiauta 1968c, 1969a as Hemianax papuensis (Burmeister, 1839) |
| 30.  | A. parthenope (Selys, 1839) | 27(26A+X) | + | Japan | Omura 1957 as A. parthenope julius Brauer, 1865 |
| 31.  | Andaeschna unicolor (Martin, 1908) | 27(26A+X) | + | Bolivia | Cuming 1964 as Aeshna cf. unicolor Martin, 1908 |
| 32.  | Austroaeschna anacantha Tillyard, 1908 | 27(26A+X) | + | Australia | Kiauta 1968c as Acanthaeschna anacantha (Tillyard, 1908) |
| 33.  | A. multipunctata (Martin, 1901) | 27(26A+X) | + | Australia | Kiauta 1968c as Acanthaeschna multipunctata (Martin, 1901) |
| 34.  | Basiaeschna janata (Selys, 1883) | 25(24A+X) | – | USA | Cruden 1968 |
| 35.  | Boyeria maclachlani (Selys, 1883) | 27(26A+X) | + | Japan | Omura 1957 |
| 36.  | B. vinao (Selys, 1839) | 27(26A+X) | – | USA | Cruden 1968 |
| 37.  | Caliaeschna microstigma (Schneider, 1845) | 16(14A+neo-XY) | + | Greece | Kiauta 1972a |
| 38.  | Castoraeschna cautor (Brauer, 1865) | 27(26A+X) | + | Brazil | Kiauta 1972b |
| 39.  | Cephalaeschna orbifrons Selys, 1883 | 25(24A+X) | + | Nepal | Kiauta 1975 |
| 40.  | Cephalaeschna sp. | 25(24A+X) | + | India | Sandhu and Malhotra 1994a |
| 41.  | Coryphaeschna adnata (Hagen, 1961) | 27(26A+X) | – | Bolivia | Cuming 1964 |
| 42.  | C. perrensi (McLachlan, 1887) | 25(24A+X) | – | Argentina | Capitulo et al. 1991 |
| 43.  | C. viriditas Calvert, 1952 | 23(22A+X) | + | Surinam | Kiauta 1979a |
| 44.  | Gynacantha bupadora Selys, 1891 | 25(24A+X) | + | India | Wala 2007 as G. millardi Brauer, 1936 |
| 45.  | G. hyalina Selys, 1882 | 28(26A+XX)* | + | Japan | Iyagi 1978a, b |
| 46.  | G. intermedius Williamson, 1923 | 26(24A+neo-XY) | + | Surinam | Kiauta 1979a |
| 47.  | G. japonica Bartenev, 1909 | 27(26A+X) | + | Japan | Omura 1957 |
| 48.  | Gynacanthaeschna sikkesma (Karsch, 1891) | 27(26A+X) | + | India | Wala et al. 2016 |
| 49.  | Oplonaeschna armata (Hagen, 1861) | 27(26A+X) | + | Mexico | Kiauta 1970a |
| 50.  | Planoeschna milnei (Selys, 1883) | 27(26A+X) | + | Japan | Kiauta 1968c, 1969a |
| 51.  | R. luteipennis (Burmeister, 1839) | 25(24A+X) | + | Surinam | Kiauta 1979a as Coryphaeschna l. luteipennis (Burmeister, 1839) |
| 52.  | R. bonariensis (Rambur, 1842) | 26(24A+neo-XY) | + | Argentina, Uruguay | Mola and Papeschi 1994 as Aeshna bonariensis Rambur, 1842 |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|---------------------|---------------|---------|------------|
| 52. *Rhionaeschna bonariensis* (Rambur, 1842) | 2n=50 | + | Argentina, Uruguay | Mola 1995 as *A. bonariensis* |
| 53. *Rh. californica* (Calvert, 1895) | 27(26A+X) | + | Canada | Kiauta 1973a as *Aeschna californica* Calvert, 1895 |
| 54. *Rh. confusa* (Rambur, 1842) | 27(26A+X) | + | Argentina, Uruguay | Mola and Papeschi 1994 as *Aeshna confusa* Rambur, 1842 |
| 55. *Rh. diffinis* (Rambur, 1842) | 21(20A+X) | + | Bolivia | Cumming 1964 as *Aeshna d. diffinis* Rambur, 1842 |
| 56. *Rh. intricata* (Martin, 1908) | 19(18A+X) | + | Bolivia | Cumming 1964 as *Aeshna intricata* Martin, 1908 |
| 57. *Rh. peralta* (Ris, 1918) | 27(26A+X) | + | Bolivia | Cumming 1964 as *Aeshna peralta* Ris, 1918 |
| 58. *Rh. planaltica* (Calvert, 1945) | 16(14A+neo-XY) | + | Argentina | Mola and Papeschi 1994 as *Aeshna cornigera planaltica* Calvert, 1952 |
| 59. *Staurophlebia reticulata* (Burmeister, 1839) | 27(26A+X) | + | Brazil | Souza Bueno 1982 (*S. r. reticulata* (Burmeister, 1839)) |
| 60. *Tachopteryx thoreyi* (Hagen, 1857) | 19(18A+X) | + | USA | Cumming 1964 |
| 61. *Tanypteryx hageni* (Selys, 1879) | 17(16A+X) | + | USA | Cruden 1968 |
| 62. *T. pryeri* (Selys, 1889) | 17(16A+X) | + | Japan | Kichijo 1939, 1942a |
| 63. *Uropetala carover* (White, 1846) | 17(16A+X)** | + | New Zealand | Wolfe 1953 |
| 64. *Anisogomphus bivittatus* (Selys, 1854) | 23(22A+X) | + | India | Das 1956 |
| 65. *A. occipitalis* (Selys, 1854) | 23(22A+X) | + | India | Walia and Chahal 2020 |
| 66. *Aphylla edentata* Selys, 1869 | 23(22A+X) | + | Bolivia | Cuming 1964 |
| 67. *A. producta* Selys, 1854 | 23(22A+X) | + | Bolivia | Cuming 1964 |
| 68. *A. theodorina* (Navas, 1933) | 23(22A+X) | + | Surinam | Kiauta 1979a |
| 69. *A. williamsoni* (Gloyd, 1936) | 23(22A+X) | + | USA | Kiauta and Brink 1978 |
| 70. *Aphylla sp.* | 23(22A+X) | + | Argentina | Mola 2007 |
| 71. *Arigomphus lentulus* (Needham, 1902) | 23(22A+X) | + | USA | Cruden 1968 as *Gomphus lentulus* Needham, 1902 |
| 72. *A. pallidus* (Rambur, 1842) | 23(22A+X) | + | USA | Cumming 1964 as *Gomphus pallidus* Rambur, 1842 |
| 73. *A. submedianus* (Williamson, 1914) | 23(22A+X) | + | USA | Cruden 1968 as *Gomphus submedianus* Williamson, 1914 |
| 74. *Asiagomphus melanoops* (Selys, 1854) | 23(22A+X) | + | Japan | Toyoshima and Hirai 1953 as *Gomphus melanoops* Selys, 1854 |
| 75. *Burmagomphus pyramidalis* Laidlaw, 1922 | 23(22A+X) | + | India | Tyagi 1977 |
| 76. *Davidius nanus* (Selys, 1869) | 23(22A+X) | + | Japan | Kichijo 1939, 1942a |
| 77. *Dromogomphus spinosus* (Selys, 1854) | 23(22A+X) | + | USA | Cruden 1968 |
| 78. *D. spilatus* (Hagen, 1857) | 23(22A+X) | + | USA | Cruden 1968 |
| 79. *Epigomphus llama* Calvert, 1903 | 23(22A+X) | + | Bolivia | Cuming 1964 |
| 80. *Erpetogomphus designatus* Hagen, 1857 | 23(22A+X) | + | USA | Cuming 1964 |
| 81. *E. diadophis* Calvert, 1905 | 23(22A+X) | + | USA | Cuming 1964 |
| 82. *E. ophiodorus* Calvert, 1905 | 23(22A+X) | + | Mexico | Kiauta 1970a |
| 83. *Gomphoides sp.* | 23(22A+X) | + | Bolivia | Cuming 1964 |
| 84. *Gomphus confusus* Selys, 1873 | 23(22A+X) | + | USA | Cruden 1968 |
| 85. *G. exilis* Selys, 1854 | 23(22A+X) | + | USA | Cruden 1968 |
| 86. *G. gealini* Rambur, 1842 | 12(10A+neo-neo-XY) | + | France | Kiauta 1968d, 1969a |
| Taxon                                | Karyotype formula 2n | m-chromosomes | Country       | References                                           |
|--------------------------------------|----------------------|---------------|---------------|------------------------------------------------------|
| 87. G. pulchellus Selys, 1840         | 2n(22A+X)            | +             | France        | Kiauta 1973b                                         |
| 88. G. vulgarissimus (Linnaeus, 1758) | 2n(22A+X)            | –             | Russia        | Perepelov et al. 2001                                |
| 89. Ictinogomphus t Corpus (Rambur, 1942) | 2n(22A+X)            | +             | India         | Asana and Makino 1935                                |
| 90. N. pulchellus Selys, 1878         | 2n(22A+X)            | –             | India         | Walia et al. 2006                                    |
| 91. N. vulgarissimus (Linnaeus, 1758) | 2n(22A+X)            | –             | Russia        | Perepelov et al. 2001                                |
| 92. N. viridis Selys, 1878            | 2n(22A+X)            | –             | Japan         | Omura 1957                                           |
| 93. Ictinogomphus rapax (Rambur, 1942) | 2n(22A+X)            | +             | India         | Kichijo 1942a                                        |
| 94. N. modestus Selys, 1878           | 2n(22A+X)            | +             | India         | Dasgupta 1957                                        |
| 95. Ictinogomphus forcipatus (Linnaeus, 1758) | 2n(22A+X)            | –             | India         | Tyagi 1977                                           |
| 96. O. saussurii Selys, 1854          | 2n(22A+X)            | +             | Austria       | Kiauta 1969a                                        |
| 97. Ophiogomphus bicornis (Selys, 1873) | 2n(22A+X)            | –             | USA           | Cruden 1968                                          |
| 98. O. cecilia (Fourcroy, 1785)       | 2n(22A+X)            | –             | Finland       | Kiauta 1969a                                        |
| 99. O. pulchellus Selys, 1840         | 2n(22A+X)            | +             | USA           | Cruden 1968                                          |
| 100. O. tigrinus Selys, 1854          | 2n(22A+X)            | –             | USA           | Cruden 1968                                          |
| 101. O. obscurus Bartenev, 1909       | 2n(22A+X)            | –             | Russia        | Perepelov and Bugrov 2001b                           |
| 102. O. punctulatus (Walsh, 1862)     | 2n(22A+X)            | –             | USA           | Cruden 1968                                          |
| 103. Paragomphus lividus (Selys, 1854) | 2n(22A+X)            | +             | USA           | Cruden 1968 as Gomphus lividus Selys, 1854           |
| 104. Ph. gently (Hagen, 1854)         | 2n(22A+X)            | –             | USA           | Cruden 1968 as Gomphus militaris Hagen, 1854          |
| 105. Ph. spicatus (Selys, 1854)       | 2n(22A+X)            | +             | USA           | Cruden 1968 as Gomphus spicatus Selys, 1854          |
| 106. Paragomphus lineatus (Selys, 1850) | 2n(22A+X)            | –             | Nepal         | Kiauta 1974, 1975                                   |
| 107. P. capricornis (Förster, 1914)   | 2n(22A+X)            | –             | Thailand      | Kiauta and Chaal 2014                                |
| 108. Phyllocyclus propinqua Belle, 1972 | 2n(22A+X)            | +             | Argentina     | De Gennaro 2004                                     |
| 109. Phyllocyclus sp.                 | 2n(22A+X)            | –             | Bolivia       | Cumming 1964                                        |
| 110. Phyllocyclus sp. 1              | 2n(22A+X)            | +             | Argentina     | Mola 2007                                            |
| 111. Phyllocyclus sp. 2              | 2n(22A+X)            | –             | Argentina     | Mola 2007                                            |
| 112. Phyllogomphoides undulatus (Needham, 1944) | 2n(22A+X)            | +             | Suriname      | Kiauta 1979a                                        |
| 113. Progomphus borealis McLachlan, 1873 | 2n(22A+X)            | –             | USA           | Cruden 1968                                          |
| 114. P. intricatus (Hagen, 1857)      | 2n(22A+X)            | –             | Bolivia       | Cumming 1964                                        |
| 115. P. obscurus (Kambur, 1942)       | 2n(22A+X)            | –             | USA           | Cruden 1968                                          |
| 116. P. phylachromus Roi, 1918        | 2n(22A+X)            | +             | Bolivia       | Cumming 1964                                        |
| 117. Scalmogomphus biregatus (Hagen, 1854) | 2n(22A+X)            | –             | Nepal         | Kiauta 1974, 1975 as Onychogomphus biregatus (Hagen, 1854) |
| 118. Shaogomphus postocularis (Selys, 1869) | 2n(22A+X)            | +             | Japan         | Omura 1957 as Gomphus postocularis Selys, 1869       |
| 119. Sieboldius alboaris Selys, 1886  | 2n(22A+X)            | +             | Russia        | Perepelov et al. 2001 as Gomphus ephippia Selys, 1872 |
| 120. Stylogomphus suzukii (Matsumura, 1926) | 2n(22A+X)            | +             | Japan         | Omura 1957                                          |
| 121. Stylocnus filipes (Charpentier, 1825) | 2n(22A+X)            | +             | Japan         | Omura 1957                                          |
| 122. S. plagius Selys, 1854           | 2n(22A+X)            | +             | Russia        | Perepelov and Bugrov 2001b                           |
| 123. S. scudderi Selys, 1873          | 2n(22A+X)            | –             | USA           | Cruden 1968 as Gomphus scudder Selys, 1873            |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 124. S. townesi Gloyd, 1936 | 2(20A+neo-X+Y) | - | USA | Kiauta and Brink 1978 as Gomphus townesi Gloyd, 1936 |
| 125. Temnogomphus kivitattu (Selys, 1854) | 23(22A+X) | + | Nepal | Kiauta 1975 |
| 126. Trigomphus ritinus (Needham, 1931) | 21(20A+X) | + | Japan | Toyoshima and Hirai 1953 (T.c. tabei Asahina, 1949) |
| 127. T. interruptus (Selys, 1854) | 19(18A+X) | + | Japan | Okuma 1930 |
| 128. T. melampus (Selys, 1869) | 21(20A+X) | - | Japan | Okuma 1930, 1942 as T. unifasciatus (Okuma 1926) |
| 129. Zonophora callipus Selys, 1869 | 23(22A+X) | + | Surinam | Kiauta 1979a |

