Chromosome number evolution in skippers (Lepidoptera, Hesperiidae)

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Abstract

Lepidoptera (butterflies and moths), as many other groups of animals and plants, simultaneously represent preservation of ancestral karyotype in the majority of families with a high degree of chromosome number instability in numerous independently evolved phylogenetic lineages. However, the pattern and trends of karyotype evolution in some Lepidoptera families are poorly studied. Here I provide a survey of chromosome numbers in skippers (family Hesperiidae) based on intensive search and analysis of published data. I demonstrate that the majority of skippers preserve the haploid chromosome number n=31 that seems to be an ancestral number for the Hesperiidae and the order Lepidoptera at whole. However, in the tribe Baorini the derived number n=16 is the most typical state which can be used as a (syn)apomorphic character in further phylogenetic investigations. Several groups of skippers display extreme chromosome number variations on within-species (e.g. the representatives of the genus Carcharodus Hübner, [1819]) and between-species (e.g. the genus Agathymus Freeman, 1959) levels. Thus, these groups can be used as model systems for future analysis of the phenomenon of chromosome instability. Interspecific chromosomal differences are also shown to be useful for discovering and describing new cryptic species of Hesperiidae representing in such a way a powerful tool in biodiversity research. Generally, the skipper butterflies promise to be an exciting group that will significantly contribute to the growing knowledge of patterns and processes of chromosome evolution.

Keywords

Lepidoptera, Hesperiidae, karyotype evolution, chromosome number, cryptic species, phylogeny, chromosomal conservatism, chromosomal instability
Introduction

The main karyotypic features of organisms, particularly the number of chromosomes, tend to be stable within species (White 1973, King 1993). New chromosomal rearrangements usually originate as heterozygotes and are often – although not always (Lukhtanov et al. 2011) – associated with heterozygote disadvantage. The spread of such rearrangements to fixation within a large population has low probability (King 1993). Therefore, many organisms are characterized by chromosomal conservatism, a situation in which all closely related taxa demonstrate the same chromosome number.

In contrast to chromosomal conservatism, chromosomal instability characterizes situations where multiple closely related taxa (populations, subspecies and/or species) belonging to a single phylogenetic lineage differ drastically from each other by major chromosomal rearrangements, sometimes resulting in high variability in chromosome number.

Both phenomena - chromosomal conservatism and chromosomal instability - are clearly expressed in insects of the order Lepidoptera (butterflies and moths). The modal haploid number of chromosomes (n) of n = 31 or n = 30 (Suomalainen 1969, Lukhtanov 2000) is preserved in the majority of lepidopteran families (Robinson 1971). At the same time, numerous cases of chromosomal instability have been discovered in the butterfly families, e.g. in Papilionidae (Emmel et al. 1995), Pieridae (Lukhtanov 1991, Lukhtanov et al. 2011, Dinca et al. 2011), Nymphalidae (Brown et al. 1992, 2004, 2007a, 2007b) and Riodinidae (Brown et al. 2012). This phenomenon was analyzed in more detail in the family Lycaenidae (Kandul et al. 2004, 2007, Lukhtanov et al. 2005, 2006, 2008, Vershinina and Lukhtanov 2010, 2013, Vila et al. 2010, Talavera et al. 2013, Przybyłowicz et al. 2014).

Skippers (the family Hesperiidae) are studied to a lesser extent with the respect of karyotype evolution than the other butterfly families mentioned above (but see: Emmel and Trew 1973, Saura et al. 2013). This family includes about 4000 species under 567 genera and is a globally distributed group found in all continents except Antarctica (Warren et al. 2008). The tribal level classification of skippers, based on combined analysis of molecular and morphological data, was recently elaborated by Warren and colleagues (Warren et al. 2008, 2009).

Here I provide a first world-wide survey of chromosome numbers in skippers based on intensive search and analysis of published data.

Results

The results of literature search are presented in the Table below. It includes all the discovered chromosome counts except n=13 for Ochlodes venatus (Bremer et Grey, 1853), noted by Bigger (1960) as “Augiades venata”. The name Ochlodes venatus was long used for the Ochlodes species of Europe, but it actually refers to its Far Eastern sister species, and the European taxon is now called O. sylvanus (Esper, 1777) (ICZN 2000). Both European and Far Eastern species have the same chromosome number n=29 (Federley
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1938, Lorković 1941, Abe et al. 2006), not n=13 as indicated by Bigger (1960). Thus, the species name used by Bigger (1960) was probably misidentification.

The classification of skippers accepted in this paper follows Warren and colleagues (Warren et al. 2008, 2009).

Discussion

Modal chromosomal numbers

The table gives the chromosome numbers of 205 species of skippers, i.e. about 5% of the species of the world fauna. This number is not enough to infer any final statements about peculiarities of chromosome numbers distribution within the Hesperiidae. However, several tentative conclusions can be made. The haploid chromosome number n=31 was found in 50 studied species of skippers and, thus, it is a clear modal number for the family at whole. Interestingly, n=31 was found in representatives of all investigated subfamilies, except for Heteropterinae. However, in the last subfamily only one species was karyologically studied until now, and discovery of n=31 in Heteropterinae is not excluded in future. The next most common numbers are n=29 (43 species), n=30 (33 species) and n=28 (13 species).

Subfamilies Coeliadinae and Eudaminae have a sharp peak at n=31. In the subfamily Trapezitinae n=31 was also found (only one species studied).

Within the subfamily Pyrginae, the modal number n=31 is found in the tribe Erynnini. The tribe Pyrrhopygini is characterized by the most common n=28. The modal number in the tribe Tagiadini is n=30. The tribe Carcharodini has peaks at n=30 and n=31. In the tribe Pyrgini, n=29, n=30 and n=31 were found as the most common numbers.

