CompCytogen 8(4): 275–291 (2014)
doi: 10.3897/CompCytogen.v8i4.8789
http://compcytogen.pensoft.net

RESEARCH ARTICLE

COMPARATIVE Cytogenetics
A peer-reviewed open-access journal
International Journal of Plant & Animal Cytogenetics, Karyosystematics, and Molecular Systematics

Chromosome number evolution in skippers (Lepidoptera, Hesperiidae)

Vladimir A. Lukhtanov[1,2]

1 *Department of Entomology, Faculty of Biology, St. Petersburg State University, Universitetskaya nab. 7/9, 199034 St. Petersburg, Russia* **2** *Department of Karyosystematics, Zoological Institute of Russian Academy of Science, Universitetskaya nab. 1, 199034 St. Petersburg, Russia*

Corresponding author: *Vladimir A. Lukhtanov* (lukhtanov@mail.ru)

Academic editor: *N. Shapoval* | Received 21 October 2014 | Accepted 29 October 2014 | Published 14 November 2014

http://zoobank.org/C1B405AA-DFE2-401B-B25A-31E8D7794B99

Citation: Lukhtanov VA (2014) Chromosome number evolution in skippers (Lepidoptera, Hesperiidae). Comparative Cytogenetics 8(4): 275–291. doi: 10.3897/CompCytogen.v8i4.8789

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

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 Hesperiidae 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 Hesperiidae.

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	*Choaspes benjaminii* (Guérin-Méneville, 1843)	31	Japan	Maeki 1953
	Ch. b. japonica (Murray, 1875)	31	Japan	Saitoh et al. 1978
4	*Coeliades 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. fulgerator* (Walch, 1775)	31	Peru	Kumagai et al. 2010
14	*A. naxos* (Hewitson, 1867)	31	Brazil	Saura et al. 2013
15	*A. phalaecus* (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
	Ch. albofasciatus (Hewitson, 1867)	31	USA (Texas)	Emmel and Trew 1973
19	*Entheus priassus pralina* Evans, 1952	22	Brazil	Saura et al. 2013
20	*Epargyreus 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	*Oechydrus chersis* (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	*Tarsoctenus praecia plutia* (Hewitson, 1857)	15	Brazil	Saura et al. 2013
26	*Thorybes pylades pylades* (Scudder, 1870)	31	USA (Connecticut)	Maeki 1961
27	*Udranomia 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				
33	*Elbella lamprus* (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. nurscia* (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				
44	*Daimio tethys* (Ménétriés, 1857)	30	Japan	Maeki 1953, Maeki and Makino 1953
45	*D. t. moorei* Mabille, 1876	30	Taiwan	Maeki and Ae 1968b
46	*Eagris lucetia* (Hewitson, 1876)	30	Uganda	de Lesse 1968
47	*E. sabadius astoria* Holland, 1896	30	Kenya	de Lesse 1968
48	*Eretis lugens* (Rogenhofer, 1891	28	Kenya	de Lesse 1968
Tribe Celaenorrhinini				
49	*Sarangesa phidyle* (Walker, 1870)	29	Senegal	de Lesse and Condamin 1962
Tribe Carcharodini				
50	*Carcharodus alceae* (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. lavatherae* (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
		30–37 (with Us)	Turkey (Amasya)	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. proteides* (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				
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. osyris* (Staudinger, 1876)	31	Argentina	de Lesse 1967a
70	*Erynnis baptisiae* (W. Forbes, 1936)	31	USA (Connecticut)	Maeki 1961
71	*E. funeralis* (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