**Macromiidae**

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 130. Didynops transversa (Say, 1839) | 25(24A+X) | + | USA | Cruden 1968 |
| 131. Epoptohelmina frontalis (Selys, 1871) | 25(24A+X) | + | India | Dasgupta 1957 (E. f. frontalis (Selys, 1871)) |
| 132. Macromia daimoji Okumura, 1949 | 25(24A+X) | - | Japan | Katatani 1987 |
| 133. M. magnifica (McLachlan, 1874) | 25(24A+X) | + | USA | Cruden 1968 |
| 134. M. moorei Selys, 1874 | 25(24A+X) | - | USA | Kiauta 1977 |

**Corduliidae**

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 135. Cordulia senea (Linnaeus, 1758) | 25(24A+X) | - | Finland | Oksala 1939a |
| 137. C. shurtleffii Scudder, 1866 | 25(24A+X) | + | USA | Cruden 1968 |
| 138. Dorocordulia libera (Selys, 1871) | 11(10A+X) | - | USA | Cruden 1968 |
| 139. Epicordulia princeps (Hagen, 1861) | 25(24A+X) | + | USA | Hung 1971 |
| 140. Epitheca bimaculata (Charpentier, 1825) | 25(24A+X) | - | Russia | Perepelov 2003 |
| 141. E. canis McLachlan, 1886 | 25(24A+X) | + | USA | Cruden 1968 |
| 142. E. spinigera (Selys, 1871) | 25(24A+X) | - | USA | Cruden 1968 |
| 143. E. petechialis (Murtkowski, 1911) | 21(20A+X) | - | USA | Cumming 1964 as Tetragnenewia petechialis Murtkowski, 1911 |
| 144. E. persica (Burmeister, 1839) | 25(24A+X) | - | USA | Cruden 1968 |
| 145. E. spinigera (Selys, 1871) | 25(24A+X) | + | USA | Cruden 1968 |
| 146. Procordulia graysi (Selys, 1871) | 25(24A+X) | + | New Zealand | Jensen 1980 |
| 147. P. smithii (White, 1846) | 25(24A+X) | + | New Zealand | Jensen 1980 |
| 148. Rialia vilina Rambur, 1842 | 25(24A+X) | + | Argentina | De Gennaro 2004 |
| 149. Somatochlora alpinae (Selys, 1840) | 25(24A+X) | - | Switzerland | Kiauta and Kiauta 1980a |
| 150. S. arctica (Zetterstedt, 1840) | 25(24A+X) | + | Russia | Perepelov 2003 |
| 151. S. bontii Marinov, 2001 | 20(18A+XY) | - | Bulgaria | Grozeva and Marinov 2007 |
| 152. S. flavomaculata (Van der Linden, 1825) | 25(24A+X) | + | Former USSR | Makalowskaia 1940 |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|---------------------|---------------|---------|------------|
| 153. S. graeseri Selys, 1887 | 25(24A+X) | – | Russia | Perepelov et al. 2001 |
| 154. S. meridianalis Nielsen, 1935 | 25(24A+X) | – | Slovenia | Kiauta and Kiauta 1995 |
| 155. S. metallica (Van der Linden, 1825) | 26(24A+XX)* | – | Finland | Oksala 1945 |
| 156. S. semicirculata (Selys, 1871) | 25(24A+X) | – | USA | Cruden 1968 |
| 157. S. uchidai Fürster, 1909 | 25(24A+X) | + | Japan | Oguma 1915, 1930 |
| 158. S. viridissima (Uhler, 1858) | 25(24A+X) | – | Japan | Oguma 1915, 1930 |

**Libellulidae**

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|---------------------|---------------|---------|------------|
| 159. Acisoma panorpoides Rambur, 1842 | 25(24A+X) | + | Bangladesh, India | Dasgupta 1957 (A. p. panorpoides) |
| 160. Aethriamanta brevipennis (Rambur, 1842) | 25(24A+X) | + | India | Dasgupta 1957 |
| 161. Anthopteryx guttata (Erichson, 1848) | 25(24A+X) | – | Surinam | Kiauta 1979a |
| 162. Atocoreura litorinae Karsch, 1899 | 21(20A+X) | + | Sudan | Wasscher 1985 |
| 163. Brachydiplax chalybea Breuer, 1868 | 25(24A+X) | + | India | Dasgupta 1957 |
| 164. B. farinosa Krueger, 1902 | 25(24A+X) | + | India | Dasgupta 1957 |
| 165. B. sobrina (Rambur, 1842) | 25(24A+X) | + | India | Ray Chandhuri and Dasgupta 1949 |
| 166. Brachymesia furcata (Hagen, 1861) | 25(24A+X) | + | Surinam | Kiauta 1979a |
| 167. B. gravida (Calvert, 1890) | 25(24A+X) | + | USA | Dasgupta 1957 (C. p. panorpoides) |
| 168. B. peruviana (Rambur, 1842) | 25(24A+X) | + | Republic of South Africa | Boys et al. 1980 |
| 169. B. nubecula (Rambur, 1842) | 25(24A+X) | + | India | Dasgupta 1957 |
| 170. B. lucidula (Hagen, 1861) | 25(24A+X) | + | India | Dasgupta 1957 |
| 171. B. persimilis (Hagen, 1861) | 25(24A+X) | + | India | Dasgupta 1957 |
| 172. B. nubecula (Rambur, 1842) | 25(24A+X) | + | Bolivia | Cumming 1964 |
| 173. B. persimilis (Hagen, 1861) | 25(24A+X) | + | Bolivia | Cumming 1964 |
| 174. C. asiatica Kirby, 1889 | 25(24A+X) | + | USA | Cumming 1964 (R. p. persimilis) |
| 175. C. asiatica Kirby, 1889 | 25(24A+X) | + | USA | Cumming 1964 (R. p. persimilis) |
| 176. C. asiatica Kirby, 1889 | 25(24A+X) | + | USA | Cumming 1964 (R. p. persimilis) |
| 177. C. asiatica Kirby, 1889 | 25(24A+X) | + | USA | Cumming 1964 (R. p. persimilis) |

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| Taxon                          | Karyotype formula | m-chromosomes | Country                  | References                           |
|-------------------------------|-------------------|---------------|--------------------------|--------------------------------------|
| C. ornata (Rambur, 1842)      | 25(24A+X)         | +             | USA                      | Kiauta and Brink 1978                |
| Crocothemis erythraea (Brulle, 1832) | 25(24A+X)         | +             | India                    | Dasgupta 1957                        |
|                               |                   | +             | Italy                    | Kiauta 1971a                         |
|                               |                   | +             | India                    | Prasad and Thomas 1992               |
|                               |                   | +             | Republic of South Africa | Boyes et al. 1980                    |
| C. sanguinolenta (Burmeister, 1839) | 25(24A+X)         | +             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980                    |
| C. servilia (Drury, 1773)     | 25(24A+X)         | +             | India                    | Asana and Makino 1935                |
|                               |                   | +             | India                    | Makino 1935                          |
|                               |                   | +             | India                    | Kichijo 1942b                        |
|                               |                   | +             | India                    | Ray Chaudhuri and Dasgupta 1949      |
|                               |                   | +             | Nepal                    | Kiauta 1975                          |
|                               |                   | +             | Philippines              | Kiauta and Kiauta 1980b              |
|                               |                   | +             | Nepal                    | Kiauta and Kiauta 1982               |
|                               |                   | +             | India                    | Tyagi 1982                           |
|                               |                   | +             | Thailand                 | Kiauta and Kiauta 1983               |
|                               |                   | +             | Japan                    | Katatani 1987                        |
|                               |                   | +             | Japan                    | Higashi and Kayano 1993              |
|                               |                   | +             | Japan                    | Omura 1955                           |
|                               |                   | +             | Japan                    | Kiauta 1983                          |
|                               |                   | +             | Japan                    | Kiauta 1983                          |
|                               |                   | +             | Japan                    | Higashi et al. 2001                  |
|                               |                   | +             | Bolivia                  | Cumming 1964                         |
|                               |                   | +             | Brazil                   | Souza Bueno 1982                     |
| D. venosa (Burmeister, 1839)  | 25(24A+X)         | +             | Brazil                    | Kiauta and Boyes 1972                |
| D. obscura (Fabricius, 1775)  | 25(24A+X)         | +             | Bolivia                  | Cumming 1964                         |
| D. pullata (Burmeister, 1839) | 23(22A+X)         | +             | Surinam                  | Kiauta 1979a                         |
| D. haematodes (Burmeister, 1839) | 25(24A+X)         | +             | Australia                | Kiauta 1969b                         |
| D. lefebvrei (Rambur, 1842)   | 25(24A+X)         | +             | Madagascar               | Kiauta 1968c, 1969b                  |
| D. nebulea (Fabricius, 1793)  | 25(24A+X)         | +             | India                    | Dasgupta 1957                        |
| D. trivialis (Rambur, 1842)   | 25(24A+X)         | +             | India                    | Asana and Makino 1935                |
|                               |                   | +             | India                    | Makino 1935                          |
| D. rufinefris (Burmeister, 1839) | 25(24A+X)         | +             | Jamaica                  | Cumming 1964                         |
| D. velox Hagen, 1861          | 25(24A+X)         | +             | Bolivia                  | Cumming 1964                         |
| E. williamsoni (Ris, 1919)    | 22(20A+neo-XY)     | –             | Surinam                  | Kiauta 1979a as Dythemis williamsoni (Ris, 1919) |