In the family Heteropterinae n=29 was found (only one species studied).

Within the subfamily Hesperiinae, the tribes Taractrocerini, Thymelicini, Calpodini, Moncini and Hesperiini are characterized by the most common n=29. Very variable chromosome numbers (from n=5 to n=50) were found in the tribe Aeromachini. It is difficult to infer the modal number for the last tribe. However, it should be noted that one species, *Thoressa varia*, has n=31 as the majority of other skippers. The tribe Baorini (subfamily Hesperiinae) has a clear peak at n=16, so it is exceptional with respect to the modal number of chromosomes.

The overall evidence indicates that chromosome numbers of Coeliadinae, Eudaminae, Trapezitinae, Pyrginae and Hesperiinae conform to the lepidopteran modal of n=31 (Robinson 1971). This number seems to be an ancestral one for the Hesperiiidae as for the order Lepidoptera at whole (Suomalainen 1969, Lukhtanov 2000). This modal number (or its deviation to n=30, n=29 and 28) were preserved in the majority of skippers. However, in the tribe Baorini the number n=16 was evolved and, thus, represents a derived trait which can be used as a (syn)apomorphic character in further phylogenetic studies of the family Hesperiiidae.
Table 1. Chromosome number of skippers (Lepidoptera, Hesperiidae) of the world fauna (Us are univalents; 2n is diploid chromosome number).

Years of the species descriptions are given square brackets in cases where they were not stated in the original sources but were inferred from reliable external evidence.

| # | Species | Haploid chromosome number | Country | Reference |
|---|---------|---------------------------|---------|-----------|
| **Subfamily Coeliadinae** | | | | |
| 1 | *Bibasis aquilina* (Speyer, 1879) | 29 | Japan | Maeki 1953 |
| | *B. a. chrysaeglia* (Butler, 1881) | 31 (2n=62) | Japan | Abe et al. 2006 |
| 2 | *B. jaina formosana* Fruhstorfer, 1911 | 31 | Taiwan | Maeki and Ae 1968b |
| 3 | *Choatpes benjaminaii* (Guérin-Méneville, 1843) | 31 | Japan | Maeki 1953 |
| | *Ch. b. japonica* (Murray, 1875) | 31 | Japan | Saitoh et al. 1978 |
| 4 | *Coelides anchises jucunda* (Butler, 1881) | 30 | Oman | Saitoh 1982 |
| 5 | *C. ernesti* (Grandidier, 1867) | 31 | Madagascar | de Lesse 1972 |
| 6 | *C. fervida* (Butler, 1880) | 23 | Madagascar | de Lesse 1972 |
| 7 | *C. forestan arbogastes* (Guenee, 1863) | 31 | Madagascar | de Lesse 1972 |
| 8 | *C. ramanatek* (Boisduval, 1833) | 31 | Madagascar | de Lesse 1972 |
| **Subfamily Euschemoninae** | no chromosomal data available | | | |
| **Subfamily Eudaminae** | | | | |
| 9 | *Achalarus casica* (Herrich-Schäffer, 1869) | 29 | USA (Texas) | Emmel and Trew 1973 |
| 10 | *A. lyciades* (Geyer, 1832) | 31 | USA (Connecticut) | Maeki 1961 |
| 11 | *A. toxeus* (Plötz, 1882) | 16 | Mexico | Maeki and Remington 1960 |
| 12 | *Astraptes anaphus* (Godman et Salvin, 1896) | 31 | Bolivia | de Lesse 1967a |
| 13 | *A. fidigerator* (Walch, 1775) | 31 | Peru | Kumagai et al. 2010 |
| 14 | *A. naxos* (Hewitson, 1867) | 31 | Brazil | Saura et al. 2013 |
| 15 | *A. phaleaeus* (Godman et Salvin, 1893) | 25 | Guatemala | de Lesse 1967a |
| 16 | *A. longipennis* (Plötz, 1882) | 31 | Costa Rica | Kumagai et al. 2010 |
| | | 31 | Peru | Kumagai et al. 2010 |
| | | 31 | Brazil | Kumagai et al. 2010 |
| 17 | *Autochton* sp. | 20, 21 | Brazil | Kumagai et al. 2010 |
| 18 | *Chioides albofasciatus* (Hewitson, 1867) | 31 | Mexico | de Lesse 1970a |
| | *Ch. albofasciatus* (Hewitson, 1867) (as *Ch. catillus*) | 31 | Mexico | Maeki and Remington 1960 |
| 19 | *Entheus priarius pralina* (Hewitson, 1867) | 22 | Brazil | Saura et al. 2013 |
| 20 | *Epagyrus barisses* (Hewitson, 1874) | 31 | Argentina | de Lesse 1967 |
| 21 | *E. clarus* (Cramer, 1775) | 31 | USA (Florida) | Maeki 1961 |
| 22 | *E. clavicornis tenda* (Evans, 1955) | ca 29–30 | Guatemala | de Lesse 1970a |
| 23 | *Oedrydryus cheris* (Herrich-Schäffer, 1869) | 31 | Bolivia | de Lesse 1967a |
| #  | Species                                                                 | Haploid chromosome number | Country            | Reference                        |
|----|------------------------------------------------------------------------|---------------------------|--------------------|----------------------------------|
| 24 | Phocides polybius phanias (Burmeister, 1880)                           | 16                        | Brazil             | Saura et al. 2013                |
| 25 | Tarsocetus praecia phutia (Hewitson, 1857)                             | 15                        | Brazil             | Saura et al. 2013                |
| 26 | Tborytes pylades pylades (Scudder, 1870)                               | 31                        | USA (Connecticut)  | Maeki 1961                       |
| 27 | Udronomia spitzi (Hayward, 1942)                                      | 29                        | Brazil             | de Lesse and Brown 1971          |
| 28 | Urbanus dorantes dorantes (Stoll, 1790)                               | 31                        | Mexico             | de Lesse 1970a                   |
| 29 | U. doryssus doryssus (Swainson, 1831)                                 | 14                        | Costa Rica         | Kumagai et al. 2010              |
| 30 | Urbanus proteus (Linnaeus, 1758)                                      | 31                        | Bolivia            | de Lesse 1967a                   |
|    |                                                                        | 31                        | Mexico             | de Lesse 1970a                   |
|    |                                                                        | 31                        | USA (Florida)      | Maeki 1961                       |
| 31 | U. simplicius (Stoll, 1790)                                           | 31                        | Argentina          | de Lesse 1967a                   |
| 32 | U. teleus (Hübner, 1821)                                              | 31                        | Argentina          | de Lesse 1967a                   |