#	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
		31	France	de Lesse 1960
		31	England	Bigger 1960
80	*E. tristis tatius* (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				
84	*Achlyodes pallida* (R. Felder, 1869) (as *A. selva*)	15	Bolivia	de Lesse 1967a
		15	Mexico	de Lesse 1970a
85	*Zera zera zera* (Butler, 1870)	34	Brazil	de Lesse and Brown 1971
Tribe Pyrgini				
86	*Anisochoria sublimbata* Mabille, 1883	31	Argentina	de Lesse 1967a
87	*Antigonus erosus* (Hübner, [1812])	31	Mexico	de Lesse 1970a
88	*A. liborius* Plötz, 1884	31	Argentina	de Lesse 1967a
89	*Celotes nessus* (W. H. Edwards, 1877)	14, 13	USA (Texas)	Emmel and Trew 1973
90	*Heliopetes arsalte* (Linnaeus, 1758)	30	Bolivia	de Lesse 1967a
	H. arsalte (Linnaeus, 1758)	30	Mexico	de Lesse 1970a
91	*H. laviana* (Hewitson, 1868)	29	USA (Texas)	Emmel and Trew 1973
92	*H. macaira* (Reakirt, [1867])	29	USA (Texas)	Emmel and Trew 1973
93	*H. omrina* (Butler, 1870)	30	Argentina	de Lesse 1967a
94	*Heliopyrgus americanus* (Blanchard, 1852)	30	Chile	de Lesse 1967a
95	*Paches loxus* (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
	P. albescens Plötz, 1884	28	USA (Texas)	Emmel and Trew 1973
98	*P. alveus* (Hübner, [1803])	24	Finland	Federley 1938
		24	Croatia	Lorkovic 1941
		24	Turkey	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. bolkariensis* 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. maculates* (Bremer et Grey, 1852)	31 (2n=62)	Japan	Abe et al. 2006
108	*P. malvae* (Linnaeus, 1758)	31	Finland	Federley 1938
		33	England	Bigger 1960
109	*P. oileus* (Linnaeus, 1767)	30 (2n=60)	USA (Texas)	Goodpasture 1976
		32	USA (Texas)	Emmel and Trew 1973
110	*P. onopordi* (Rambur, [1839])	30	France	Lorkovic 1941
111	*P. serratulae* (Rambur, [1839])	30	France	Lorkovic 1941
112	*Trina geometrina geometrina* (C. Felder et R. Felder, 1867)	31	Brazil	de Lesse and Brown 1971
Subfamily Heteropterinae				
113	*Butleria quilla* Evans, 1939	29	Chile	de Lesse 1967a
Subfamily Trapezitinae				
114	*Trapezites eliena* Hewitson, 1868	31	Australia	Maeki and Ogata 1971
Subfamily Hesperiinae				
Tribe Aeromachini				
115	*Aegiale hesperiaris* (Walker, 1856)	24	Mexico	Freeman 1969
116	*Agathymus alliae* (Stallings et Turner, 1957)	38	USA (Arizona)	Freeman 1969
117	*A. aryxna* (Dyar, 1905)	5	Mexico	Freeman 1969
118	*A. baueri* (Stallings et Turner, 1954)	15	USA (Arizona)	Freeman 1969
119	*A. chisosensis* (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. freemani* 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 lajitaensis 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. neumoegeni florenceae* (Stallings et Turner, 1957)	10	USA (Texas)	Freeman 1969
	A. neumoegeni macalpinei (Freeman, 1955)	10	USA (Texas)	Freeman 1969
126	*A. polingi* (Skinner, 1905)	10	USA (Arizona)	Freeman 1969
127	*A. remingtoni* (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 leptosema* Mabille, 1891	ca28	Argentina	de Lesse 1967a
133	*Megathymus coloradensis coloradensis* Riley, 1877	27	USA	Freeman 1969
134	*M. coloradensis kendalli* Freeman, 1965	27	USA (South central Texas)	Freeman 1969
	M. coloradensis louiseae Freeman, 1963	27	USA (Western Texas)	Freeman 1969
	M. coloradensis navajo Skinner, 1911	27	USA	Freeman 1969
	M. coloradensis reinthali Freeman, 1963	27	USA (Texas)	Freeman 1969
	M. coloradensis reubeni Stallings, Turner et Stallings, 1963	27	USA (Texas)	Freeman 1969
	M. coloradensis stallingsi Freeman, 1943	27	USA	Freeman 1969
	M. coloradensis wilsonorum 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	*Pardaleodes incerta* (Snellen, 1872)	17	Uganda	de Lesse 1968
138	*Stallingsia maculosus* (Freeman, 1955)	50	USA (Texas)	Maeki 1961, Freeman 1969
139	*Suastus gremius* (Fabricius, 1798)	23	Taiwan	Maeki and Ae 1968b
140	*Thoressa varia* (Murray, 1875)	31 (2n=62)	Japan	Abe et al. 2006
141	*T. varia* (Murray, 1875)	31	Japan	Maeki 1953
Tribe Baorini				
142	*Gegenes gambica* (Mabille, 1878)	41	Yemen	Saitoh 1984
		41	Turkey	de Lesse 1960
		41	Lebanon	Larsen 1982
143	*Gegenes nostrodamus* (Fabricius, 1793)	15	Egypt	Larsen 1982
		15	Israel	Saitoh 1979, Larsen 1982
144	*Gegenes pumilio* (Hoffmansegg, 1804)	24	France	de Lesse 1960
		24	Alger	de Lesse 1967b
145	*Parnara guttata* (Bremer et Grey, 1852)	16	Japan	Maeki 1953, Maeki and Makino 1953
		16	China	Saitoh and Abe 1981
146	*Pelopidas conjucta 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
		16	Japan	Maeki and Remington 1960
152	*Zenonia zeno* (Trimen, 1864)	16	Uganda	de Lesse 1968
Tribe Taractrocerini				
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 stinga* Evans, 1949	29	Japan (Okinava)	Abe et al. 2006
157	*T. ohara formosana* Fruhstorfer, 1911	29 (2n=58)	Taiwan	Abe et al. 2006
Tribe Thymelicini				
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. hyrax* (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 Calpodini				
165	*Ebusus ebusus* (Cramer, [1780])	29	Mexico	de Lesse 1970a
166	*Lychnuchus celsus* (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 (Florida)	Maeki 1961
170	*P. panoquinoides* (Skinner, 1891)	29	USA (Texas)	Emmel and Trew 1973
Tribe Anthoptini no chromosomal data available				
Tribe Moncini				
171	*Amblyscirtes aenus* W.H. Edwards, 1878	28, 29	USA (Texas)	Emmel and Trew 1973
172	*A. cassus* 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. texanae* 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	Wesley and Emmel 1975