Karyotypes of Odonata: a check-list
## Taxon Karyotype

### formula 2n  ♂

### m-chromaticosomes

### Country

### References

| Taxon                                      | Karyotype formula 2n  ♂ | m-chromosomes | Country     | References                  |
|--------------------------------------------|------------------------|---------------|-------------|-----------------------------|
| 201. *Erythemis attala* (Selys, 1857)       | 25(24A+X)              | –             | Bolivia     | Cumming 1964                |
|                                            |                        |               | Argentina   | Agopian and Mola 1988       |
| 202. *E. colourata* (Hagen, 1861)           | 25(24A+X)              | +             | USA         | Cruden 1968                 |
| 203. *E. crochita* (Hagen, 1861)            | 25(24A+X)              | +             | Surinam     | Kiauta 1979a                |
| 204. *E. buenasargentina* (Burmeister, 1839) | 25(24A+X)              | –             | Surinam     | Kiauta 1979a                |
| 205. *E. peruviana* (Rambur, 1842)          | 25(24A+X)              | –             | Surinam     | Kiauta 1979a                |
| 206. *E. plebeja* (Burmeister, 1839)        | 25(24A+X)              | –             | Bolivia     | Cumming 1964                |
| 207. *E. simplicicollis* (Say, 1839)        | 25(24A+X)              | +             | USA         | Cruden 1968                 |
| 208. *E. vesiculosa* (Fabricius, 1775)      | 25(24A+X)              | –             | Bolivia     | Cumming 1964 as *Lepthemis vesiculosa* (Fabricius, 1775) |
|                                            |                        |               | Surinam     | Kiauta 1979a as *L. vesiculosa* |
|                                            |                        |               | Brasil      | Ferreira et al. 1979 as *L. vesiculosa* |
| 209. *Erythrodiplax anomala* (Brauer, 1865) | 25(24A+X)              | +             | Brazil      | Souza Bueno 1982            |
| 210. *E. atrouterminata* Ris, 1911           | 25(24A+X)              | +             | Uruguay     | Goni and Abenante 1982      |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 211. *E. attenuata* (Kirby, 1889)           | 25(24A+X)              | +             | Surinam     | Kiauta 1979a                |
|                                            |                        |               | Brasil      | Ferreira et al. 1979 (E. b. basalis (Kirby, 1897)) |
| 212. *E. basalis* (Kirby, 1897)             | 25(24A+X)              | –             | Bolivia     | Cumming 1964                |
|                                            |                        |               | Surinam     | Kiauta 1979a (E. b. basalis (Kirby, 1897)) |
|                                            |                        |               | Brasil      | Ferreira et al. 1979 (E. b. basalis (Kirby, 1897)) |
| 213. *E. berenice* (Drury, 1770)            | 25(24A+X)              | –             | USA         | Cruden 1968                 |
|                                            |                        |               | USA         | Hung 1971                   |
| 214. *E. catanae* (Burmeister, 1839)        | 25(24A+X)              | –             | Bolivia     | Cumming 1964                |
| 215. *E. chromopterus* Borror, 1942         | 23(22A+X)              | +             | Uruguay     | Goni and Abenante 1982      |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 216. *E. cleopatra* Ris, 1911               | 25(24A+X)              | +             | Peru        | Kiauta and Boyes 1972       |
| 217. *E. connata* (Burmeister, 1839)        | 25(24A+X)              | +             | Chile       | Kiauta and Boyes 1972 (E. c. connata (Burmeister, 1839)) |
|                                            |                        |               | USA         | Kiauta and Brink 1978 (E. c. minuscule (Rambur, 1842)) |
|                                            |                        |               | Surinam     | Kiauta and Brink 1978 (E. c. minuscule (Rambur, 1842)) |
|                                            |                        |               | Brasil      | Ferreira et al. 1979 as *E. c. minuscule* (Rambur, 1842) |
|                                            |                        |               | Argentina   | Capitulo et al. 1991        |
|                                            |                        |               | Brasil      | Ferreira et al. 1979 (E. c. minuscule (Rambur, 1842)) |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 220. *E. fusca* (Rambur, 1842)              | 25(24A+X)              | –             | Bolivia     | Cumming 1964 as *E. connata fusca* (Rambur, 1842) |
|                                            |                        |               | Guatemala   | Cruden 1968 as *E. c. fusca* |
|                                            |                        |               | Surinam     | Kiauta 1979a as *E. c. fusca* |
|                                            |                        |               | Brasil      | Ferreira et al. 1979 as *E. c. fusca* |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 221. *E. fervida* (Erichson, 1848)          | 25(24A+X)              | +             | Argentina   | Mola 1996                   |
| 222. *E. justinsiana* Selys, 1857           | 25(24A+X)              | +             | Jamaica     | Cumming 1964                |
| 223. *E. juliana* Ris, 1911                 | 25(24A+X)              | +             | Brazil      | Souza Bueno 1982            |
| 224. *E. latermaculata* Ris, 1911           | 25(24A+X)              | +             | Surinam     | Kiauta 1979a                |
|                                            |                        |               | Brasil      | Ferreira et al. 1979        |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 225. *E. lygea* Ris, 1911                   | 25(24A+X)              | +             | Argentina   | Capitulo et al. 1991        |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 226. *E. media* Borror, 1942                | 21(20A+X)              | +             | Bolivia     | Cumming 1964                |
|                                            |                        |               | Brasil      | Kiauta and Boyes 1972       |
|                                            |                        |               | Argentina   | Capitulo et al. 1991        |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 227. *E. melanorubra* Borror, 1942          | 25(24A+X)              | +             | Bolivia     | Cumming 1964                |
|                                            |                        |               | Venezuela   | Kiauta and Boyes 1972       |
|                                            |                        |               | Argentina   | Capitulo et al. 1991        |
|                                            |                        |               | Argentina   | Mola 1996                   |
| 228. *E. minuscula* (Rambur, 1842)          | 25(24A+X)              | +             | USA         | Kiauta and Brink 1978       |
|                                            |                        |               | Argentina   | Mola and Agopian 1985       |
| 229. *E. nigricans* (Rambur, 1842)          | 25(24A+X)              | +             | Uruguay     | Goni and Abenante 1982      |
| Taxon                                | Karyotype formula 2n | m-chromosomes | Country       | References                  |
|--------------------------------------|----------------------|---------------|--------------|-----------------------------|
| 229. *E. nigricans* (Rambur, 1842)   | 25(24A+X)            | +             | Argentina    | Mola 1996                   |
|                                      | 25(24A+X)            | −             | Argentina    | De Gennaro 2004             |
|                                      | 25(24A+X)            | +             | Argentina    | De Gennaro et al. 2008      |
| 230. *E. ochracea* (Burmeister, 1839)| 23(22A+X)            | +             | Bolivia      | Cumming 1964                |
|                                      | 23(22A+X)            | +             | Dominica     | Cruden 1968                 |
|                                      | 23(22A+X)            | +             | Surinam      | Kiauta 1979a                |
| 231. *E. paraguayensis* (Foerster, 1904) | 25(24A+X)            | +             | Bolivia      | Cumming 1964                |
|                                      | 25(24A+X)            | +             | Dominica     | Cruden 1968                 |
|                                      | 25(24A+X)            | +             | Surinam      | Kiauta 1979a                |
|                                      | 25(24A+X)            | +             | Brazil       | Ferreira et al. 1979        |
| 232. *E. umbrata* (Linnaeus, 1758)  | 23(22A+X)            | +             | Bolivia      | Cumming 1964                |
|                                      | 23(22A+X)            | +             | Dominica     | Cruden 1968                 |
|                                      | 23(22A+X)            | +             | Surinam      | Kiauta 1979a                |
|                                      | 23(22A+X)            | +             | Brazil       | Ferreira et al. 1979        |
| 233. *E. unimaculata* (DeGeer, 1773) | 25(24A+X)            | −             | Bolivia      | Cumming 1964                |
|                                      | 25(24A+X)            | +             | Bolivia      | Cumming 1964                |
|                                      | 25(24A+X)            | +             | Dominica     | Cruden 1968                 |
|                                      | 25(24A+X)            | +             | Surinam      | Kiauta 1979a                |
|                                      | 25(24A+X)            | +             | Brazil       | Ferreira et al. 1979        |
| 234. *Hydrobasileus croceus* (Brauer, 1867) | 26(24A+XX)*          | +             | India        | Prasad and Thomas 1992      |
| 235. *Ladona julia* (Uhler, 1857)    | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 236. *Lathrecista asiatica* (Fabricius, 1798) | 25(24A+X)            | +             | India        | Dasgupta 1957               |
| 237. *Leucorrhina alxbiron* (Burmeister, 1839) | 25(24A+X)            | +             | India        | Tyagi 1982                  |
| 238. *L. dubia* (Van der Linden, 1825) | 26(24A+XX)*          | −             | Finland      | Oksala 1939a, 1945          |
| 239. *L. frigida* Hagen, 1890        | 21(20A+X)            | +             | USA          | Cruden 1968                 |
| 240. *L. glacialis* Hagen, 1890      | 23(22A+X)            | +             | USA          | Cruden 1968                 |
| 241. *L. hudsonica* (Selys, 1830)    | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 242. *L. intacta* (Hagen, 1861)      | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 243. *L. pectoralis* (Charpentier, 1825) | 26(24A+XX)*          | −             | Finland      | Oksala 1939a, 1945          |
| 244. *L. proxima* Calvert, 1890      | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 245. *L. rubicunda* (Linnaeus, 1857) | 25(24A+X)            | −             | Finland      | Oksala 1939a, 1945          |
| 246. *Libellula angelinea* Selys, 1883 | 25(24A+X)            | +             | Japan        | Oguma 1915, 1930             |
|                                      | 25(24A+X)            | +             | Japan        | Kichijo 1942a               |
| 247. *L. auripennis* Burmeister, 1839 | 25(24A+X)            | +             | USA          | Kiauta and Brink 1978       |
| 248. *L. axilena* Westwood, 1837     | 25(24A+X)            | +             | USA          | Cumming 1964                |
| 249. *L. basalis* (Say, 1840)        | 25(24A+X)            | −             | USA          | Smith 1916                  |
| 250. *L. composita* Hagen, 1873      | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 251. *L. croceipennis* Selys, 1868   | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 252. *L. cyanea* Fabricius, 1775     | 25(24A+X)            | −             | USA          | Cruden 1968                 |
| 253. *L. depressa* Linnaeus, 1758    | 23(22A+X)            | −             | Belgium      | Carnoy 1885                 |
|                                      | 25(24A+X)            | −             | England      | Hogben 1921                 |
|                                      | 25(24A+X)            | −             | Austria      | Kiauta 1968c, 1969b         |
|                                      | 23(22A+X)            | −             | Croatia      | Francovi and Jurčič 1986, 1989 |
|                                      | 25(24A+X)            | +             | Russia       | Perepelov et al. 1998       |
| 254. *L. flatida* Rambur, 1842       | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 255. *L. forestis* Hagen, 1861       | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 256. *L. fulva* Muller, 1764         | 25(24A+X)            | +             | Switzerland  | Kiauta and Kiauta 1979      |
|                                      | 27(26A+X)            | +             | Croatia      | Francovi and Jurčič 1986, 1989 |
| 257. *L. insecta* Hagen, 1861        | 25(24A+X)            | −             | USA          | Cumming 1964                |
|                                      | 25(24A+X)            | +             | USA          | Cruden 1968                 |
| 258. *L. lactuosa* Burmeister, 1839  | 25(24A+X)            | −             | USA          | Smith 1916                  |
| 259. *L. palchella* Drury, 1773      | 25(24A+X)            | +             | USA          | Cruden 1968                 |
|                                      | 25(24A+X)            | +             | Canada       | Kiauta 1969a                |
| 260. *L. quadrinaculata* Linnaeus, 1758 | 25(24A+X)            | +             | Japan        | Oguma 1915, 1930 (L. q. asahinai Schmidt, 1957) |
| Taxon                              | Karyotype formula 2n | m-chromosomes | Country       | References                                      |
|-----------------------------------|----------------------|---------------|---------------|------------------------------------------------|
| 260. *L. quadrimaculata* Linnaeus, 1758 | 25(24A+X)            | +             | Japan         | Kichijo 1942d (*L. q. asahinai*)               |
|                                   | +                    | +             | Japan         | Omura 1955 (L. q. asahinai)                    |
|                                   | +                    | +             | Japan         | Kiauta 1968b, c (*L. q. asahinai*)             |
|                                   | +                    | +             | Former USSR  | Fuchsówna and Sawczyńska 1928 (L.            |
|                                   |                      |               |               | *quadrimaculata* Linnaeus, 1758)              |
|                                   | +                    | +             | Finland       | Oksala 1939a, b, 1945 (L. *quadrimaculata*)  |
|                                   | +                    | +             | Former USSR  | Makalowska 1940 (L. *quadrimaculata*)        |
|                                   | +                    | +             | Netherlands   | Kiauta 1968b, c (L. *quadrimaculata*)        |
|                                   | +                    | +             | USA           | Cruden 1968 (L. *quadrimaculata*)             |
|                                   | +                    | +             | Russia        | Perepelov et al. 1998 (L. *quadrimaculata*)  |
| 261. *L. saturata* Uhler, 1857     | 25(24A+X)            | +             | USA           | Cruden 1968                                   |
| 262. *L. semifasciata* Burmeister, 1839 | 25(24A+X)        | +             | USA           | Cruden 1968                                   |
| 263. *L. vibrans* Fabricius, 1793 | 25(24A+X)            | +             | USA           | Cruden 1968                                   |
| 264. *Lyriothemis* pachygastra (Selys, 1878) | 25(24A+X)     | –             | Japan         | Omura 1955                                   |
| 265. *Macrothemis* decilisata Calvert, 1909 | 23(22A+X)       | +             | Brazil        | Kiauta and Boyes 1972                        |
| 266. *M. bimichlora* (Burmeister, 1839) | 6(4A+neo-X)    | +             | Bolivia       | Cumming 1964                                 |
| 267. *M. imitans* Karsch, 1890    | 25(24A+X)            | +             | Brazil        | Kiauta and Boyes 1972                        |
|                                   |                      |               | (M. i. imitans Karsch, 1890)               |
| 268. *M. mortoni* Ris, 1913       | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
| 269. *M. musiva* Calvert, 1898    | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
| 270. *Macrothemis* sp.            | 25(24A+X)            | +             | Argentina     | Mola 2007                                    |
| 271. *Miathyria* artemis (Selys, 1857) | 25(24A+X)       | +             | Surinam       | Kiauta 1979a                                 |
| 272. *M. marcella* (Selys, 1857) | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
|                                   |                      |               | Surinam       | Kiauta 1979a                                 |
|                                   |                      |               | Argentina     | Mola and Agopian 1985                         |
|                                   |                      |               | Brazil        | Ferreira et al. 1979                          |
| 273. *Microathyria* artemis Ris, 1911 | 25(24A+X)        | +             | Brazil        | Ferreira et al. 1979                          |
|                                   |                      |               | Brazil        | Souza Bueno 1982                              |
| 274. *M. atra* (Martin, 1897)     | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
| 275. *M. ctenata* Calvert, 1909   | 25(24A+X)            | +             | Bolivia       | Souza Bueno 1982                              |
|                                   |                      |               | Argentina     | Mola 2007                                    |
| 276. *M. didyma* (Selys, 1857)    | 25(24A+X)            | +             | Jamaica       | Cumming 1964                                 |
| 277. *M. exima* Kirby, 1897       | 25(24A+X)            | +             | Surinam       | Kiauta 1979a                                 |
| 278. *M. hagenii* Kirby, 1890     | 25(24A+X)            | +             | Jamaica       | Cumming 1964                                 |
|                                   |                      |               | Surinam       | Kiauta 1979a                                 |
| 279. *M. hesperis* Ris, 1911      | 25(24A+X)            | +             | Surinam       | Kiauta 1979a                                 |
|                                   |                      |               | Brazil        | Ferreira et al. 1979                          |
|                                   |                      |               | Argentina     | Mola et al. 1999                              |
| 280. *M. hypodiptina* Calvert 1906 | 23(22A+X)          | +             | Brazil        | Souza Bueno 1982                              |
|                                   |                      |               | Argentina     | Agopian and Mola 1988                         |
| 281. *M. iheringi* Santos, 1946   | 23(22A+X)            | +             | Bolivia       | Cumming 1964                                 |
| 282. *M. larcigata* Calvert, 1909 | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
|                                   |                      |               | Brazil        | Kiauta and Boyes 1972                        |
| 283. *M. longifasciata* Calvert, 1909 | 24(22A+neo-XY)  | –             | Argentina     | Agopian and Mola 1988                         |
| 284. *M. ocellata* (Martin, 1897) | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
|                                   |                      |               | (M. o. dentiens Calvert, 1909)             |
| 285. *M. sparia* (Selys, 1900)    | 25(24A+X)            | +             | Bolivia       | Cumming 1964                                 |
|                                   |                      |               | Argentina     | Mola et al. 1999                              |
| 286. *M. stawiarksi* Santos, 1953 | 25(24A+X)            | +             | Brazil        | Souza Bueno 1982                              |
| 287. *M. unguulata* Foerster, 1907 | 23(20A+X, X, Y)   | –             | Argentina     | Mola et al. 1999                              |
| 288. *M. cf. eximia* Kirby, 1879  | 21(20A+X)            | –             | Bolivia       | Cumming 1964                                 |
| 289. *M. sp. (anguulata Foerster, 1907-group)* | 23(22A+X)     | –             | Bolivia       | Cumming 1964                                 |
| 290. *Nannothemis bella* (Uhler, 1857) | 25(24A+X)        | +             | USA           | Cruden 1968                                   |
| 291. *Nesiothemis farinosa* (Foerster, 1898) | 25(24A+X)    | +             | Kenya         | Kiauta 1969c                                  |
|                                   |                      |               | Kenya         | Wascher 1985                                  |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|----------------|---------|------------|
| 292. *Nesogonia blackburni* (McLachlan, 1883) | 25(24A+X) | + | Hawaii | Kiauta 1969a |
| 293. *Neurothemis fulva* (Drury, 1773) | 25(24A+X) | + | Nepal | Kiauta 1974, 1975 |
| 294. *N. intermedia* (Rambur, 1842) | 25(24A+X) | + | Nepal | Kiauta 1974, 1975 (N. i. intermedia (Rambur, 1842)) |
| | | | | Kiauta and Kiauta 1982 (N. i. degener (Sel., 1842)) |
| 295. *N. terminata* Ris, 1911 | 25(24A+X) | + | Philippines | Kiauta and Kiauta 1980b |
| 296. *N. tullia* (Drury, 1773) | 28(26A+neo-XY) | + | India | Ray Chaudhuri and Dasgupta 1949 |
| | | + | India | Tyagi 1982 (N. t. tullia) |
| | 25(24A+X) | + | Thailand | Kiauta and Kiauta 1983 |
| 297. *Oligoclada amphinome* Ris, 1919 | 25(24A+X) | + | Surinam | Kiauta 1979a |
| 298. *O. laetitia* Ris, 1911 | 23(22A+X) | + | Argentina | Mola and Agopian 1985 |
