1 Evolutionary mechanisms of runaway

chromosome number change in Agrodiaetus

2 butterflies

7

- 3 Alisa O. Vershinina and Vladimir A. Lukhtanov
- 4 Supplementary information
- 5 **Supplementary Table S1.** Karyotypes and *COI*, *trnL*, *COII*, 5.8S *rDNA*, *ITS2*, 28S *rDNA* sequence
- 6 data for the studied samples of the subgenus *Agrodiaetus*.

*Modal chromosome number (in brackets) reflects haploid karyotype in most of the individuals studied. "NSh" abbreviation corresponds to the Nazar Shapoval's sequence ID.

·		Sequence ID			
species name	n (modal n)*	COI+trnL+COII	COI	5.8S rDNA + ITS2+28S rDNA	
icarus (outgroup)	23	AY496815	AY556927	AY556590	
achaemenes	134	EF104615	AY557140	AY556740	
actinides	NA	EF104621	GU559748	AY556753	
actis	26-28 (27)	EF104606	AY556999	AY556633	
admetus	80	AY496711	AY556867	AY556733	
admetus ssp. malievi	79	EF104617	-	HM210176	
alcestis	20-21 (20)	-	AY557008	AY556641	
alcestis ssp. karacetinae	19	AY954018	-	AY556574	
altivagans	20- 23 (21)	AY496716	AY556846	AY556717	
antidolus	42-44 (42)	AY496717	AY557095	AY556692	
zarathustra	20-22 (21)	AY953994	AY557141	AY556741	
arasbarani	25	AY496718	-	-	
ardschira	113	AY954001	-	-	
aroaniensis	48	-	AY556725	AY556856	
artvinensis	21-22 (21)	-	AY557038	AY556663	
baltazardi	45	AY954008	-	-	
baytopi	27-28 (27)	AY496720	AY557087	AY556688	
bilgini	25	AY496721	-	-	
birunii	10	AY953985	AY556912	AY556578	
bogra	53		NSh J318		
caeruleus	10	AY953987	AY556926	AY556589	
carmon	81-82	AY496722	AY556981	AY556622	
ciscaucasicus	16	AY496724	-	-	
cyaneus ssp. damalis	20	EF104610	AY557143	-	

cyaneus ssp. kernmansis	22	AY954003	_	_
cyaneus ssp. paracyaneus	19	AY953993	_	_
dagestanicus	39-40 (39)	AY954025	_	_
dagmara	NA	EF104618	AY556852	_
dama	41	-	AY557007	AY556640
damocles ssp. kanduli	25	AY496726	-	-
damocles ssp. krymaeus	26	AY496727	_	HM210178
damon	45	AY496732	AY557131	AY556714
damone ssp. altaicus	67	AY496734	FJ663228	-
dantchenkoi	40-42	AY496737	AY557073	AY556679
demavendi race-68 ssp. lorestanus	ca68	AY953995	AY557142	AY556743
demavendi race-73	73	EF104630	-	-
demavendi race-79	79	AY954007	_	_
dizinensis	17	EF104638	AY556939	AY556599
dolus ssp. virgilia	122	HM210162	-	HM210180
dolus ssp. vittatus	124-125 (124)	AY496740	-	-
ectabanensis	18	AY953992	-	-
elbursicus	17	AY953999	AY556877	AY556555
elbursicus from Veresk	20	AY953986	-	-
elbursicus ssp. gilanensis	18	EF104637	-	-
eriwanensis	29-35 (32)	AY496742	-	-
ernesti	18	-	AY556989	AY556626
erschoffii	13-15 (13)	AY496743	AY556925	AY556588
fabressei	90	AY496744	AY556952	AY556608
faramarzii	107	AY954017	-	-
femininoides	27	EF104636	AY557150	AY556749
firdussii from Shahkuh	30-34 (30)	AY953997	-	-
firdussii ssp. vilai	35	EF104607	-	-
firdussii from Zanjan	28	EF104623	-	AY556576
fulgens	108-110 (109)	AY496712	AY556954	AY556610
glaucias	56	AY496747	AY557134	AY556736
gorbunovi	20	AY954022	AY556899	AY556569
guezelmavi	41-42 (42)	-	AY557022	AY556651
haigi	25	AY496750	AY557069	AY556677
hamadanensis	21-22	AY502112	AY556875	AY556554
hopfferi	15	AY496751	AY557005	AY556638
huberti	35-37 (35)	AY496753	AY557123	AY556707
humedasae	39	HM210170	AY557127	HM210193
interjectus	29-32 (31)	-	AY557059	AY556671
iphicarmon	29	EF104608	AY556990	AY556627
iphidamon	14	AY953988	AY556913	AY556584
iphigenia race-12	12	AY496757	AY557061	AY556656
iphigenia from Armenia	14	AY556849	-	-
iphigenia ssp. araratensis	13	AY496756	-	-