#	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
		29	USA (Texas)	Emmel and Trew 1973
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 Hesperiini				
186	*Asbolis capucinus* (Lucas, 1857)	48	USA (Florida)	Maeki 1961
187	*Cynea iquita* (Bell, 1941)	29	Argentina	de Lesse 1967a
188	*Hesperia comma* (Linnaeus, 1758)	28	Italy	de Lesse 1970c
		28	Lebanon	Larsen 1975
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	Argentia	de Lesse 1967a
		29	USA (Florida)	Maeki 1961
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. sylvanoides* (Boisduval, 1852)	29	USA	Maeki 1961
195	*O. sylvanus* (Esper, 1777)	29	Finland	Federley 1938
		29	Croatia	Lorkovic 1941
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	*Poanes hobomok hobomok* (Harris, 1862)	29	?USA	Lorkovic in Robinson 1971
199	*P. taxiles* (W. H. Edwards, 1881)	29	USA	Maeki 1961
200	*P. zabulon* (Boisduval et Le Conte, [1837]) (as *Polites zabulon*)	29	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
	P. vibex praeceps (Scudder, 1872)	27	USA (Texas)	Emmel and Trew 1973
	P. vibex vibex (Geyer, 1832)	29	USA (Florida)	Maeki 1961
203	*Wallengrenia egeremet* (Scudder, 1863)	28	USA (Texas)	Emmel and Trew 1973
204	*W. otho curassavica* (Snellen, 1887)	28–30	USA (Texas)	Emmel and Trew 1973
205	*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. aryxna* 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.