| | | – | Brazil | Souza Bueno 1982 |
| 299. *O. monosticha* Borror, 1931 | 23(22A+X) | + | Surinam | Kiauta 1979a |
| | | + | Brazil | Ferreira et al. 1979 |
| 300. *O. pachystigma* Karsch, 1890 | 23(22A+X) | + | Brazil | Souza Bueno 1982 |
| 301. *Orthemis aequilibris* Calvert, 1909 | 12(10A+neo-XY) | + | Surinam | Kiauta 1979a |
| 302. *O. ambigna* Calvert, 1909 | 12(10A+neo-XY) | + | Argentina | Agopian and Mola 1984 |
| 303. *O. biolleyi* Calvert, 1906 | 23(22A+X) | + | Bolivia | Cumming 1964 |
| 304. *O. cutiforvis* Calvert, 1906 | 23(22A+X) | + | Surinam | Kiauta 1979a |
| | | + | Brazil | Ferreira et al. 1979 |
| 305. *O. discolor* Burmeister, 1839 | 23(22A+X) | + | Argentina | Mola 2007 |
| 306. *O. ferruginea* (Fabricius, 1775) | 10(8A+neo-XY)** | – | Bolivia | Cumming 1964 |
| | 23(22A+X) | – | USA | Cruden 1968 |
| | | + | Guatemala, Dominica | Cruden 1968 |
| | | + | Peru | Kiauta 1969a, 1971c |
| | | + | Peru | Kiauta and Bojes 1972 |
| | 23(22A+X) | + | Surinam | Kiauta 1979a |
| | 25(24A+X) | + | Brazil | Ferreira et al. 1979 |
| 307. *O. levis* Calvert, 1906 | 24(22A+XX)*** | + | Brazil, Argentina | Mola and Agopian 1985 |
| 308. *O. nodiplaga* Karsch, 1891 | 6(4A+neo-XY)*** | + | Bolivia | Cumming 1964 |
| 309. *Orthetrum abbotti* Calvert, 1892 | 25(24A+X) | + | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980 |
| 310. *O. albistylum* (Selys, 1848) | 25(24A+X) | + | Italy | Kiauta 1971a (O. a. albistylum (Selys, 1848)) |
| | | + | Russia | Perepelov et al. 1998 |
| | | + | Japan | Oguma 1915, 1917, 1930 (O. a. specium (Uhler, 1858)) |
| | | + | India | Kichijo 1942b (O. a. specium) |
| | | + | Japan | Omura 1955 (O. a. specium) |
| 311. *O. azureum* (Rambur, 1842) | 25(24A+X) | + | Madagascar | Kiauta 1969b, c |
| 312. *O. brachiale* (Beauvois, 1805) | 21(20A+X) | – | Kenya | Kiauta 1969b, c |
| | | + | Burkina Faso (Former Voltiac Republic) | Kiauta and Ochse 1979 (O. b. brachiale (Beauvois, 1805)) |
| 313. *O. brunneum* (Fonscolombe, 1837) | 25(24A+X) | + | Italy | Kiauta 1971a |
| | | + | Russia | Perepelov et al. 1998 |
| 314. *O. cancellatum* (Linnaeus, 1758) | 25(24A+X) | + | Finland | Öksala 1939a |
| | | + | India | Dasgupta 1957 |
| | | + | Netherlands | Kiauta 1969a, b |
| | | + | India | Tyagi 1982 |
| | | + | Russia | Kuznetsova et al. 2018 |
| Taxon               | Karyotype formula 2n | m-chromosomes | Country                      | References                      |
|--------------------|----------------------|---------------|------------------------------|---------------------------------|
| O. chrysostigma    | 25(24A+X)            | +             | Burkina Faso (Former Voltaic Republic) | Kiauta and Ochse 1979         |
|                    | − o −               | +             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980              |
|                    | − o −               | +             | Kenya                         | Wascher 1985                   |
| O. coerulescens    | 25(24A+X)            | +             | Austria                       | Kiauta 1969c                   |
|                    | 23(22A+X)           | −             |                               |                                 |
|                    | 25(24A+X)            | +             | Italy                         | Kiauta 1971a                   |
|                    | 27(26A+X)           | +             |                               |                                 |
| O. glaucum         | 25(24A+X)            | +             | India                         | Dasgupta 1957                  |
|                    | − o −               | +             | India                         | Handa and Batra 1980           |
|                    | − o −               | +             | India                         | Tyagi 1982                     |
|                    | − o −               | +             | India                         | Handa et al. 1984              |
|                    | − o −               | +             | India                         | Walia and Sandhu 2002          |
|                    | − o −               | +             | India                         | Kumari and Gautam 2017         |
| O. guineae         | 25(24A+X)            | +             | Burkina Faso (Former Voltaic Republic) | Kiauta and Ochse 1979         |
| O. japonicum       | 25(24A+X)            | +             | Japan                         | Oguma 1917, 1930 (O. j. internum) McLachlan, 1894 |
|                    | − o −               | +             | Japan                         | Kichijo 1942b (O. j. internum)  |
|                    | − o −               | +             | Japan                         | Omura 1955 (O. j. internum)     |
|                    | − o −               | +             | Nepal                         | Kiauta 1975 (O. j. internum)    |
|                    | − o −               | +             | Nepal                         | Kiauta and Kiauta 1976 (O. j. internum) |
|                    | − o −               | +             | Nepal                         | Kiauta and v. 1977 (O. j. internum) |
|                    | − o −               | +             | Nepal                         | Prasad and Thomas 1992         |
|                    | − o −               | +             | Nepal                         | Ojima 1917                     |
|                    | − o −               | +             | Japan                         | Oguma 1955                     |
|                    | − o −               | +             | Russia                        | Perpelev 2003                  |
| O. julia Kirby, 1900 | 25(24A+X)           | +             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980 (O. j. falsum Longfeld, 1955) |
|                    | − o −               | +             | Kenya                         | Wascher 1985 (O. j. falsum)    |
| O. leuconicum      | 25(24A+X)            | +             | Nepal                         | Kiauta 1975                    |
|                    | − o −               | +             | Nepal                         | Kjaup and Kiauta 1982          |
|                    | − o −               | +             | Nepal                         | Thomas and Prasad 1981         |
|                    | − o −               | +             | India                         | Thomas and Prasad 1992         |
| O. melanina        | 25(24A+X)            | +             | Japan                         | Oguma 1917                      |
|                    | − o −               | +             | Japan                         | Omura 1955                     |
|                    | − o −               | +             | Russia                        | Perepelov 2003                 |
| O. monardi         | 25(24A+X)            | +             | Burkina Faso (Former Voltaic Republic) | Kiauta and Ochse 1979         |
| O. poecilops       | 25(24A+X)            | +             | Japan                         | Suzuki et al. 1991 (O. p. miyajimaensis Yuki et Doi, 1958) |
| O. praunorum       | 25(24A+X)            | +             | India                         | Dasgupta 1957 (O. p. neglectum Rambus, 1842) |
|                    | − o −               | +             | Taiwan                        | Kiauta 1969a, c (O. p. neglectum) |
|                    | − o −               | +             | India                         | Tyagi 1982 (O. p. neglectum)    |
|                    | − o −               | +             | India                         | Prasad and Thomas 1992 (O. p. neglectum) |
|                    | − o −               | +             | India                         | Tyagi 1978a, b (O. p. neglectum) |
|                    | − o −               | +             | Nepal                         | Kjaup and Kjaup 1982 (O. p. neglectum) |
|                    | − o −               | +             | India                         | Walia and Sandhu 2002 (O. p. neglectum) |
|                    | − o −               | +             | India                         | Kumari and Gautam 2017 (O. p. neglectum) |
| O. sabina          | 25(24A+X)            | +             | India                         | Asana and Makino 1935          |
|                    | − o −               | +             | India                         | Makino 1935                    |
|                    | − o −               | +             | India                         | Kichijo 1942b                  |
|                    | − o −               | +             | India                         | Ray Chandhuri and Dasgupta 1949 |
|                    | − o −               | +             | Nepal                         | Kiauta 1975                    |
| Taxon                               | Karyotype formula 2n | m-chromosomes | Country          | References                     |
|------------------------------------|----------------------|---------------|-----------------|-------------------------------|
| 326. *O. sabina* (Drury, 1773)     | 2n – m-chromosomes   | +             | India           | Tyagi 1982                    |
|                                    | 2n – m-chromosomes   | +             | India           | Prasad and Thomas 1992        |
|                                    | 2n – m-chromosomes   | +             | India           | Walia and Sandhu 2002         |
|                                    | 25(24A+X)            | +             | Greece          | Kiauta 1972a                  |
| 327. *O. taeniolatum* (Schneider, 1845) | 25(24A+X) | +             | Nepal           | Tyagi 1975                    |
|                                    | 2n – m-chromosomes   | +             | India           | Tyagi 1978a, b                |
|                                    | 2n – m-chromosomes   | +             | India           | Handa and Barra 1980          |
|                                    | 2n – m-chromosomes   | +             | India           | Tyagi 1982                    |
|                                    | 2n – m-chromosomes   | +             | India           | Handa et al. 1984             |
|                                    | 2n – m-chromosomes   | +             | India           | Thomas and Prasad 1986        |
|                                    | 2n – m-chromosomes   | +             | India           | Walia and Sandhu 2002a        |
|                                    | 2n – m-chromosomes   | +             | India           | Walia et al. 2015             |
| 328. *O. testaceum* (Burmeister, 1839) | 25(24A+X) | +             | Nepal           | Kiauta and Kiauta 1982        |
| 329. *O. triangulare* (Selys, 1878) | 25(24A+X)   | +             | Japan           | Kiauta 1955 (O. t. melanica)  |
|                                    | 2n – m-chromosomes   | +             | Taiwan          | Kiauta 1969a, b (O. t. triangulare) |
|                                    | 2n – m-chromosomes   | +             | Nepal           | Kiauta 1975 (O. t. triangulare) |
|                                    | 2n – m-chromosomes   | +             | India           | Tyagi 1978a, b (O. t. triangulare) |
|                                    | 2n – m-chromosomes   | +             | India           | Handa and Barra 1980 (O. t. triangulare) |
|                                    | 2n – m-chromosomes   | +             | India           | Tyagi 1982 (O. t. triangulare) |
|                                    | 2n – m-chromosomes   | +             | India           | Walia and Sandhu 2002 (O. t. triangulare) |
| 330. *Pachydiplax longipennis* (Burmeister, 1839) | 25(24A+X) | –             | USA             | Cumming 1964                  |
|                                    | 2n – m-chromosomes   | +             | USA             | Cruden 1968                   |
|                                    | 2n – m-chromosomes   | +             | USA             | Kiauta and Brink 1978         |
| 331. *Palpopleura jucunda* Rambur, 1842 | 25(24A+X) | +             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980 |
| 332. *P. lucia* (Drury, 1773)      | 25(24A+X)   | +             | Burkina Faso (Former Voltiac Republic) | Kiauta and Ochssee 1979 (P. l. portia) (Drury, 1773) |
|                                    | 2n – m-chromosomes   | +             | Kenya           | Wascher 1985 (P. l. portia)    |
| 333. *P. sexmaculata* (Fabricius, 1787) | 25(24A+X) | +             | Nepal           | Kiauta 1974, 1975             |
|                                    | 2n – m-chromosomes   | +             | India           | Tyagi 1982 (P. s. sexmaculata) (Fabricius, 1787) |
| 334. *Pantala flavescens* (Fabricius, 1798) | 25(24A+X) | +             | India           | Asana and Makino 1935         |
|                                    | 2n – m-chromosomes   | +             | India           | Makino 1935                   |
|                                    | 2n – m-chromosomes   | +             | India           | Kichij 1942h                  |
|                                    | 2n – m-chromosomes   | +             | India           | Dasgupta 1957                 |
|                                    | 2n – m-chromosomes   | +             | India           | Seshachar and Bagga 1963      |
|                                    | 2n – m-chromosomes   | +             | Bolivia         | Cumming 1964                  |
|                                    | 2n – m-chromosomes   | +             | Suriname        | Kiauta 1979a                  |
|                                    | 2n – m-chromosomes   | +             | Brazil          | Ferreira et al. 1979          |
|                                    | 2n – m-chromosomes   | +             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980 |
|                                    | 2n – m-chromosomes   | +             | Brazil          | Souza Bueno 1982              |
|                                    | 2n – m-chromosomes   | +             | Argentina       | Agopian and Mola 1988         |
|                                    | 2n – m-chromosomes   | +             | India           | Prasad and Thomas 1992        |
|                                    | 2n – m-chromosomes   | +             | Russia          | Perepelov and Bugrov 2001b   |
| 335. *P. hymenaea* (Say, 1836)     | 25(24A+X)   | +             | Bolivia         | Cumming 1964                  |
|                                    | 2n – m-chromosomes   | +             | USA             | Cruden 1968                   |
| 336. *Perithemis cornelia* Ris, 1910 | 25(24A+X) | –             | Bolivia         | Cumming 1964                  |
| 337. *P. domitia* (Drury, 1773)    | 25(24A+X)   | +             | Jamaica         | Cumming 1964                  |
| 338. *P. electra* Ris, 1928        | 25(24A+X)   | –             | Bolivia         | Cumming 1964                  |
| 339. *P. icteropectra* (Selys in Sagra, 1857) | 25(24A+X) | +             | Argentina       | Mola and Agopian 1985         |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|---------------------|--------------|---------|------------|
| 340.  | P. lais (Perry, 1834) | 17(16A+X)   | –       | Bolivia    | Cumming 1964 |
|       |                     | –           | –       | Surinam    | Kiauta 1979a |
|       |                     | –           | –       | Brazil     | Ferreira et al. 1979 |
| 341.  | P. moona Kirby, 1889 | 25(24A+X)   | +       | Bolivia    | Cumming 1964 |
|       |                     | –           | –       | Surinam    | Kiauta 1979a |
|       |                     | –           | –       | Brazil     | Ferreira et al. 1979 |
|       |                     | –           | +       | Argentina  | Mola and Agopian 1985 |
| 342.  | P. tenax (Say, 1839) | 25(24A+X)   | +       | USA        | Kiauta and Brink 1978 |
| 343.  | P. similalis Calvert, 1907 | 25(24A+X)   | +       | USA        | Cumming 1964 |
| 344.  | Perithemis sp.       | 25(24A+X)   | –       | Bolivia    | Cumming 1964 |
| 345.  | Planiplex erythropyga (Karsch, 1891) | 25(24A+X)   | +       | Argentina  | Mola et al. 1999 |
|       |                     | –           | +       |           | De Gennaro 2004 |
| 346.  | P. sanguiniventris (Calvert, 1907) | 25(24A+X)   | +       | USA        | Cumming 1964 |
| 347.  | Plathemis hydia (Drury, 1773) | 25(24A+X)   | +       | USA        | Cumming 1964 |
|       |                     | –           | +       | USA        | McGill 1907 |
| 348.  | Potanarcha congener (Rambur, 1842) | 25(24A+X)   | +       | India      | Asana and Makino 1935 as P. obscura (Rambur, 1842) |
|       |                     | –           | +       | India      | Makino 1935 as P. obscura |
|       |                     | –           | +       | India      | Kichijo 1942b as P. obscura |
|       |                     | –           | +       | India      | Dasgupta 1937 as P. obscura |
|       |                     | –           | +       | India      | Tyagi 1982 as P. obscura |
|       |                     | –           | +       | India      | Prasad and Thomas 1992 |
|       |                     | –           | +       | India      | Sandhu and Wala 1995 |
| 349.  | Pseudothemis sinita (Burmeister, 1839) | 24(22A+2neo-XY) | –       | Japan      | Omura 1955 |
| 350.  | Pseudotramoae laestera Fraser, 1920 | 25(24A+X)   | +       | Nepal      | Kiauta 1974, 1975 |
| 351.  | Rhodopipta cardinalis (Erichson, 1848) | 25(24A+X)   | +       | Bolivia    | Cumming 1964 |
| 352.  | R. evanir Belle, 1964 | 25(24A+X)   | +       | Surinam    | Kiauta 1979a |
| 353.  | Rhodothyemis ruje (Rambur, 1842) | 25(24A+X)   | +       | India      | Prasad and Thomas 1992 |
| 354.  | Rhynothemis fuliginosa Selys, 1883 | 25(24A+X)   | +       | Japan      | Toyoshima and Hiroi 1953 |
|       |                     | –           | +       | Japan      | Omura 1955 |
|       |                     | –           | +       | Japan      | Hiroi 1956 |
|       |                     | 25(24A+X)   | +       | Japan      | Kiauta 1969c |
| 355.  | R. variegata (Linnaeus et Johansson, 1763) | 25(24A+X)   | +       | India      | Ray Chaudhuri and Dasgupta 1949 |
|       |                     | –           | +       | Nepal      | Kiauta 1975 |
| 356.  | Scapanes frontalis (Burmeister, 1839) | 25(24A+X)   | +       | Jamaica    | Cumming 1964 |
| 357.  | Symphoropum commixtum (Selys, 1884) | 25(24A+X)   | –       | India      | Tyagi 1978a, b, 1982 |
| 358.  | S. corruptum (Hagen, 1861) | 25(24A+X)   | +       | USA        | Cruden 1968 as Tarnetrum corruptum (Hagen, 1861) |
|       |                     | –           | +       | USA        | Kiauta 1969a, c as T. corruptum |
| 359.  | S. castor (Hagen, 1861) | 25(24A+X)   | +       | USA        | Cruden 1968 |
| 360.  | S. cruceolum (Selys, 1840) | 25(24A+X)   | +       | Russia     | Perepelov 2003 |
| 361.  | S. danae (Sulzer, 1776) | 25(24A+X)   | +       | Former USSR Makalowskaja 1940 |
|       |                     | –           | +       | Finland    | Oksala 1945 |
|       |                     | –           | +       | USA        | Cruden 1968 |
|       |                     | –           | +       | Russia     | Perepelov 2003 |
|       |                     | –           | +       | Russia     | Kuznetsova et al. 2018 |
| 362.  | S. euruticum (Selys, 1883) | 21(20A+X)   | –       | Japan      | Kichijo 1942b, c |
|       |                     | –           | –       | Japan      | Hiroi 1956 |
|       |                     | –           | –       | Japan      | Kiauta 1969c |
| 363.  | S. flavescens (Linnaeus, 1758) | 25(24A+X)   | +       | Former USSR Makalowskaja 1940 |
|       |                     | –           | +       | Russia     | Perepelov 2003 |
| 364.  | S. fonecolombiensis (Selys, 1840) | 25(24A+X)   | +       | Russia     | Perepelov 2003 |
| 365.  | S. frequens (Selys, 1883) | 23(22A+X)   | –       | Japan      | Oguma 1917, 1930 |
|       |                     | –           | –       | Japan      | Kichijo 1942a, b |
|       |                     | –           | –       | Japan      | Kiauta 1969c |
| 366.  | S. infuscatum (Selys, 1883) | 25(24A+X)   | +       | Russia     | Perepelov 2003 |
| 367.  | S. internum Montgomery, 1943 | 27(26A+X)   | +       | Canada     | Kiauta 1973a |
| 368.  | S. madidum (Hagen, 1861) | 25(24A+X)   | +       | USA        | Cruden 1968 |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|---------------------|---------------|---------|------------|
| 368.  | S. madidum (Hagen, 1861) | 25(24A+X) | + | Japan | Oguma 1917, 1930 (S. p. elatum (Selys, 1872)) |
| 369.  | S. meridionale (Selys, 1841) | 25(24A+X) | + | Switzerland | Kiauta 1966 |
| 370.  | S. obtusum (Hagen, 1867) | 25(24A+X) | + | USA | Cruden 1968 |
| 371.  | S. parvulum Bartenev, 1912 | 25(24A+X) | + | Japan | Kiauta 1968c |
| 372.  | S. pedemontanum Müller in Allioni, 1766 | 25(24A+X) | + | USSR | Perepelov et al. 1998 (S. p. pedemontanum) |
| 373.  | S. rubicundulum (Say, 1839) | 25(24A+X) | + | USA | Cruden 1968 |
| 374.  | S. sanguineum (Müller, 1764) | 25(24A+X) | + | Italy | Kiauta 1971a |
| 375.  | S. semicinctum (Say, 1839) | 25(24A+X) | + | USA | Smith 1916 |
| 376.  | S. striatum (Charpentier, 1840) | 25(24A+X) | + | USSR | Perepelov et al. 2001b |
| 377.  | S. vicinum (Hagen, 1861) | 25(24A+X) | + | USA | Cruden 1968 |
| 378.  | S. vulgatum (Linnaeus, 1758) | 25(24A+X) | + | USSR | Perepelov 2003 |
| 379.  | Tarnetrum illotum (Hagen, 1861) | 25(24A+X) | + | Jamaica | Cumming 1964 |
| 380.  | Tauriphila australis (Hagen, 1867) | 25(24A+X) | + | USA | Cruden 1968 |
| 381.  | T. attica Calvert, 1906 | 25(24A+X) | + | Mexico | Cruden 1968 |
| 382.  | T. rii Martin 1896 | 25(24A+X) | + | Argentina, Uruguay | Mola and Agopian 1985 |
| 383.  | Tholymis citrina Hagen, 1867 | 25(24A+X) | + | Surinam | Kiauta 1979a |
| 384.  | Th. tillagra (Fabricius, 1798) | 25(24A+X) | + | Brazil | Ferreira et al. 1979 |
| 385.  | Tramea abdominalis (Rambur, 1842) | 25(24A+X) | + | Bolivia | Cumming 1964 |
| 386.  | T. basilaris (Palisot de Beauvois, 1817) | 25(24A+X) | + | India | Das 1956 (T. b. burmeisteri (Kirby, 1889)) |
| 387.  | T. binotata (Rambur, 1842) | 25(24A+X) | + | Surinam | Kiauta 1979a |
| 388.  | T. carolina (Linnaeus, 1763) | 25(24A+X) | + | USA | Cumming 1964 |
| 389.  | T. cphinx (Hagen, 1867) | 25(24A+X) | + | USA | Cruden 1968 |
| 390.  | T. lacerata (Hagen, 1861) | 25(24A+X) | + | USA | Cruden 1968 |
| 391.  | T. limbata (Desjardins, 1832) | 25(24A+X) | + | India | Asana and Makino 1935 |
| 392.  | T. virginia (Rambur, 1842) | 25(24A+X) | + | India | Kichijo 1942b |
| 393.  | Trithemis annulata (Palisot de Beauvois, 1805) | 25(24A+X) | + | Republic of South Africa | Boyes et al. 1980 |
| 394.  | T. arteriosa (Burmester, 1839) | 25(24A+X) | + | Kenya | Wasscher 1985 |