**Subfamily Pyrginae**

**Tribe Pyrrhopygini**

| #  | Species                                                                 | Haploid chromosome number | Country            | Reference                        |
|----|------------------------------------------------------------------------|---------------------------|--------------------|----------------------------------|
| 33 | Elbella lampra (Hopffer, 1874)                                         | 40                        | Brazil             | de Lesse 1970a                   |
| 34 | (?) Jemadia sp.                                                        | 32(?)                     | Brazil             | Saura et al. 2013                |
| 35 | Mimoniades montana J. Zikán, 1938                                      | 27                        | Brazil             | Saura et al. 2013                |
| 36 | M. nurcia (Swainson, 1821)                                             | 28                        | Ecuador            | de Lesse 1967a                   |
|    | M. n. malis (Godman et Salvin, 1879)                                    | 28                        | Colombia           | Saura et al. 2013                |
| 37 | Mimoniades sp.                                                          | 21                        | Colombia           | Saura et al. 2013                |
| 38 | Mimoniades sp.                                                          | 28                        | Colombia           | Saura et al. 2013                |
| 39 | M. versicolor (Latreille, [1824])                                      | 28                        | Brazil             | de Lesse and Brown 1971          |
| 40 | Pyrrhopyge charybdis Westwood, 1852                                    | 14(?)                     | Brazil             | Saura et al. 2013                |
| 41 | P. pelota Plötz, 1879                                                  | 28                        | Argentina          | de Lesse 1967a                   |
| 42 | Pyrrhopyge sp.                                                          | 15                        | Brazil             | Saura et al. 2013                |
| 43 | Sarbia sp.                                                             | 30                        | Brazil             | Saura et al. 2013                |

**Tribe Tagiadini**

| #  | Species                                                                 | Haploid chromosome number | Country     | Reference                           |
|----|------------------------------------------------------------------------|---------------------------|-------------|-------------------------------------|
| 44 | Daimio tethys (Ménétriès, 1857)                                        | 30                        | Japan       | Maeki 1953, Maeki and Makino 1953   |
| 45 | D. t. moorei Mabille, 1876                                             | 30                        | Taiwan      | Maeki and Ae 1968b                 |
| 46 | Eagnis lucetia (Hewitson, 1876)                                        | 30                        | Uganda      | de Lesse 1968                       |
| 47 | E. saladius astoria Holland, 1896                                      | 30                        | Kenya       | de Lesse 1968                       |
| 48 | Eretis lugens (Rogenhofer, 1891)                                       | 28                        | Kenya       | de Lesse 1968                       |

**Tribe Celaenorrhinini**

| #  | Species                                                                 | Haploid chromosome number | Country     | Reference                           |
|----|------------------------------------------------------------------------|---------------------------|-------------|-------------------------------------|
| 49 | Sarangesa phidyle (Walker, 1870)                                       | 29                        | Senegal     | de Lesse and Condamin 1962          |