Acknowledgements

I thank A. Warren (University of Florida) for help and consultations in taxonomy and nomenclature of skippers. The study was supported by the Russian Foundation for Basic Research: mainly by grant RFBR 13-04-92716-IND-a and partially by grant RFBR 14-04-01051-a.

References

Abe A, Kushibiki M, Kudoh K (2006) A study of male germ-line chromosomes in 14 species of the Hesperiidae (Lepidoptera). Transactions of the Lepidopterological Society of Japan 57(3): 217–228.

Bigger TRL (1960) Chromosome numbers of Lepidoptera. Entomologist's Gazette 11: 149–152.

Brown KS Jr, Emmel TC, Eliazar PJ, Suomalainen E (1992) Evolutionary patterns in chromosome numbers in neotropical Lepidoptera. I. Chromosomes of the Heliconiini (Family Nymphalidae: Subfamily Nymphalinae). Hereditas 117(2): 109–125. doi: 10.1111/j.1601-5223.1992.tb00165.x

Brown KS Jr, Freitas AVL, von Schoultz B, Saura AO, Saura A (2007a) Chromosomal evolution of South American frugivorous butterflies in the Satyroid clade (Nymphalidae: Charaxinae, Morphinae and Satyrinae). Biological Journal of the Linnean Society 92: 467–481. doi: 10.1111/j.1095-8312.2007.00872.x

Brown KS Jr, Freitas AVL, Wahlberg N, von Schoultz B, Saura AO, Saura A (2007b) Chromosomal evolution in the South American Nymphalidae. Hereditas 144(4): 137–148. doi: 10.1111/j.2007.0018-0661.02015.x

Brown KS Jr, von Schoultz B, Suomalainen E (2004) Chromosome evolution in Neotropical Danainae and Ithomiinae (Lepidoptera). Hereditas 141(3): 216–236. doi: 10.1111/j.1601-5223.2004.01868.x

Brown KS Jr, von Schoultz B, Saura AO, Saura A (2012) Chromosomal evolution in the South American Riodinidae (Lepidoptera: Papilionoidea). Hereditas 149(4): 128–138. doi: 10.1111/j.1601-5223.2012.02250.x

Camacho JPM, Sharbel TF, Beukeboom LW (2000) B-chromosome evolution. Philosophical Transactions of the Royal Society London B 355: 163–178. doi: 10.1098/rstb.2000.0556

de Lesse H (1960) Spéciation et variation chromosomique chez les Lépidoptères Rhopalocères. Annales des Sciences Naturelles (Ser. 12) 2: 1–223.

de Lesse H (1967a) Les nombres de chromosomes chez les Lépidoptères Rhopalocères néotropicaux. Annales de la Societe Entomologique de France (NS) 3: 67–136.

de Lesse H (1967b) Formules chromosomiques de Lépidoptères Rhopalocères d'Afrique du Nord. Bulletin de la Société entomologique de France 72: 20–25.

de Lesse H (1968) Formules chromosomiques de Lépidoptères Rhopalocères d´Uganda et du Kenya. Annales de la Societe Entomologique de France (NS) 4: 581–599.

de Lesse H (1970a) Les nombres de chromosomes chez les Lépidoptères Rhopalocères en Amérique centrale et Colombie. Annales de la Societe Entomologique de France (NS) 6: 347–358.

de Lesse H (1970b) Formules chromosomiques de quelques Lépidoptères Rhopalocères de Guyane. Annales de la Societe Entomologique de France (NS) 6: 849–855.

de Lesse H (1970c) Formules chromosomiques de quelques Rhopalocères paléarctiques [Lep.]. Bulletin de la Société entomologique de France 75: 214–218.

de Lesse H (1972) Nombres de chromosomes de quelques Lépidoptères Rhopalocères de Madagascar. Bulletin de la Société entomologique de France 77: 9–11.

de Lesse H, Brown KS Jr (1971) Formules chromosomiques de Lépidoptères Rhopalocères du Bresil. Bulletin de la Société entomologique de France 76: 131–137.

de Lesse H, Condamin M (1962) Formules chromosomiques de quelques Lépidoptères Rhopalocères du Sénégal. Bulletin de L'Institut Français d'Afrique Noire. Série A, Sciences Naturalles 24(2): 464–473.