Karyotypes of Odonata: a check-list
| Taxon                      | Karyotype formula 2n | m-chromosomes | Country                  | References                  |
|---------------------------|----------------------|---------------|--------------------------|-----------------------------|
| T. arna Pinhey, 1961      | 25(24A+X)            | +             | Burkina Faso (Former Voltiac Republic) | Kiauta and Ochse 1979       |
| T. aurora (Burmeister, 1839) | 25(24A+X)            | +             | India                    | Oguma and Asana 1932        |
| T. doradis (Rambur, 1842) | 25(24A+X)            | +             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980           |
| T. festiva (Rambur, 1842) | 25(24A+X)            | +             | Nepal                    | Kiauta 1975                 |
| T. furva Karsch, 1899     | 25(24A+X)            | +             | Sudan                    | Wasscher 1985               |
| T. kirbyi Selys, 1891     | 25(24A+X)            | +             | Kenya                    | Wasscher 1985 (T. k. ardens) |
| T. pallatinervis (Kirby, 1889) | 25(24A+X)          | +             | Asana and Makino 1935    |                             |
| T. signata (Rambur, 1842) | 25(24A+X)            | +             | India                    | Das 1956 (U. s. signata (Rambur, 1842)) |
| Z. torrida (Kirby, 1889)  | 25(24A+X)            | +             | Thailand                  | Kiauta and Kiauta 1983      |
| Zyxomma petiolatum (Rambur, 1842) | 25(24A+X)       | +             | India                    | Prasad and Thomas 1992      |

Cordulegastroidae

Chlorogomphidae

414. Watanaheoptera askarsemi (Selys, 1878) 25(24A+X) + India | Wu and Chahal 2019 |

Cordulegastridae

415. Anotogaster basalis Selys, 1854 23(22A+X) + India | Sandhu and Malhotra 1994b |
416. A. kuchenbeseri (Förster, 1899) 25(24A+X) + China | Zhu and Wu 1986 |
417. A. sieboldii (Selis, 1854) 25(24A+X) + Japan | Oguma 1930 |
418. Cordulegaster boltoni (Donovan, 1807) 25(24A+X) + Finland | Oksala 1939, a |
419. C. brevisignata Selys, 1854 25(24A+X) + India | Wu and Chahal 2019 |
420. C. dianator (Selys, 1854) 25(24A+X) + USA |Crudens 1968 |
421. C. doradis Hagen, 1857 25(24A+X) + USA |Crudens 1968 |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 422.  | C. maculata Selys, 1854 | 25(24A+X) | + | USA | Cruden 1968 |
| 423.  | Neallagaster hermosae (Fraser, 1927) | 25(24A+X) | + | Nepal | Kiauta and Kiauta 1976 |

**Zygoptera**

**Lestioidea**

**Lestidae**

424. *Austrolestes colensoi* (White, 1846) 25(24A+X) + New Zealand Jensen 1980

425. *Chalcolestes viridis* (Van der Linden, 1825) 25(24A+X) + Netherlands Kiauta 1969a