**Tribe Carcharodini**

| #  | Species                                                                 | Haploid chromosome number | Country     | Reference                           |
|----|------------------------------------------------------------------------|---------------------------|-------------|-------------------------------------|
| 50 | Carcharodus alicae (Esper, [1780])                                      | 31                        | Croatia     | Lorkovic 1941                       |
| 51 | C. boeticus Reverdin, 1913                                              | 43–47                     | Spain       | de Lesse 1960                       |
|    | C. boeticus Reverdin, 1913                                              | 40–52                     | France      | de Lesse 1960                       |
|    | C. boeticus Reverdin, 1913                                              | 38–46                     | Italy       | de Lesse 1960                       |
| #  | Species                                      | Haploid chromosome number | Country        | Reference       |
|----|----------------------------------------------|---------------------------|----------------|-----------------|
| 52 | *C. dravira* (Moore, 1874)                   | 37–48 (with Us)           | Iran           | de Lesse 1960   |
| 53 | *C. flocciferus* (Zeller, 1847)              | 32–41 (with Us)           | France (Cauterets) | de Lesse 1960 |
| 54 | *C. flocciferus* (Zeller, 1847)              | 42–58 (with Us)           | Italy          | de Lesse 1960   |
| 55 | *C. lavathenerae* (Esper, [1783])            | 30                        | France (Salau, Ariege) | de Lesse 1960 |
| 56 | *C. orientalis* Reverdin, 1913               | 31–32                     | Lebanon        | de Lesse 1960   |
|    |                                             |                           |                |                 |
|    |                                             | 30                        | Turkey (Van)   | de Lesse 1960   |
| 57 | *C. stauderi ambiguus* Verity, 1925          | 30                        | Lebanon        | de Lesse 1960   |
|    |                                             | 30                        | Turkey         | de Lesse 1960   |
| 58 | *Hesperopsis alpheus* (W. H. Edwards, 1876) (as *Pholisora*) | 34               | USA (Texas)    | Emmel and Trew 1973 |
| 59 | *Muschampia nomas* (Lederer, 1855)           | 30                        | Lebanon        | de Lesse 1960   |
| 60 | *M. proteoides* (Wagner, 1929)               | 30                        | Lebanon        | Larsen 1975     |
| 61 | *M. proto* (Ochsenheimer, 1808)              | 30                        | Spain          | de Lesse 1960   |
|    |                                             | 30                        | Lebanon        | Larsen 1975     |
| 62 | *Pholisora catullus* (Fabricius, 1793)       | 29                        | USA            | Lorkovic in Robinson 1971 |
| 63 | *Spialia orbifer* (Hübner, [1823])           | 30                        | Croatia        | Lorkovic 1941   |
|    |                                             | 31                        | Turkey         | de Lesse 1960   |
| 64 | *S. phlomidis* (Herrich-Schäffer, [1845])  | 31                        | Turkey         | de Lesse 1960   |
| 65 | *S. sertorius* (Hoffmannsegg, 1804)         | 31                        | Slovenia       | Lorkovic 1941   |

**Tribe Erynnini**

| #  | Species                                      | Haploid chromosome number | Country        | Reference       |
|----|----------------------------------------------|---------------------------|----------------|-----------------|
| 66 | *Chiomara asychis georgina* (Reakirt, 1868) | 31                        | Mexico         | de Lesse 1970a  |
|    | *Ch. asychis georgina* (Reakirt, 1868)       | 32                        | USA (Texas)    | Emmel and Trew 1973 |
| 67 | *Chiomara sp.*                               | 31                        | Trinidad       | Wesley and Emmel 1975 |
| 68 | *Ebrietas anacreon* (Staudinger, 1876)       | 31                        | Argentina      | de Lesse 1967a  |
| 69 | *E. oyris* (Staudinger, 1876)                | 31                        | Argentina      | de Lesse 1967a  |
| 70 | *Erynnis baptitae* (W. Forbes, 1936)         | 31                        | USA (Connecticut) | Maeki 1961 |
| 71 | *E. funeritalis* (Scudder et Burgess, 1870)  | 31                        | Argentina      | de Lesse 1967a  |
| 72 | *E. horatius* (Scudder et Burgess, 1870)     | 31                        | USA (Florida)  | Maeki 1961      |
| 73 | *E. icelus* (Scudder et Burgess, 1870)       | 30                        | USA (Connecticut) | Maeki 1961 |
| 74 | *E. juvenalis juvenalis* (Fabricius, 1793)  | 30                        | USA (Connecticut) | Maeki 1961 |
| 75 | *E. lucilius* (Scudder et Burgess, 1870)     | 31                        | USA (Connecticut) | Maeki and Remington 1960a |
| 76 | *E. marloyi* (Boisduval, [1834])             | 31                        | Lebanon        | de Lesse 1960   |
| 77 | *E. montanus* (Bremer, 1861)                | 31 (2n=62)                | Japan          | Abe et al. 2006 |
|    | *E. montanus* (Bremer, 1861)                | 31                        | Japan          | Maeki 1953      |
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| #  | Species                        | Haploid chromosome number | Country          | Reference                  |
|----|--------------------------------|---------------------------|------------------|----------------------------|
| 78 | *E. persius* (Scudder, 1863)    | 31                        | USA (Connecticut) | Maeki 1961                 |
| 79 | *E. tages* (Linnaeus, 1758)    | 31                        | Croatia          | Lorkovic 1941              |
|    |                                |                           | France           | de Lesse 1960              |
|    |                                |                           | England          | Bigger 1960                |
| 80 | *E. tristis tattius* (W. H. Edwards, 1883) | 31                     | USA (Texas)      | Emmel and Trew 1973       |
| 81 | *Gesta gesta* (Herrich-Schäffer, 1863) | 32                     | Tobago           | Wesley and Emmel 1975     |
| 82 | *Grais stigmaticus* (Mabille, 1883) | 31                     | Mexico           | Maeki and Remington 1960a |
| 83 | *Theagenes albiplaga* (C. Felder et R. Felder, 1867) | 31                     | Bolivia          | de Lesse 1967a             |

### Tribe Achlyodidini

| #  | Species                        | Haploid chromosome number | Country | Reference                  |
|----|--------------------------------|---------------------------|---------|----------------------------|
| 84 | *Achlyodes pallida* (R. Felder, 1869) (as *A. selva*) | 15                     | Bolivia | de Lesse 1967a             |
|    |                                |                           |         | de Lesse 1970a             |
| 85 | *Zera zera zera* (Butler, 1870) | 34                     | Brazil  | de Lesse and Brown 1971   |