De Prins W, van der Poorten D (1995) Rhopalocera and Grypocera of Turkey 14. Taxonomic revision of the *Pyrgus alveus* (Hübner, [1803]) complex from Greece to West China, with description of two new species from southern Turkey (Lepidoptera: Hesperiidae). Phegea 23(1): 1–44.

Emmel TC, Eliazar PJ, Brown KS Jr, Suomalainen E (1995) Chromosome evolution in the Papilionidae. In: Scriber JM, Tsubaki Y, Lederhouse RC (Eds) Swallowtail butterflies: their ecology and evolution. Scientific Publishers, Gainesville, 283–298.

Emmel TC, Trew HR (1973) Chromosomes of skipper butterflies from Southwestern North-America (Lepidoptera, Hesperiidae). Cytologia 38(1): 45–53. doi: 10.1508/cytologia.38.45

Federley H (1938) Chromosomenzahlen finnländischer Lepidopteren. I. Rhopalocera. Hereditas 24: 397–464. doi: 10.1111/j.1601-5223.1938.tb03219.x

Freeman HA (1969) Systematic review of the Megathymidae. Journal of the Lepidopterist's Society 23(Supplement 1): 1–59.

Goodpasture C (1976) High-resolution chromosome analysis in Lepidoptera. Annals of the Entomological Society of America 69(4): 764–771.

Dinca V, Lukhtanov VA, Talavera G, Vila R (2011) Unexpected layers of cryptic diversity in Wood White *Leptidea* butterflies. Nature Communications 2: 1–234. doi: 10.1038/ncomms1329

Hesselbarth G, Van Oorschot H, Wagener S (1995) Die Tagfalter der Türkei unter Berücksichtigung der angrenzenden Länder. Vol. 1-3. Bocholt, Selbstverlag S. Wagener, 1354 pp.

ICZN (2000) Opinion 1944: *Papilio sylvanus* Esper, 1777 (currently known as *Ochlodes sylvanus* or *O. venatus faunus*; Insecta, Lepidoptera: specific name conserved. Bulletin of Zoological Nomenclature 57: 56–57.

Jones RN, González-Sánchez M, González-García M, Vega JM, Puertas MJ (2008) Chromosomes with a life of their own. Cytogenetic and Genome Research 120: 265–280. doi: 10.1159/000121076

Kandul NP, Lukhtanov VA, Dantchenko AV, Coleman JWS, Sekercioglu CH, Haig D, Pierce NE (2004) Phylogeny of *Agrodiaetus* Hübner 1822 (Lepidoptera: Lycaenidae) inferred from mtDNA sequences of *COI* and *COII* and nuclear sequences of *EF1-α*: Karyotype diversification and species radiation. Systematic Biology 53(2): 278–298. doi: 10.1080/10635150490423692

Kandul NP, Lukhtanov VA, Pierce NE (2007) Karyotypic diversity and speciation in *Agrodiaetus* butterflies. Evolution 61(3): 546–559. doi: 10.1111/j.1558-5646.2007.00046.x

King M (1993) Species evolution. Cambridge, 336 pp.

Kumagai Y, Abe A, Kudoh K (2010) A survey of chromosome numbers of seven species of Hesperiidae in the neotropical region (Lepidoptera). Transactions of the Lepidopterological Society of Japan 61(1): 87–91.