426. *Indolestes cyanus* (Selys, 1862) 25(24A+X) + Nepal Kiauta and Kiauta 1976 as *I. cyanus* (Selys, 1862)

427. *Lestes barbarus* (Fabricius, 1798) 25(24A+X) + Former Yugoslavia Kiauta 1972a

428. *L. congener* Hagen, 1861 25(24A+X) + USA Cruden 1968

429. *L. disjunctus* Selys, 1862 25(24A+X) – USA Cruden 1968

430. *L. dorothea* Fraser, 1924 25(24A+X) + Nepal Kiauta 1974, 1975

431. *L. dorys* Kirby, 1890 25(24A+X) – USA Cruden 1968

432. *L. forcipatus* Rambur, 1842 21(20A+X) – USA Cruden 1968

433. *L. forficula* Rambur, 1842 25(24A+X) + Jamaica Cumming 1964

434. *L. pauletus* Calvert, 1909 25(24A+X) + Brazil Souza Bueno 1982

435. *L. rectangularis* Say, 1839 25(24A+X) + USA Cruden 1968

436. *L. similatrix* McLeachlan, 1895 25(24A+X) + Madagascar Kiauta 1969b

437. *L. spongia* (Hansemann, 1823) 25(24A+X) – Former USSR Makalowskaja 1940

438. *L. stultus* Hagen, 1861 25(24A+X) – USA Cruden 1968

439. *L. viridis* Hagen, 1861 25(24A+X) + USA Cumming 1964

440. *L. viridac* Selys, 1862 19(18A+X) – USA Kiauta and Brink 1978

441. *L. virens* Charpentier, 1825 25(24A+X) + Netherlands Kiauta 1969a (*L. v. vestalis* Rambur, 1842)

442. *Sympecma fusca* (Van der Linden, 1823) 25(24A+X) + Japan Kiauta and Brink 1975 (*S. annulata braueri* Bianchi, 1904)

443. *S. paedisca* (Brauer, 1877) 25(24A+X) + Netherlands Kiauta and Brink 1975 (*S. annulata braueri* Bianchi, 1904)

**Synlestidae**

444. *Megaselastes major* Selys, 1862 25(24A+X) – Nepal Kiauta 1974, 1975

**Platystictidae**

445. *Drepanosticta* sp. 25(24A+X) – Nepal Kiauta and Kiauta 1976

446. *Drepanosticta* sp. 25(24A+X) – India Iyagi 1978a, b

447. *Palaemnema paulina* (Drury, 1773) 25(24A+X) + Costa Rica Cumming 1964

448. *Protosticta* sp. 25(24A+X) – Thailand Kiauta and Kiauta 1983

**Calopterygidae**

**Caleopterygidae**

449. *Arthrocalopteryx atrata* (Selys, 1853) 25(24A+X) + Japan Oguma 1930 as *Calopteryx atrata* Selys, 1853

450. *Calopteryx aequabilis* Say, 1839 25(24A+X) + USA Cruden 1968

451. *C. cornelia* (Selys, 1853) 25(24A+X) + Japan Oguma 1930 as *Ancyperion cornelia* (Selys, 1853)

452. *C. dimidiata* Burmeister, 1839 25(24A+X) + USA Kiauta and Brink 1978

453. *C. japonica* Selys, 1869 25(24A+X) + Japan Kiauta 1942a

454. *C. maculata* (Beauvois, 1805) 25(24A+X) + USA Cumming 1964a

455. *C. splendidus* (Harris, 1780) 25(24A+X) + Turkey Kiauta 1972a

(C. e. annaena Bartenev, 1912)
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 455. *C. splendens* (Harris, 1780) | 2n♂ = 46 | – | Italy | Kiauta 1971a (C. s. caprae Conci, 1956) |
| | | + | Former USSR | Makalowskaia 1940 (C. s. splendens) (Harris, 1782) |
| | | – | Finland | Oksala 1945 (C. s. splendens) |
| | | – | Germany | Kiauta 1969a, 1971b (C. s. splendens) |
| | | – | France | Kiauta 1973b (C. s. splendens) |
| | | – | Russia | Perspelev et al. 1998 (C. s. splendens) |
| | | + | Russia | Kuznetsova et al. 2020b |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 456. *C. virgo* (Linnaeus, 1758) | 2n♂ = 46 | + | Spain | Kiauta 1971b (C. v. meridionalis Selys, 1873) |
| | | + | Belgium | Carnoy 1885 (C. v. virgo) |
| | | – | Finland | Oksala 1939 (C. v. virgo) |
| | | + | Former USSR | Makalowskaia 1940 (C. v. virgo) |
| | | + | Germany, Luxembourg | Kiauta 1968e, f (C. v. virgo) |
| | | + | Netherlands | Kiauta 1972c (C. v. virgo) |
| | | + | Russia | Kuznetsova et al. 2020b |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 457. *Hetaerina americana* (Fabricius, 1798) | 2n♂ = 46 | + | USA | Cumming 1964 |
| | | – | USA | Cruden 1968 |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 458. *H. charca* Calvert, 1909 | 2n♂ = 46 | + | Bolivia | Cumming 1964 |
| 459. *H. longipes* (Hagen in Selys, 1853) | 2n♂ = 46 | + | Brazil | Souza Bueno 1982 as *H. carinifex* Hagen in Selys, 1853 |
| | | – | Brazil | Ferreira et al. 1979 |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 460. *H. rosea* Selys, 1853 | 2n♂ = 46 | – | Bolivia | Cumming 1964 |
| 461. *H. titia* (Drury, 1773) | 2n♂ = 46 | + | USA | Cumming 1964 |
| | | – | Mexico | Kiauta 1970a as *H. tricolor* (Burmeister, 1839) |
| 462. *H. vulnerata* (Selys, 1853) | 2n♂ = 46 | + | Mexico | Kiauta 1970a |
| 463. *Matrona basilaris* Selys, 1853 | 2n♂ = 46 | – | Taiwan | Kiauta 1968c |
| 464. *Mnais costalis* Selys, 1869 | 2n♂ = 46 | + | Japan | Oguma 1930 |
| | | – | Japan | Kichijo 1942a |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 465. *M. pruinosa* Selys, 1853 | 2n♂ = 46 | + | Japan | Oguma 1930 as *M. irrigata* Selys, 1855 |
| | | – | Japan | Kichijo 1942a as *M. irrigata* |
| | | – | Japan | Omura 1957 as *M. irrigata* |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 466. *Neurobasis chinensis* (Linnaeus, 1758) | 2n♂ = 46 | + | Nepal | Kiauta and Kiauta 1975 (*N. c. chinensis*) (Linnaeus, 1758) |
| | | – | India | Tyagi 1978b (*N. c. chinensis*) |
| | | – | Nepal | Kiauta and Kiauta 1982 (*N. c. chinensis*) |
| | | – | Thailand | Kiauta and Kiauta 1983 (*N. c. chinensis*) |
| | | + | India | Wala and Sandhu 2002 (*N. c. chinensis*) |
| | | – | India | Wala et al. 2016 (*N. c. chinensis*) |

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 467. *Phaon iridipennis* (Burmeister, 1839) | 2n♂ = 46 | + | Republic of South Africa | Boyes et al. 1980 |