### Tribe Pyrgini

| #  | Species                        | Haploid chromosome number | Country          | Reference                  |
|----|--------------------------------|---------------------------|------------------|----------------------------|
| 86 | *Anisochoria sublimbata* Mabille, 1883 | 31                     | Argentina        | de Lesse 1967a             |
| 87 | *Antigonus eurus* (Hübner, [1812]) | 31                        | Mexico           | de Lesse 1970a             |
| 88 | *A. loborius* Plötz, 1884       | 31                        | Argentina        | de Lesse 1967a             |
| 89 | *Celotes nessus* (W. H. Edwards, 1877) | 14, 13                   | USA (Texas)      | Emmel and Trew 1973       |
| 90 | *Heliopetes arsala* (Linnaeus, 1758) | 30                     | Bolivia          | de Lesse 1967a             |
|    | *H. arsala* (Linnaeus, 1758)    | 30                        | Mexico           | de Lesse 1970a             |
| 91 | *H. laviana* (Hewitson, 1868)   | 29                        | USA (Texas)      | Emmel and Trew 1973       |
| 92 | *H. macaina* (Reakirt, [1867])  | 29                        | USA (Texas)      | Emmel and Trew 1973       |
| 93 | *H. omrina* (Butler, 1870)      | 30                        | Argentina        | de Lesse 1967a             |
| 94 | *Heliiopyrgus americanus* (Blanchard, 1852) | 30                     | Chile            | de Lesse 1967a             |
| 95 | *Paches locus* (Westwood, [1852]) | 31                     | Guatemala        | de Lesse 1970a             |
| 96 | *Pyrgus aladaghensis* De Prins et van der Poorten, 1995 | ca 18–21            | Turkey           | Lukhtanov and Kandul 1995 (in Hesselbarth et al. 1995) |
| 97 | *P. albescens* Plötz, 1884      | 30 (2n=60)                | USA (Texas)      | Goodpasture 1976           |
|    |                                |                           |                  | Emmel and Trew 1973       |
| 98 | *P. alveus* (Hübner, [1803])    | 24                        | Finland          | Federley 1938             |
|    |                                |                           |                  | Lorkovic 1941             |
|    |                                |                           |                  | Lukhtanov and Kandul 1995 (in Hesselbarth et al. 1995) |
| 99 | *P. bellieri* (Oberthür, 1910)  | 27                        | France           | de Lesse 1960              |
| 100| *P. bocchoris* (Hewitson, 1874) | 30                        | Argentina        | de Lesse 1967a             |
| 101| *P. bolkarriensis* De Prins et van der Poorten, 1995 | 30         | Turkey           | Lukhtanov and Kandul 1995 (in Hesselbarth et al. 1995) |
| 102| *P. cacaliae* (Rambur, 1839)    | 30                        | Italy            | de Lesse 1960              |
| 103| *P. carlinae* (Rambur, [1839])  | 30                        | Italy            | de Lesse 1960              |
| 104| *P. carthami* (Hübner, [1813])  | 29                        | Italy            | de Lesse 1960              |
| #   | Species                          | Haploid chromosome number | Country                       | Reference                  |
|-----|----------------------------------|---------------------------|-------------------------------|----------------------------|
| 105 | *P. cirsii* (Rambur, [1839])      | 30                        | France (Peyreleau, Aveyron)   | de Lesse 1960              |
| 106 | *P. fides* Hayward, 1940          | 30                        | Chile                         | de Lesse 1967a             |
| 107 | *P. maculatus* (Bremer et Grey, 1852) | 31 (2n=62)               | Japan                         | Abe et al. 2006            |
| 108 | *P. malvar* (Linnaeus, 1758)      | 31                        | Finland                       | Federley 1938              |
|     |                                  |                           |                               |                            |
| 109 | *P. oileus* (Linnaeus, 1767)      | 30 (2n=60)                | USA (Texas)                   | Goodpasture 1976           |
| 110 | *P. onopordi* (Rambur, [1839])    | 30                        | France                        | Lorkovic 1941              |
| 111 | *P. serratum* (Rambur, [1839])    | 30                        | France                        | Lorkovic 1941              |
| 112 | *Trina geometrina geometrina*     | 31                        | Brazil                        | de Lesse and Brown 1971    |

**Subfamily Heteropterinae**

| #   | Species                          | Haploid chromosome number | Country                  | Reference                  |
|-----|----------------------------------|---------------------------|--------------------------|----------------------------|
| 113 | *Butleria quilla* Evans, 1939     | 29                        | Chile                    | de Lesse 1967a             |

**Subfamily Trapezitinae**

| #   | Species                          | Haploid chromosome number | Country                  | Reference                  |
|-----|----------------------------------|---------------------------|--------------------------|----------------------------|
| 114 | *Trapezites eliena* Hewitson, 1868 | 31                       | Australia                | Maeki and Ogata 1971       |