Larsen TB (1975) Chromosome numbers and notes on testicular morphology of some Lebanese Rhopalocera (Insecta Lepidoptera). Entomologica Scandinavica 6(3/4): 253–260. doi: 10.1163/187631275X00091

Larsen TB (1982) *Gegenes pumilio* Hoffmannsegg, 1804; a review with cytological evidence that two species are involved (Hesperiidae). Nota Lepidopterologica 5(2/3): 103–110.

Lorković Z (1941) Die Chromosomenzahlen in der Spermatogenese der Tagfalter. Chromosoma 2: 155–191. doi: 10.1007/BF00325958

Lorković Z (1990) The butterfly chromosomes and their application in systematics and phylogeny. In: Kudrna O (Ed.) Butterflies of Europe. Volume 2. Wiesbaden, Aula-Verlag, 332–396.

Lukhtanov VA (1991) Evolution of the karyotype and system of higher taxa of the Pieridae (Lepidoptera) of the world fauna. Entomologicheskoe Obozrenie 70(3): 619–641.

Lukhtanov VA (2000) Sex chromatin and sex chromosome systems in nonditrysian Lepidoptera (Insecta). Journal of Zoological Systematics and Evolutionary Research 38(2): 73–79. doi: 10.1046/j.1439-0469.2000.382130.x

Lukhtanov VA, Dinca V, Talavera G, Vila R (2011) Unprecedented within-species chromosome number cline in the Wood White butterfly *Leptidea sinapis* and its significance for karyotype evolution and speciation. BMC Evolutionary Biology 11: 109. doi: 10.1186/1471-2148-11-109

Lukhtanov VA, Kandul NP, Plotkin JB, Dantchenko AV, Haig D, Pierce NE (2005) Reinforcement of pre-zygotic isolation and karyotype evolution in *Agrodiaetus* butterflies. Nature 436(7049): 385–389. doi: 10.1038/nature03704

Lukhtanov VA, Shapoval NA, Dantchenko AV (2008) *Agrodiaetus shahkuhensis* sp. n. (Lepidoptera, Lycaenidae), a cryptic species from Iran discovered by using molecular and chromosomal markers. Comparative Cytogenetics 2(2): 99–114.

Lukhtanov VA, Vila R, Kandul NP (2006) Rearrangement of the *Agrodiaetus dolus* species group (Lepidoptera, Lycaenidae) using a new cytological approach and molecular data. Insect Systematics and Evolution 37(3): 325–334. doi: 10.1163/187631206788838563

Maeki K (1953) A chromosome study of Japanese butterflies. Kwansei Gakuin Iniversity Annual Studies 1: 67–70.

Maeki K (1961) Chromosome numbers of butterflies from North America. Zoological Magazine (Tokyo) 70: 165–169.

Maeki K, Ae A (1968a) A chromosome study of seventeen species of butterflies from Hong Kong (Lep. Rhopalocera). Kontyu 36(1): 65–74.

Maeki K, Ae A (1968b) Studies of the chromosomes of Formosan Rhopalocera. 1. Papilionidae and Hesperiidae. Kontyu 36(2): 116–123.

Maeki K, Ae A (1979) Chromosomal studies in interspecific hybrids of butterflies (Papilionidae, Lepidoptera). XV. Proceedings of the Japan Academy (B) 55: 295–299.

Maeki K, Makino S (1953) Chromosome numbers of some Japanese Rhopalocera. Lepidoptera News 7: 36–38.

Maeki K, Ogata M (1971) A chromosome study of eighteen species of butterflies from Australia (Lep. Rhopalocera). Kontyu 39(1): 1–8.

Maeki K, Remington CL (1960) Studies of the chromosomes of North American Rhopalocera 2. Hesperiidae, Megathymidae and Pieridae. The Journal of the Lepidopterists' Society 14: 37–57.

Przybyłowicz Ł, Lukhtanov V, Lachowska-Cierlik D (2014) Towards the understanding of the origin of the Polish remote population of *Polyommatus* (*Agrodiaetus*) *ripartii* (Lepidoptera: Lycaenidae) based on karyology and molecular phylogeny. Journal of Zoological Systematics and Evolutionary Research 52(1): 44–51. doi: 10.1111/jzs.12040

Robinson R (1971) Lepidoptera genetics. Pergamon Press, Oxford, 687 pp.