Chlorocyphidae

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 468. *Aristocypha fenestrella* Rambur, 1842 | 2n♂ = 46 | – | Thailand | Kiauta and Kiauta 1983 as *Rhinocypha fenestrella* Rambur, 1842 |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| A. quadrimaculata (Selys, 1853) | 23(22A+X) | + | India | Chatterjee and Kiauta 1973 as Rhinocypha quadrimaculata Selys, 1853 |
| A. trifasciata (Selys, 1853) | 23(22A+X) | – | India | Tyagi 1978a, b as Rhinocypha trifasciata Selys, 1853 |
| Heliocypha biforata (Selys, 1859) | 23(22A+X) | – | India | Tyagi 1978a, b as Rhinocypha biforata beetoni Selys, 1859 |
| H. biseriata (Selys, 1859) | 23(22A+X) | – | Thailand | Kiauta and Kiauta 1983 as Rhinocypha b. biforata Selys, 1859 |
| Libellula lineata (Burmeister, 1839) | 23(22A+X) | – | India | Walia et al. 2018 (L. l. lineata (Burmeister, 1839)) |
| Paracypha unimaculata (Selys, 1879) | 23(22A+X) | + | Nepal | Kiauta and Kiauta 1982 as Rhinocypha unimaculata Selys, 1879 |
| Rhinocypha colorata Selys, 1869 | 23(22A+X) | – | Philippines | Kiauta and Kiauta 1980b |
| Polythore boliviana (McLachlan, 1878) | 23(22A+X) | – | Bolivia | Cumming 1964 |
| Antiploura conus Hagen, 1880 | 25(24A+X) | + | Nepal | Kiauta and Kiauta 1976, 1982 |
| Beyadera indica (Selys, 1853) | 25(24A+X) | + | Nepal | Chatterjee and Kiauta 1973 |
| Euphasa guerini Rambus, 1842 | 25(24A+X) | – | Thailand | Kiauta and Kiauta 1983 |
| Epallage fatime (Charpentier, 1840) | 25(24A+X) | – | Greece | Kiauta 1970b |
| Allopodagrion contortum (Selys, 1862) | 25(24A+X) | + | Brazil | Kiauta 1972b as Megapodagrion contortum (Selys, 1862) |
| Teinopodagrion macropus (Selys, 1862) | 25(24A+X) | – | Bolivia | Cumming 1964 as Megapodagrion macropus (Selys, 1862) |
| T. setigerum (Selys, 1886) | 25(24A+X) | – | Bolivia | Cumming 1964 as Megapodagrion setigerum Selys, 1886 |
| Heteragrion flavidorsum Calvert, 1909 | 25(24A+X) | – | Bolivia | Cumming 1964 |
| H. inca Calvert, 1909 | 25(24A+X) | + | Bolivia | Cumming 1964 |
| Philogenia carrillica Calvert, 1907 | 25(24A+X) | + | Costa Rica | Cumming 1964 |
| Hypolestes clara (Calvert, 1891) | 17(16A+X) | – | Jamaica | Cumming 1964 |
| Calicnemia miniatia (Selys, 1886) | 25(24A+X) | + | Nepal | Kiauta and Kiauta 1982 |
| C. paloeulana (Selys, 1886) | 25(24A+X) | – | Nepal | Kiauta 1975 |
| Calicnemia sp. | 25(24A+X) | – | Nepal | Kiauta 1975 |
| Calicnemia sp. | 25(24A+X) | – | India | Tyagi 1978b |
| Caleticia chromobulax (Selys, 1891) | 25(24A+X) | – | India | Walla and Devi 2020b |
| C. bimaculata (Laidlaw, 1914) | 25(24A+X) | – | India | Walla and Devi 2020b |
| C. didyma (Selys, 1863) | 25(24A+X) | – | India | Walla and Devi 2020b |
| C. faereri (Laidlaw, 1932) | 25(24A+X) | – | India | Walla and Devi 2020b |
| C. renifer (Selys, 1886) | 25(24A+X) | – | Nepal | Kiauta 1974, 1975 |
| Copera annulata (Selys, 1863) | 25(24A+X) | + | Japan | Kichijo 1941, 1942a, c |
| – – – | + | India | Dasgupta 1957 |
| – – – | – | Thailand | Kiauta and Kiauta 1983 |
| – – – | + | India | Walia and Devi 2018 |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 501. *C. marginipes* (Rambur, 1842) | 25(24A+X) | – | India | Tyagi 1978a, b |
|  | | – | Thailand | Kiauta and Kiauta 1983 |
|  | | – | India | Walia and Devi 2018 |
| 502. *C. vittata* (Selys, 1863) | 25(24A+X) | + | India | Walia and Devi 2018 |
|  | | – | India | Walia and Devi 2018 (C. v. assamensis (Laidlaw, 1914)) |
| 503. *Disparoneura quadrivacuata* (Rambur, 1842) | 25(24A+X) | – | India | Walia and Devi 2020a |
| 504. *Eume cyanovittata* Fraser, 1922 | 25(24A+X) | – | India | Walia and Devi 2020a |
| 505. *E. longistyla* Fraser, 1931 | 25(24A+X) | – | India | Walia and Devi 2020a |
| 506. *Onychagrion atracynae* (Selys, 1865) | 25(24A+X) | – | Thailand | Kiauta and Kiauta 1983 |
| 507. *Platycnemis penipes* (Pallas, 1771) | 25(24A+X) | – | Finland | Oklads 1945 |
|  | | – | – | India | Kiauta 1971a |
|  | | – | – | – | Russia | Perepelov and Bugrov 2001b |
| 508. *Prodasineura australis* (Fraser, 1922) | 25(24A+X) | + | Thailand | Kiauta and Kiauta 1983 |
| 509. *P. nigra* (Fraser, 1922) | 25(24A+X) | – | India | Walia and Devi 2020a |
| 510. *P. verticilis* (Selys, 1860) | 25(24A+X) | – | India | Walia and Devi 2020a |
| 511. *Prodasineura sp.1* | 25(24A+X) | – | Thailand | Kiauta and Kiauta 1983 |
| 512. *Prodasineura sp.2* | 25(24A+X) | – | Thailand | Kiauta and Kiauta 1983 |
| 513. *Acanthagrion ascendens* Calvert, 1909 | 27(26A+X) | + | Bolivia | Cumming 1964 |
| 514. *A. clavatum* Calvert, 1909 | 27(26A+X) | + | Bolivia | Cumming 1964 |
| 515. *A. gracile* (Rambur, 1842) | 27(26A+X) | – | Surinam | Kiauta 1979a (A. g. minarum Selys, 1876) |
|  | | – | – | Brazil | Ferreira et al. 1979 (A. g. minarum Selys, 1876) |
| 516. *Aeolagrion inca* Selys, 1876 | 27(26A+X) | – | Bolivia | Cumming 1964 as *A. felacenum* (Sjostedt, 1918) |
| 517. *Agriocnemis clauseni* Fraser, 1922 | 27(26A+X) | + | India | Tyagi 1978a, b |
| 518. *A. femina* (Brauer, 1868) | 27(26A+X) | – | Philippines | Kiauta and Kiauta 1980b |
|  | | – | + | Thailand | Kiauta and Kiauta 1983 |
| 519. *A. pygmaea* (Rambur, 1842) | 27(26A+X) | – | India | Tyagi 1978b |
|  | | – | + | Thailand | Kiauta and Kiauta 1983 |
| 520. *Amphiagrion abbreviatum* (Selys, 1876) | 27(26A+X) | – | USA | Cruden 1968 |
| 521. *Amphiallagma parsuum* (Selys, 1876) | 27(26A+X) | + | India | Honda and Kochhar 1985 as *Enallagma parsuum* Selys, 1876 |
| 522. *Argia apicalis* (Say, 1839) | 37(36A+X) | – | USA | Kiauta and Kiauta 1980b |
| 523. *A. fumipennis* (Burmeister, 1839) | 27(26A+X) | – | USA | Kiauta and Kiauta 1980c (A. f. atria Gloyd, 1968) |
|  | | – | USA | Kiauta and Brink 1978 (A. f. fumipennis (Burmeister, 1839)) |
|  | | – | USA | Kiauta and Kiauta 1980c (A. f. fumipennis) |
|  | | – | * + | Canada | Kiauta and Kiauta 1980c (A. f. violacea (Hagen, 1861)) |
| 524. *A. funebris* (Hagen, 1861) | 27(26A+X) | – | USA | Cruden 1968 |
| 525. *A. immunda* (Hagen, 1861) | 27(26A+X) | – | USA | Cruden 1968 |
| 526. *A. moesta* (Hagen, 1861) | 25(24A+X) | – | Canada | Cruden 1968 |
| 527. *A. nahuana* Calvert, 1902 | 25(24A+X) | – | USA | Kiauta and Kiauta 1980c |
| 528. *A. sedula* (Hagen, 1861) | 27(26A+X) | – | USA | Kiauta and Kiauta 1980c |
| 529. *A. tibialis* (Rambur, 1842) | 37(36A+X) | – | USA | Kiauta and Kiauta 1980c |
| 530. *A. translata* Hagen, 1865 | 25(24A+X) | + | USA | Kiauta and Kiauta 1980c |
| 531. *A. violaceus* (Hagen, 1861) | 27(26A+X) | – | USA | Cruden 1968 |
| 532. *A. viridia* (Hagen, 1861) | 27(26A+X) | – | USA | Cruden 1968 |
| 533. *Ceriagrion auranticum* Fraser, 1922 | 27(26A+X) | + | Thailand | Kiauta and Kiauta 1983 as *C. latericium* Liefenick, 1951 |
| 534. *C. azureum* (Selys, 1891) | 27(26A+X) | – | Nepal | Kiauta 1974, 1975 |
| 535. *C. cerinomelas* Liefenick, 1927 | 27(26A+X) | – | Nepal | Kiauta 1974, 1975 |
| Taxon                                           | Karyotype formula 2n | m-chromosomes | Country                   | References                              |
|------------------------------------------------|-----------------------|---------------|---------------------------|-----------------------------------------|
| 536. *C. cerinorubellum* (Brauer, 1866)         | 27(26A+X)             | +             | India                     | Dasgupta 1957                           |
| 537. *C. coronandelianum* (Fabricius, 1798)     | 27(26A+X)             | +             | India                     | Prasad and Thomas 1992                  |
| 538. *C. fallax* Ris, 1914                     | 27(26A+X)             | +             | Republic of South Africa   | Dasgupta 1957                           |
| 539. *C. glabrum* (Burmeister, 1839)           | 27(26A+X)             | –             | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980                      |
| 540. *C. rubiae* Laidlaw, 1916                  | 27(26A+X)             | +             | Asana and Makino 1935      |                                        |
| 541. *C. tenellum* (Villers, 1789)             | 27(26A+X)             | +             | Italy                     | Kiauta 1971a (C. t. tenellum (Villers, 1789)) |
| 542. *Chromagrion conditum* (Hagen, 1876)      | 27(26A+X)             | –             | USA                       | Cruden 1968                             |
| 543. *Coenagrion armatum* (Charpentier, 1840)   | 27(26A+X)             | –             | Former USSR               | Makalowskaja 1940                      |
| 544. *C. hastulatum* (Charpentier, 1825)       | 27(26A+X)             | –             | Former USSR               | Makalowskaja 1940                      |
| 545. *C. hastulatum* (Charpentier, 1840)       | 27(26A+X)             | –             | Russia                    | Perepelov and Bugrov 2001b             |
| 546. *C. laevigatum* (Charpentier, 1889)       | 27(26A+X)             | –             | Austria                   | Kiauta and Kiauta 1991                 |
| 547. *C. lacustris* (Vander Linden, 1823)       | 27(26A+X)             | –             | Former USSR               | Makalowskaja 1940                      |
| 548. *C. puella* (Linnaeus, 1758)              | 27(26A+X)             | +             | Russia                    | Kuznetsova et al. 2020b                |
| 549. *C. resolutum* (Hagen, 1876)              | 27(26A+X)             | –             | USA                       | Cruden 1968                             |
| 550. *Coenagrion sp.*                         | 27(26A+X)             | +             | Japan                      | Kichijo 1941, 1942d, e                   |
| 551. *Diceratobasis macrogaster* (Selys, 1875) | 27(26A+X)             | +             | Jamaica                   | Cumming 1964                           |
| 552. *Enallagma aspersum* (Hagen, 1861)        | 27(26A+X)             | –             | USA                       | Cruden 1968                             |
| 553. *E. boreale* Selys, 1875                  | 27(26A+X)             | –             | USA                       | Cruden 1968                             |
| 554. *E. carunculatum* Morse, 1895             | 27(26A+X)             | –             | USA                       | Cruden 1968                             |
| 555. *E. cirrulatum* Selys, 1883               | 27(26A+X)             | +             | Russia                    | Perepelov and Bugrov 2001b             |
| 556. *E. cistula* (Hagen, 1861)                | 27(26A+X)             | –             | USA                       | Cruden 1968                             |
| 557. *E. cyathigerum* (Charpentier, 1840)      | 27(26A+X)             | –             | Finland                   | Oksala 1939a, 1945                      |
| 558. *E. ebrium* (Hagen, 1861)                 | 27(26A+X)             | –             | Former USSR               | Makalowskaja 1940                      |
| 559. *E. eximium* Hagen, 1861                  | 27(26A+X)             | –             | Netherlands               | Kiauta 1969a, c                         |
| 560. *E. najas* (Hansemann, 1823)              | 27(26A+X)             | –             | Russia                    | Perepelov and Bugrov 2001b             |
| 561. *E. nobile* (Hansemann, 1823)             | 27(26A+X)             | –             | Russia                    | Kuznetsova et al. 2020b                |
| 562. *Homeoura chelifer* (Selys, 1876)         | 27(26A+X)             | +             | Surinam                   | Kiauta 1971a as Enallagma cheliferum (Selys, 1876) |
| 563. *Ischnura aurora* (Brauer, 1865)          | 27(26A+X)             | –             | Brazil                    | Fereira et al. 1979 as *E. chelifer*    |
| 564. *I. caprella* (Hagen, 1861)               | 27(26A+X)             | –             | Bolivia                   | Cumming 1964 as Ceratia caprella (Hagen, 1861) |
| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|---------------------|----------------|---------|------------|
| 565.  | I. cervula Selys, 1876 | 27(26A+X) | – | USA | Cruden 1968 |
| 566.  | I. denticularis (Burmeister, 1839) | 27(26A+X) | – | USA | Cruden 1968 |
| 567.  | I. elegani (Van der Linden, 1823) | 27(26A+X) | – | Finland | Okasa 1939a, 1945 |
|       |                     | – – – | – | Netherlands | Kiauta 1969a |
| 568.  | I. flaviatilis Selys, 1876 | 27(26A+X) | – | Bolivia | Cumming 1964 |
| 569.  | I. forejata Morton, 1907 | 27(26A+X) | – | Nepal | Kiauta 1974, 1975 |
| 570.  | I. ilusiae (Morton, 1907) | 25(24A+X) | + | India | Tyagi 1978b as Rhodichthys ilusiae (Morton, 1907) |
| 571.  | I. pumilio (Charpentier, 1825) | 27(26A+X) | – | Netherlands | Kiauta 1976 |
| 572.  | I. perparva Selys, 1876 | 27(26A+X) | – | USA | Cruden 1968 |
| 573.  | I. ramburi (Selys, 1860) | 27(26A+X) | + | USA | Kiauta and Brink 1978 |
| 574.  | I. rufostigma Selys, 1876 | 27(26A+X) | – | Nepal | Kiauta 1974, 1975 |
|       |                     | – | + | Philippines | Kiauta and Kiauta 1980b |
| 575.  | I. senegalensis (Rambur, 1842) | 27(26A+X) | + | Japan | Kichijo 1941, 1942d, e |
|       |                     | – – – | + | India | Dasgupta 1957 |
|       |                     | – – – | + | Ethiopia | Kiauta 1969b |
|       |                     | – – – | + | Thailand | Kiauta and Kiauta 1983 |
|       |                     | – – – | + | India | Praad and Thomas 1992 |
| 576.  | I. verticalis (Say, 1839) | 27(26A+X) | – | USA | Cruden 1968 |
| 577.  | I. ultima Ris, 1908 | 27(26A+X) | – | Bolivia | Cumming 1964 |
| 578.  | Leptagrion macrurum (Burmeister, 1839) | 30(28A+neo-XY) | – | Brazil | Kiauta 1971c, 1972d |
| 579.  | Mecistogaster sp. 1 | 29(28A+X) | + | Bolivia | Cumming 1964 |
| 580.  | Mecistogaster sp. 2 | 12(10A+neo-XY) | – | Brazil | Kiauta 1974, 1975 |
| 581.  | Megalagrion noburneae (Blackburn, 1884) | 27(26A+X) | + | Hawaii | Kiauta 1969b |
| 582.  | Mortonaagrion seletum (Ris, 1916) | 27(26A+X) | + | Japan | Kichijo 1941, 1942a, d, e |
| 583.  | Nesaeleia terne (Hagen, 1861) | 27(26A+X) | – | USA | Cruden 1968 |
| 584.  | N. speciosa (Charpentier, 1840) | 28(26A+XX)* | – | Finland | Okasa 1945 |
| 585.  | Oxyagrion hemplei Calvert, 1909 | 27(26A+X) | – | Brazil | Souza Bueno 1982 |
| 586.  | O. terminalae Selys, 1876 | 27(26A+X) | – | Surinam | Kiauta 1979a |
| 587.  | Parsacrion hieroglyphicum (Brauer, 1865) | 27(26A+X) | – | Brazil | Perreira et al. 1979 |
| 588.  | P. malayanum (Selys, 1876) | 27(26A+X) | + | Nepal | Kiauta 1974, 1975 |
| 589.  | Proichneura subfurcata (Selys, 1876) | 27(26A+X) | – | Kenya | Wasscher 1985 as Enallagma subfurcatum Selys, 1876 |
| 590.  | Pseudagrion acacie Förster, 1906 | 27(26A+X) | + | Republic of South Africa | Boyes et al. 1980 |
| 591.  | P. australasiae Selys, 1876 | 27(26A+X) | + | India | Dasgupta 1957 |
| 592.  | P. decorum (Rambur, 1842) | 27(26A+X) | + | India | Dasgupta 1957 |
| 593.  | P. kersteni (Gerstaker, 1869) | 27(26A+X) | – | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980 |
| 594.  | P. microcephalum (Rambur, 1842) | 27(26A+X) | – | India | Dasgupta 1957 |
| 595.  | P. pruinnum (Burmeister, 1839) | 27(26A+X) | + | Thailand | Kiauta and Kiauta 1980b |
| 596.  | P. rubripes (Selys, 1876) | 27(26A+X) | + | India | Dasgupta 1957 |
| 597.  | P. salisburyense Ris, 1921 | 27(26A+X) | + | Kingdom of Eswatini (Former Swaziland) | Boyes et al. 1980 |
| 598.  | P. spenceii Fraser, 1922 | 27(26A+X) | + | India | Dasgupta 1957 |
| 599.  | P. subulatus Pinhey, 1956 | 25(24A+X) | + | Burkina Faso (Former Voltaic Republic) | Kiauta and Ochssee 1979 |
| 600.  | Pyrrhosoma nymphula (Suter, 1776) | 28(26A+XX)* | – | Finland | Okasa 1945 |
| 601.  | Telebasis carmencia Calvert, 1909 | 27(26A+X) | – | Surinam | Kiauta 1979a |
| 602.  | Tigiaegelion aurantinigrum Calvert, 1909 | 27(26A+X) | – | Bolivia | Cumming 1964 |
Karyotypes of Odonata: a check-list

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 603. *Xanthocnemis zelandica* (McLachlan, 1873) | 27(26A+X) | – | New Zealand | Jensen 1980 as *X. zelandica* (McLachlan, 1873) |
| 604. *Zonia grion exclamationis* (Selys, 1876) | 27(26A+X) | – | USA | Cruden 1968 |

### Protoneuridae

| Taxon | Karyotype formula 2n | m-chromosomes | Country | References |
|-------|----------------------|---------------|---------|------------|
| 605. *Cacioneura autumnalis* Fraser, 1922 | 25(24A+X) | * | India | Tyagi 1978b |
| 606. *Epipleoneura sp.* | 27(26A+X) | – | Bolivia | Cumming 1964 |
| 607. *Protoneura rubriventris* (Selys, 1860) | 27(26A+X) | * | Bolivia | Cumming 1964 as *Neoneura rubriventris* Selys, 1860 |

* In the original publication, the female karyotype is given.
** Jensen (1980) considers these data as erroneous (but see section “Concluding remarks and future directions” in the present paper).
*** Karyotype formula is extrapolated based on vague descriptions by Cumming (1964).