**Subfamily Hesperiinae**

**Tribe Aeromachini**

| #   | Species                          | Haploid chromosome number | Country                  | Reference                  |
|-----|----------------------------------|---------------------------|--------------------------|----------------------------|
| 115 | *Aegiale hesperiaris* (Walker, 1856) | 24                       | Mexico                   | Freeman 1969               |
| 116 | *Agathymus alliae* (Stallings et Turner, 1957) | 38                | USA (Arizona)            | Freeman 1969               |
| 117 | *A. aryca* (Dyar, 1905)          | 5                         | Mexico                   | Freeman 1969               |
| 118 | *A. baueri* (Stallings et Turner, 1954) | 15                | USA (Arizona)            | Freeman 1969               |
| 119 | *A. chisoiensis* (Freeman, 1952) | 18                        | USA (Texas)              | Freeman 1969               |
| 120 | *A. estelleae valverdiensis* Freeman, 1966 | 9                  | USA (Texas)              | Freeman 1969               |
|     | *A. e. estelleae* (Stallings et Turner, 1958) | 9                  | Mexico                   | Freeman 1969               |
| 121 | *A. fremani* Stallings, Turner et Stallings, 1960 | 15                | USA (Arizona)            | Freeman 1969               |
| 122 | *A. gilberti* Freeman, 1964       | 21                        | USA (Texas)              | Freeman 1969               |
| 123 | *A. mariae chinatiensis* Freeman, 1964 | 22                | USA (Texas)              | Freeman 1969               |
|     | *A. mariae latitaensis* Freeman, 1964 | 22                | USA (Texas)              | Freeman 1969               |
|     | *A. mariae mariae* (Barnes et Benjamin, 1924) | 22                | USA or Mexico            | Freeman 1969               |
|     | *A. mariae rindgei* Freeman, 1964 | 22                        | USA (Texas)              | Freeman 1969               |
| 124 | *A. micheneri* Stallings, Turner et Stallings, 1961 | 20                | Mexico                   | Freeman 1969               |
| 125 | *A. neuromogeni florenceae* (Stallings et Turner, 1957) | 10                 | USA (Texas)              | Freeman 1969               |
|     | *A. neuromogeni macalpinei* (Freeman, 1955) | 10                 | USA (Texas)              | Freeman 1969               |
| 126 | *A. polangi* (Skinner, 1905)     | 10                        | USA (Arizona)            | Freeman 1969               |
| 127 | *A. remingtomi* (Stallings et Turner, 1958) | 9                  | Mexico                   | Freeman 1969               |
| #  | Species                                | Haploid chromosome number | Country          | Reference                      |
|----|----------------------------------------|---------------------------|------------------|-------------------------------|
| 128| Alera vulpina (C. Felder et R. Felder, 1867) | ca27                      | Ecuador          | de Lesse 1967a                |
| 129| Ankola fan (Holland, 1844)              | 10                        | Uganda           | De Lesse 1968                 |
| 130| Arotis derasa (Herrich-Schäffer, 1870) (as Euphyes) | 28                        | Brazil           | de Lesse and Brown 1971       |
| 131| Erionota thrax thrax (Linnaeus, 1767)   | 29                        | Malaysia         | Saitoh and Kumagai 1974       |
| 132| Euphyes leptoema Mabille, 1891          | ca28                      | Argentina        | de Lesse 1967a                |
| 133| Megathyrsus colonadensis colonadensis Riley, 1877 | 27                        | USA              | Freeman 1969                  |
| 134| M. colonadensis kendalli Freeman, 1965  | 27                        | USA (South central Texas) | Freeman 1969 |
|     | M. colonadensis louiseae Freeman, 1963  | 27                        | USA (Western Texas) | Freeman 1969                  |
|     | M. colonadensis navajo Skinner, 1911    | 27                        | USA              | Freeman 1969                  |
|     | M. colonadensis reinthali Freeman, 1963 | 27                        | USA (Texas)      | Freeman 1969                  |
|     | M. colonadensis reuben Stallings, Turner et Stallings, 1963 | 27 | USA (Texas) | Freeman 1969 |
|     | M. colonadensis stallingsi Freeman, 1943 | 27                        | USA              | Freeman 1969                  |
|     | M. colonadensis wisororum Stallings et Turner, 1958 | 27 | ?Mexico | Freeman 1969 |
| 135| M. violae Stallings et Turner, 1956     | 27                        | USA              | Maeki 1961, Freeman 1969      |
| 136| M. yuccae buchholzi Freeman, 1952       | 26                        | USA (Florida)    | Freeman 1969                  |
| 137| Paradaleodes incerta (Snellen, 1872)    | 17                        | Uganda           | de Lesse 1968                 |
| 138| Stallingsia maculosia (Freeman, 1955)   | 50                        | USA (Texas)      | Maeki 1961, Freeman 1969      |
| 139| Suastus gremitu (Fabricius, 1798)       | 23                        | Taiwan           | Maeki and Ae 1968b            |
| 140| Thoreisa varia (Murray, 1875)           | 31 (2n=62)                | Japan            | Abe et al. 2006               |
| 141| T. varia (Murray, 1875)                 | 31                        | Japan            | Maeki 1953                    |

**Tribe Baorini**

| #  | Species                                | Haploid chromosome number | Country          | Reference                      |
|----|----------------------------------------|---------------------------|------------------|-------------------------------|
| 142| Gegenes gambica (Mabille, 1878)         | 41                        | Yemen            | Saitoh 1984                   |
|     |                                        |                           | Turkey           | de Lesse 1960                 |
|     |                                        |                           | Lebanon          | Larsen 1982                   |
| 143| Gegenes nostradamus (Fabricius, 1793)   | 15                        | Egypt            | Larsen 1982                   |
|     |                                        |                           | Israel           | Saitoh 1979, Larsen 1982      |
| 144| Gegenes pumilio (Hoffmansegg, 1804)     | 24                        | France           | de Lesse 1960                 |
|     |                                        |                           | Alger            | de Lesse 1967b                |
| 145| Parnara gutata (Bremer et Grey, 1852)   | 16                        | Japan            | Maeki 1953, Maeki and Makino 1953 |
|     |                                        |                           | China            | Saitoh and Abe 1981           |
| 146| Pelopidas conjuncta conjucta (Herrich-Schäffer, 1869) | 16 | Hong Kong | Maeki and Ae 1968a |
| 147| P. jansonis (Butler, 1878)              | 16 (2n=32)                | Japan            | Abe et al. 2006               |
| # | Species | Haploid chromosome number | Country | Reference |
|---|---|---|---|---|
| 148 | P. mathias (Fabricius, 1798) | 16 | Japan | Maeki and Remington 1960 |
| 149 | P. thrax (Hübner, [1821]) | 16 | Lebanon | Larsen 1975 |
| 150 | Polytremis lubricans (Herrich-Schäffer, 1869) | 16 | Taiwan | Maeki and Ae 1968b |
| 151 | P. pellucida (Murray, 1875) | 16, 17, 18 (2n=32, 33) | Japan | Abe et al. 2006 |
| 152 | Zenonia zeno (Trimen, 1864) | 16 | Uganda | de Lesse 1968 |
| 153 | Ocybadistes walkeri sothis Waterhouse, 1933 | 28 | Australia | Maeki and Ogata 1971 |
| 154 | Potanthus flavus (Murray, 1875) | 29 (2n=58) | Japan | Abe et al. 2006 |
| 155 | Telicota ancilla horisha Evans, 1934 | 29 | Taiwan | Maeki and Ae 1968b |
| 156 | Telicota colon stings Evans, 1949 | 29 | Japan (Okinawa) | Abe et al. 2006 |
| 157 | T. ohara formosana Fruhstorfer, 1911 | 29 (2n=58) | Taiwan | Abe et al. 2006 |