Saitoh K (1979) A note on the haploid karyotype of the Mediterranean skipper *Gegenes nostrodamus* (Lepidoptera, Hesperiidae) from Israel. Chromosome Information Service 27: 8–9.

Saitoh K (1982) Spermatocyte chromosomes of five taxa of Rhopalocera from Oman. Chromosome Information Service 33: 10–12.

Saitoh K (1984) Chromosomes of three butterfly taxa from Yemen. Tyo to Ga 34(4): 167–170.

Saitoh K, Abe A (1981) Chromosome numbers in twenty-four taxa of Rhopalocera from the People's Republic of China. Chromosome Information Service 31: 18–19.

Saitoh K, Kumagai Y (1974) Notes on the spermatocyte chromosomes of four species of west Malaysian butterflies. Chromosome Information Service 16: 4–6.

Saitoh K, Abe A, Kudoh K (1978) Meiotic chromosomes of *Choaspes benjaminii japonica* (Lepidoptera, Hesperiidae). Chromosome Information Service 25: 28–29.

Saitoh K, Kumagai Y, Abe A (1991) Notes on the spermatocyte chromosomes of six taxa of Formosan butterflies. Tyo to Ga 42(2): 47-51.

Saura A, von Schoultz B, Saura AO, Brown KS Jr (2013) Chromosome evolution in Neotropical butterflies. Hereditas 150: 26–37. doi: 10.1111/j.1601-5223.2013.00008.x

Suomalainen E (1969) Chromosome evolution in the Lepidoptera. Chromosomes Today 2: 132–138.

Talavera G, Lukhtanov V, Rieppel L, Pierce NE, Vila R (2013) In the shadow of phylogenetic uncertainty: the recent diversification of *Lysandra* butterflies through chromosomal change. Molecular Phylogenetics and Evolution 69: 469–478. doi: 10.1016/j.ympev.2013.08.004

Vershinina AO, Lukhtanov VA (2010) Geographical distribution of the cryptic species *Agrodiaetus alcestis alcestis*, *A. alcestis karacetinae* and *A. demavendi* (Lepidoptera, Lycaenidae) revealed by cytogenetic analysis. Comparative Cytogenetics 4(1): 1–11. doi: 10.3897/compcytogen.v4i1.21

Vershinina AO, Lukhtanova VA (2013) Dynamics of chromosome number evolution in the *Agrodiaetus phyllis* species complex (Insecta: Lepidoptera). Cell and Tissue Biology 7(4): 379–381. doi: 10.1134/S1990519X13040159

Vila R, Lukhtanov VA, Talavera G, Gil-T F, Pierce NE (2010) How common are dot-like distribution ranges? Taxonomical oversplitting in Western European *Agrodiaetus* (Lepidoptera, Lycaenidae) revealed by chromosomal and molecular markers. Biological Journal of the Linnean Society 101: 130–154. doi: 10.1111/j.1095-8312.2010.01481.x

Warren AD, Ogawa J, Brower AVZ (2008) Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperiidae (Lepidoptera: Hesperiodea). Cladistics 24: 642–676. doi: 10.1111/j.1096-0031.2008.00218.x

Warren AD, Ogawa JR, Brower AVZ (2009) Revised classification of the family Hesperiidae (Lepidoptera: Hesperioidea) based on combined molecular and morphological data. Systematic Entomology 34(3): 467–523. doi: 10.1111/j.1365-3113.2008.00463.x

Wesley DJ, Emmel TC (1975) The chromosomes of Neotropical butterflies from Trinidad and Tobago. Biotropica 7: 24–31. doi: 10.2307/2989796

White MJD (1973) Animal cytology and evolution. Cambridge, 961 pp.