Table 2. The diversity of chromosome numbers and sex chromosome mechanisms, and modal karyotypes in 23 families of Odonata: a summary.

| Taxon | N of species/genera described* | N of species/genera studied | Male karyotypes | Modal karyotype | N of species/genera with modal karyotype (occurrence in percent) |
|-------|--------------------------------|----------------------------|----------------|----------------|---------------------------------------------------------------|
| Anisogomphoptera | Anisoptera | Epiophlebioidea | Epiophlebiidae (4/1) | 1/1 | 25, X0 | 24A + X | 1 (100) / 1 (100) |
| Aeshnoidea | Aeshnidae (456/51) | 58/18 | 13, X0; 14, neo-XY; 15, X0; 16, neo-XY; 19, X0; 21, X0; 24, neo-XY; 25, X0; 26, neo-XY; 27, X0 | 26A + X | 44 (76) / 14 (78) |
| Petaluroidea | Petaluridae (10/5) | 4/3 | 17, X0; 19, X0; 25, X0 | 16A + X | 3 (75) / 2 (67) |
| Gomphoidea | Gomphidae (980/87) | 66/31 | 12, neo-neo-XY; 21, X0; 22, neo-XY; 23, X0; 24, neo-XY; 25, X0 | 22A + X | 57 (86) / 28 (90) |
| Libelluloidea | Macromiidae (125/4) | 6/3 | 25, X0 | 24A + X | 6 (100) / 3 (100) |
| Cordulegastridea | Corduliidae (154/20) | 23/7 | 10, neo-XY; 11, X0; 13, X0; 14, neo-XY; 20, X0; 21, X0; 25, X0; 26, neo-XY; 27, X0 | 24A + X | 19 (83) / 6 (86) |
| Libellulidae (1037/142) | 255/59 | 6, neo-XY; 6 neo-XY; 8, neo-XY; 10, neo-XY; 12, neo-XY; 17, X0; 21, X0; 22, neo-XY; 23, X0; 23, X1X2Y; 24, neo-XY; 25, X0; 27, X0; 28, neo-XY; 29, X0; 41, X0 | 24A + X | 227 (89) / 57 (97) |
| Chlorogomphidae (47/3) | 9/3 | 23, X0; 25, X0 | 24A + X | 8 (89) / 3 (100) |
| Zygoptera | Lestoidea | Lestidae (151/9) | 20/5 | 19, X0; 21, X0; 25, X0 | 24A + X | 18 (90) / 5 (100) |
| Platystictoidea | Platystictidae (224/6) | 4/3 | 25, X0 | 24A + X | 4 (100) / 3 (100) |
| Calopterygoidea | Calopterygidae (185/21) | 20/8 | 23, X0; 25, X0; 27, X0 | 24A + X | 20 (100) / 8 (100) |
| Chlorocyphidae (144/19) | 9/6 | 23, X0; 25, X0 | 24A + X | 22 (89) / 5 (84) |
| Polythoridae (59/7) | 2/2 | 23, X0 | 22A + X | 2 (100) / 2 (100) |
| Euphaeidae (68/12) | 4/4 | 25, X0 | 24A + X | 4 (100) / 4 (100) |
| Megapodagrionidae (296/42) | 3/2 | 25, X0 | 24A + X | 3 (100) / 2 (100) |
| Heteragrionidae (57/2) | 2/1 | 25, X0 | 24A + X | 2 (100) / 1 (100) |
| Philogeniidae (40/2) | 1/1 | 25, X0 | 24A + X | 1 (100) / 1 (100) |
| Hypolestidae (6/4) | 1/1 | 17, X0 | 16A + X | 1 (100) / 1 (100) |
| Coenagrionoidea | Platycnemididae (404/40) | 22/8 | 25, X0 | 24A + X | 19 (100) / 7 (100) |
| Coenagrionidae (1267/114) | 92/28 | 12, neo-XY; 25, X0; 27, X0; 29, X0; 30, neo-XY; 37, X0 | 24A + X | 81 (89) / 26 (90) |
| Protoneuridae (260 / 25) | 3/3 | 25, X0; 27, X0 | 24A + X | 2 (70) / 2 (70) |

* Taken from Dijkstra et al. 2013
Concluding remarks and future directions

In total, karyotypes of 607 species (198 genera, 23 families) of Odonata are studied up to now. Table 1, presented in our work, includes 423 species (125 genera, 8 families) of the Anisoptera, 184 species (72 genera, 14 families) of the Zygoptera, and one species of the Anisozygoptera. Thus, the presently available karyotype data cover about 10% of the world species diversity of the order in general.
Within Odonata, chromosome numbers in males vary over a relatively wide range, from \(2n = 6\) in *Macrothemis hemichlora* and *Orthemis levis* to \(2n = 41\) in *O. nodiplaga*. Both low chromosome number species are suggested to have an evolutionarily secondary neo-XY system (Cumming 1964; Kiauta 1972c) that could have arisen through an X-autosome fusion from an X(0) system. All three of the above species belong to the largest dragonfly family Libellulidae, in which nearly 89% of studied species (255 in total) have the karyotype \(2n = 25(24A + X)\). The last one is the most common in Odonata in general: it occurs in each of the three suborders, Zygoptera, Anisoptera and Anisozygoptera, and in all families with the exception of two damselfly families, the Polythoridae with only two studied species sharing \(2n = 23(22A + X)\) and a monotypic family Hypolestidae with \(2n = 17(16A + X)\) in male *Hypolestes clara*. Besides Libellulidae, the karyotype \(2n = 25(24A + X)\) is currently the presumed modal one in 14 other families, such being the case at least in six better covered (at species and/or generic level) families, i.e. the dragonfly families Corduliidae, Cordulegastridae, and Macromiidae, and the damselfly families Lestidae, Calopterygidae, and Platycnemididae (Table 2, Fig. 1). This chromosome set is suggested to be an ancestral one for the order Odonata in general (Oguma 1930; Kuznetsova et al. 2020b) although this suggestion remains questionable at this stage.

Chromosomal rearrangements, among which fission and fusions apparently predominated (Kiauta 1969c, 1972c), led to the appearance of divergent karyotypes in the evolution of Odonata. As a result, in many dragonfly and damselfly families, other karyotypes, when occurring, are of secondary origin as indicated by either a diverged number of autosomes or a secondary sex chromosome system of an XY-type or both (e.g. Cumming 1964; Kiauta 1969a, c; Agopian and Mola 1984, 1988; Mola et al. 1999; Perepelov and Bugrov 2002). Some interesting examples of this kind can be found in the family Libellulidae, in which \(2n = 25(24A + X)\) is most likely an evolutionarily initial karyotype (e.g. Agopian and Mola 1988). These examples are as follows (see Table 1): *Orthemis nodiplaga* and *O. ambinigra* with \(2n = 41(40A + X)\) and \(2n = 12(10A + \text{neo-XY})\), respectively; *Erythrodiplax media* and *E. minuscula*, both with \(2n = 22(20A + \text{neo-XY})\); *Micrathyria longifasciata* and *M. ungulata* with \(2n = 24(22A + \text{neo-XY})\) and \(2n = 23(20A + X_1X_2Y)\), respectively. In some families, any of these presumably derived karyotypes not only occurs but also prevails and may be considered modal (see Table 2 and Fig. 1). Within Anisoptera, such families are Aeshnidae (\(2n = 26A + X\)) and Gomphidae (\(2n = 22A + X\)), whereas within Zygoptera, these are Chlorocyphidae (\(2n = 22A + X\)) and Coenagrionidae (\(2n = 26A + X\)). Thus, Odonata, despite the fact that they have holokinetic chromosomes (Nokkala et al. 2002), demonstrate rather high karyotypic stability, with most species showing \(2n = 25\) (found in 60% of studied species), \(2n = 27(21%)\) and \(2n = 23(13%)\) which may point to some selective constraints acting to stabilize chromosome number in their evolution (Kuznetsova et al. 2020b).

There are the species for which different authors give various karyotypes that are sometimes difficult to interpret (see Table 1). In some cases, this might be due to
misidentifications of a particular species or an error in determining the karyotype. For example, Wolfe (1953) reported $2n = 17(16A + X)$ for males of *Uropetala carovei* (Petaluridae, Anisoptera) from New Zealand. However, according to later studies of this species in the same locality (Jensen and Mahanty 1978; Jensen 1980), it has $2n = 25(24A + X)$, and Jensen (1980) therefore considers the Wolfe data as erroneous. We cannot exclude, however, that the above authors studied different *U. carovei* subspecies, *U. c. carovei* White, 1846 and *U. c. chiltoni* Tillyard, 1921, that may indeed have different karyotypes. In other cases, the chromosome number difference between geographic populations might be indicative of the inter-population variation within the bounds of one taxonomic species or even the existence of a species complex with several morphologically cryptic species. For example, 4 of the 17 studied species of the dragonfly genus *Aeshna* Fabricius, 1775 were reported to have different karyotypes in different populations. These are: *Aeshna grandis* – $2n = 26A + X$ (former USSR), $2n = 24A + X$ (former USSR, Finland), and $2n = 24A + neo-XY$ (Netherlands, Finland); *A. isoceles* – $2n = 26A + X$ (USA) and $2n = 24A + X$ (Russia); *A. juncea* – $2n = 26A + X$ (Italy) and $2n = 24A + neo-XY$ (Finland, former USSR, Italy); *A. mixta* – $2n = 26A + X$ (Netherlands) and $2n = 24A + X$ (India) (Table 1). In all such cases, special studies involving a combined analysis of karyotypes, morphology, distribution patterns and molecular markers are needed.

Approximately 80% of Odonata species have a pair of very small chromosomes, i.e. microchromosomes or m-chromosomes (Mola 2007, Table 1). A number of speculations have been forwarded to explain the origin of these chromosomes in Odonata. Kiauta (1968e) suggested m-chromosomes to be fragments of “normal” chromosomes, whereas Oguma (1930) considered them the remnants of an autosome pair in the process of its elimination by progressive loss of chromatin. The size of the smaller chromosome pair was shown to be variable within different species (Kiauta 1968e; see Mola 2007 for other references) which is consistent with both hypotheses. Closely related species and different populations of the same species often differ from each other in the presence/absence of m-chromosomes (Table 1). This is most likely due to the lack of clear criteria for the identification of a small chromosome pair as m-chromosomes in a particular karyotype (Mola 2007; Kuznetsova et al. 2020b).

Most cytogenetic studies of Odonata have been made only to determine the chromosome number and sex chromosome mechanism for which the routine staining was used. Although a considerable amount of such data was obtained (Table 1, 2), standard karyotypes of many Odonata taxa remain totally unknown (Fig. 1). Lack of data on more “primitive” families of Zygoptera (e.g. Hemiphlebiidae) and Anisoptera (e.g. Austropetaliidae and Neopetaliidae) makes difficult understanding karyotype evolution of the order in general.

During the last decades, karyotypes of a few dozen Odonata species were studied using various techniques of differential staining of chromosomes such as C-banding, AgNOR-staining and DNA specific fluorochrome banding visualizing constitutive heterochromatin, nucleolus organizing regions (NORs) and AT- and GC-rich chromosome segments, respectively. Such data can be found in the following publica-
tions: Thomas and Prasad (1986), Prasad and Thomas (1992), Perepelov et al. (1998), Perepelov and Bugrov (2001a, b, 2002), Grozeva and Marinov (2007), De Gennaro et al. (2008), Walia et al. (2011, 2018), Walia and Chahal (2014, 2018), Walia and Devi (2018), Walia and Katnoria (2018), Walia and Devi (2020a, b). Unfortunately, these data alone did not shed much light on the karyotypic evolution of Odonata.

Although the classical cytological techniques remain necessary starting points for cytogenetic studies of Odonata to get an overview of their genomes, the future of Odonata cytogenetics must be coupled with the application of new cytogenetic molecular techniques that enable the localization of specific DNA sequences in chromosomes and the identification of individual chromosomes in karyotypes. In the article by Frydrychová et al. (2004) and, on a larger scale, in two of our recent publications (Kuznetsova et al. 2018, 2020b), the fluorescence in situ hybridization (FISH) technique was used for the first time for analyzing Odonata karyotypes. Several species belonging to the Anisoptera (from the families Aeshnidae, Libellulidae, and Corduliidae) and the Zygoptera (from the families Coenagrionidae and Calopterygidae) were studied regarding the occurrence of the TTAGG telomeric repeats and the distribution of the 18S rRNA genes in their karyotypes. The TTAGG repeats proved to be the canonical motif of telomeres in the class Insecta in general, which, however, was repeatedly lost in the evolution of different phylogenetic lineages (Kuznetsova et al. 2020a). It was shown in the listed Odonata publications that the (TTAGG)$_n$ motif does not occur in all but one (Sympetrum vulgatum) species, and the 18S is located on one of the largest pairs of autosomes in all studied dragonfly species but on m-chromosomes in all studied damselfly species (Kuznetsova et al. 2020b).

The results obtained showed great promise of the combined use of FISH and classical and banding cytogenetics in order to identify new chromosomal markers, reveal differences between species, particularly when they share the same or very close karyotypes, and speculate about the mechanisms involved in the karyotype evolution of Odonata (Kuznetsova et al. 2020b). Another promising line of future research could be to test hypotheses (Mola and Papeschi 1994; Ardila-Garcia and Gregory 2009) about whether there is a relationship between karyotype evolution and genome size diversity in the Odonata or there is no such relationship.

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