**Tribe Taractrocerini**

| # | Species | Haploid chromosome number | Country | Reference |
|---|---|---|---|---|
| 158 | Copaeodes minima (W.H. Edwards, 1870) | 29 | USA (Florida) | Maeki 1961 |
| 159 | Thymelicus sylvestris (Poda, 1761) | 27 | England | Bigger 1960 |
| 160 | Th. sylvaticus (Bremer, 1861) | 10 (2n=20) | Japan | Abe et al. 2006 |
| 161 | Th. acteon (Rottemburg, 1775) | 28 | Spain | de Lesse 1970c |
| 162 | Th. hyrinx (Lederer, 1861) | 29 | Lebanon | Larsen 1975 |
| 163 | Th. leoninus (Butler, 1878) | 9 (2n=18) | Japan | Abe et al. 2006 |
| 164 | Th. lineola (Ochsenheimer, 1808) | 29 | Finland | Federley 1938 |
| | | | 29 | Lebanon | Larsen 1975 |

**Tribe Thymelicinini**

| # | Species | Haploid chromosome number | Country | Reference |
|---|---|---|---|---|
| 165 | Ebusus ebous (Cramer, [1780]) | 29 | Mexico | de Lesse 1970a |
| 166 | Lychnuchus celius (Fabricius, 1793) | 30 | Brazil | de Lesse and Brown 1971 |
| 167 | Panoquina hecebolus (Scudder, 1872) | 29 | USA (Texas) | Emmel and Trew 1973 |
| 168 | Panoquina ocola (W. H. Edwards, 1863) | 29 | USA (Texas) | Emmel and Trew 1973 |
| 169 | P. panoquin (Scudder, 1863) | 29 | USA (Texas) | Maeki 1961 |
| 170 | P. panoquinoides (Skinner, 1891) | 29 | USA (Texas) | Emmel and Trew 1973 |

**Tribe Anthoptini** no chromosomal data available

**Tribe Moncini**

| # | Species | Haploid chromosome number | Country | Reference |
|---|---|---|---|---|
| 171 | Amblyscirtes aenus (W.H. Edwards, 1878) | 28, 29 | USA (Texas) | Emmel and Trew 1973 |
| 172 | A. casus W. H. Edwards, 1883 | 29 | USA (Texas) | Emmel and Trew 1973 |
| 173 | A. celia (Skinner, 1895) | 29 | USA (Texas) | Emmel and Trew 1973 |
| 174 | A. phylace W.H. Edwards, 1878 | 29 | USA (Texas) | Emmel and Trew 1973 |
| 175 | A. texanue Bell, 1927 | 29 | USA (Texas) | Emmel and Trew 1973 |
| 176 | A. vialis (W. H. Edwards, 1862) | 29 | USA (Connecticut) | Maeki 1961 |
| 177 | Cymaenes sp. | 31 | Tobago | Wesly and Emmel 1975 |
### Chromosome number evolution in skippers (Lepidoptera, Hesperiidae)

| #  | Species                                      | Haploid chromosome number | Country         | Reference                  |
|----|----------------------------------------------|---------------------------|-----------------|----------------------------|
| 178| Enosis immaculata immaculata (Hewitson, 1868) | 29                        | Ecuador         | Kumagai et al. 2010        |
| 179| Lerema accius (Smith, 1797)                   | 29 (2n=58)                | USA (Texas)     | Goodpasture 1976           |
| 180| Moeris vopiscus (Herrich-Schäffer, 1869)     | 27                        | Peru            | Kumagai et al. 2010        |
| 181| Nastra lherminier (Latreille, [1824])        | 30                        | USA (Connecticut)| Maeki 1961                 |
| 182| Thargella caura (Plötz, 1882)                | 25                        | Brazil          | de Lesse and Brown 1971    |
| 183| Vettius coryna (Hewitson, [1866])            | 31, ca32                  | Ecuador         | de Lesse 1967a             |
| 184| V. phyllus prona Evans, 1955                 | 26                        | Brazil          | de Lesse and Brown 1971    |
| 185| V. triangularis (Hübner, [1831])             | 26                        | Brazil          | Kumagai et al. 2010        |

#### Tribe Hesperini

| #  | Species                                      | Haploid chromosome number | Country         | Reference                  |
|----|----------------------------------------------|---------------------------|-----------------|----------------------------|
| 186| Adobis capacitus (Lucas, 1857)               | 48                        | USA (Florida)   | Maeki 1961                 |
| 187| Cynea ignita (Bell, 1941)                    | 29                        | Argentina       | de Lesse 1967a             |
| 188| Hesperia comma (Linaeus, 1758)               | 28                        | Italy           | de Lesse 1970c             |
| 189| H. florinda Butler, 1878                     | 28 (2n=56)                | Japan           | Abe et al. 2006            |
| 190| Hylephila fasciolata (Blanchard, 1852)       | 29                        | Argentina       | de Lesse 1967a             |
| 191| H. phyleus (Drury, 1773)                     | 29                        | Argentina       | de Lesse 1967a             |
| 192| H. signata (Blanchard, 1852)                 | 29                        | Chile           | de Lesse 1967a             |
| 193| Ochlodes ochraceus (Bremer, 1861)            | 29 (2n=58)                | Japan           | Abe et al. 2006            |
|    |                                             | 24                        | Japan           | Maeki and Remington 1960   |
| 194| O. sylvamoides (Boisduval, 1852)             | 29                        | USA             | Maeki 1961                 |
| 195| O. sylvanus (Esper, 1777)                    | 29                        | Finland         | Federley 1938              |
| 196| O. venatus (Bremer et Grey, 1853) (as sylvanus Esper, 1777) | 29 (2n=58) | Japan | Abe et al. 2006 |
| 197| Oligoria maculata (W. H. Edwards, 1865)      | 29                        | USA (Florida)   | Maeki 1961                 |
| 198| Pbanes hobomok hobomok (Harris, 1862)        | 29                        | USA             | Maeki 1961                 |
| 199| P. taxile (W. H. Edwards, 1881)              | 29                        | USA             | Maeki 1961                 |
| 200| P. zabulon (Boisduval et Le Conte, [1837])   | 29 (as Polites zabulon)   | USA (Connecticut)| Maeki 1961 |
| 201| Polites themistocles (Latreille, [1824])     | 29                        | USA (Florida)   | Maeki 1961                 |
| 202| P. vibex catilina (Plötz, 1886)              | 29                        | Argentina       | de Lesse 1967a             |
| 203| Polites vibex praceps (Scudder, 1872)        | 27                        | USA (Texas)     | Emmel and Trew 1973        |
| 204| Wallengrenia egeremet (Scudder, 1863)        | 28                        | USA (Texas)     | Emmel and Trew 1973        |
| 205| W. otho curassavica (Snellen, 1887)          | 28–30                     | USA (Texas)     | Emmel and Trew 1973        |
| 206| W. premnas (Wallengren, 1860)                | 27                        | Argentina       | de Lesse 1967              |
Between- and within-species variations in chromosome number

Several groups of skippers display extreme chromosome number variations at the within-species level (Table). The most extreme variations in number of chromosome elements were observed in first meiotic metaphase of *Carcharodus boeticus*, *C. dravira* and *C. flocciferus* (Table, de Lesse 1960). The nature of these variations remains unknown, and there are two plausible explanations for this phenomenon. First, this variation can be explained by presence of so-called B-chromosomes (=additional chromosomes, =supernumerary chromosomes) (de Lesse 1960). B-chromosomes consist mainly of repetitive DNA and can sometimes accumulate through processes of mitotic or meiotic drive (Jones et al. 2008). B-chromosomes can be distinguished from normal A-chromosomes because they are usually smaller and can be seen as additional chromosomes present in only some of the individuals in a population (Camacho et al. 2000, Jones et al. 2008).

Second, this kind of variation can be caused by violations in meiotic chromosome pairing resulting in appearance of univalents (instead of bivalents) in meiotic prophase (Lorković 1990). This type of variation was studied in detail by Maeki and Ae (1979) in butterfly genus *Papilio* and is expected if regular or irregular interspecific mating occurs in nature. Anyway, the nature of intraspecific variations observed in *Carcharodus* is different from that discovered in the Wood White butterfly *Leptidea sinapis* (Linnaeus, 1758) (Pieridae). In the last species the compared range of intraspecific variation in chromosome number (from n=28 to n=53) was caused by multiple chromosome fusions/fissions accumulated within the species (Lukhtanov et al. 2011, Dinca et al. 2011).

Between-species variation exists in numerous genera of skippers (Table 1) and is especially expressed in the Nearctic genus *Agathymus* Freeman, 1959, in which the range of haploid numbers was discovered from n =5 in *A. arynna* to n=38 in *A. alliae* (Freeman 1969). This range is comparable of even exceeds the range found in chromosomally diverse genera from other butterfly families (Lorković 1990, Lukhtanov et al. 2005, Talavera et al. 2013). Thus, the genera of Hesperiidae can be used as model systems for future analysis of the phenomenon of chromosome instability.

Detecting cryptic species using analysis of chromosomal differences

Recent years karyological data have been widely used in studies of butterfly taxonomy and in biodiversity research as main or additional chracters for detecting cryptic species (e.g. Dinca et al. 2011) and for synonymizing biological entities that were incorrectly described as distinct species (e.g. Vila et al. 2010). The family Hesperiidae is not excluded in this respect. In the genus *Gegenes* Hübner, [1819], two cryptic species *G. pumilio* (n=24) and *G. gambica* (n=41) were discovered through extensive chromosome analysis of different populations (de Lesse 1960, 1967b, Larsen 1982, Saitoh 1984).
In the genus *Pyrgus* Hübner, [1819], our unpublished chromosome data (see Table) were used to recognize and then to describe two morphologically similar species, *P. bolkariensis* and *P. aladaghensis* (De Prins and van der Poorten 1995).

Thus, interspecific chromosomal differences are useful for discovering and describing new cryptic species of Hesperiidae representing in such a way a powerful tool in biodiversity research.

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