iphigenia race-15	15	EF104609	-	-
iphigenides	65-67 (67)	AY496758	FJ663236	AY556722
juldusus ssp. kasachstanus	67	AY496759	-	-
karatavicus	67	AY496760	-	-
karindus	68-73 (68)	EF104633	AY557145	NSh E398
kendevani	15-17 (15)	AY954005	-	NSh Nz3
khorasanensis	84	AY954013	AY557138	AY556737
klausschuriani	56	AY953984	AY556910	AY556577
kurdistanicus	62	AY496762	AY557074	AY556680
lukhtanovi	22	AY954021	-	-
luna	73-74	EF104624	-	NSh E154
lycius	21-22 (22)	-	AY556985	AY556625
magnificus	NA	EF104619	-	-
maraschi	16	-	AY557000	AY556634
masulensis	10	EF104613	-	GQ166175
mediator	NA	EF104602	-	-
menalcas	85	AY496763	AY557001	AY556635
merhaba	16-17 (17)	AY496764	AY557037	AY556662
mithridates from Etzincan	21-27 (22)	AY496765	-	-
mithridates from Malatya	21-27 (23)	-	AY557006	AY556639
mofidii	35	AY954012	AY557137	AY556739
morgani	25-27 (25)	-	NSh Z524	NSh W154
ninae	33-35 (34)	AY496766	AY557113	AY556701
paulae	17	-	AY556892	AY556564
peilei	38-39 (39)	EF104634	AY557144	AY556744
pfeifferi	106-108 (108)	AY954002	-	-
phyllides	66-67 (67)	AY496770	FJ663239	-
phyllis	80	AY953989	AY556923	AY556587
pierceae	22	AY496773	AY557083	AY556686
poseidon	19-21 (20)	AY496775	AY557002	AY556636
poseidonides	24	EF104622	-	AY556721
posthumus	90	AY953990	AY556922	AY556586
pseudactis	29	AY496777	AY556845	AY556716
pulcher	NA	EF104620	-	-
putnami	26	AY496778	AY557112	AY556700
ripartii	90	EF104603	AY556962	AY556727
rjabovi	49	AY954019	-	-
rjabovi from Masuleh	43	AY954006	-	-
rovshani	52-53	AY496788	AY556897	AY556567
sennanensis race-29	29	EF104616	-	-
sennanensis race-31	31	EF104625	AY557147	AY556746
sertavulensis	20	-	AY557023	AY556652
shahkuhensis	16	AY953998	-	NSh Nz7
shahrami				

shamil	17	AY954024	-	-
sigberti	29	-	AY557020	AY556650
sorkhensis	43	AY954010	-	-
stempfferi	23	AY954000	-	JX093393
surakovi	50	AY496792	AY556844	AY556715
tankeri	20-21 (21)	AY496794	AY557125	AY556709
tenhageni	54	AY954009	AY557139	AY556738
theresiae	63	-	AY557013	AY556645
transcaspicus	52-53 (52)	AY954014	-	-
turcicolus	20	AY496796	AY557110	AY556699
turcicus	24	AY496798	AY557117	AY556674
valiabadi	23	-	AY556934	AY556594
vanensis	78	AY496799	AY556850	AY556720
vaspurakani	22	AY496713	AY557085	AY556687
wagneri	16-17 (16)	-	AY556995	AY556629
zapvadi	18-19 (18)	AY496741	AY557067	AY556675
schuriani	75-80, 81-82 (80)	-	AY557014	AY556646

Хромосомные числа у изученных видов сем. Pieridae

	Место сбора		Число	Чи	сло хромосом
Вид			мета- фазных пласти- нок	основ- ное	другие най- денные числа
112	Подсем. Dismo	rphiinae	:		
Leptidea sinapis L. A	лтай, Зыряновск	1	I	4445	
	зербайджан, Талыш	3	11		28, 31, 32, 34
	Подсем. Coli	adinae			
Colias hyale L. A	лтай, Усть-Каменогорск	1	18	31	
C. thisoa Mén. A	рмения, Даралагезский хр.	2	28	31	
Тот же . А	лтай, Калбинский хр.	2 3	28	31	31+B, 32, 33, 34
Gonopteryx rhamni, L. A	лтай, Курчумский хр.	1	35	31	31+B
	Подсем. Antho	charinae			
Anthocharis car- A damines L.	лтай, Зыряновск	3	39	31	30, 30+B
	Подсем. Ріе	rinae			
Pieris brassicae L. A	зербайджан, Талыш	4	32	15	
P. rapae L. A	лтай, Зыряновск	3	20	25	26
P. napi L. A	лтай, Зыряновск	Ĭ	11	25	20
	ахичевань	1	12	25	
Pontia daplidice L. A	лтай, Курчумский хр.	4	19	26	
P. chloridice Hbn.	То же	2	19	26	
Aporia crataegi L. A	лтай, Зыряновск	1	46	25	

Таблица 2

Хромосомные числа белянок мировой фауны						
№	№ Вид	Местность	Число хромосом (n)	Источник		
	Подсем	. Dismorphiinae	Schatz, 1886			
	Триба І	Dismorhiini	Schatz, 1886			
1	Dismorphia amphione praxinoe Doubl.	Мексика	30	de Lesse, 1970a		
2	D. critomediia Hübn.	Боливия	31	de Lesse, 1967a		
	D. critomedia feodora Lucas	Колумбия	31	Тот же		
3	D. hyposticta Feld.	Колумбия	48	« «		
4	D. jethys Boisd.	Мексика	31	de Lesse, 1970a		
5	D. nemesis Latr.	Боливия	31	de Lesse, 1967a		
6	D. pinthaeus L.	Гвиана	17	de Lesse, 1970c		
7	D. psamathe F.	Аргентина	23, 24	de Lesse, 1967a		
8	D. theonoe melanina Avin.	Гвиана	14(?) + B	de Lesse, 1970c		
9	D. thermesia Godt.	Бразилия	31	de Lesse, Brown, 1971		
10	D. theucarila Doubl.	Колумбия	18	de Lesse, 1967a		
11	Preudopieris nehemia Boisd.	Аргентина	23	- Тот же		
	P. nehemia viridula Feld.	Эквадор	23	« «		
	Триба	Leptideini	Verity, 1947			
12	Leptidea amurensis Mén.	Япония	61	Maeki, 1958a, b; 1959		
13	L. duponcheli Stgr.	Франция	104	Lorković, 1941; 1949		
	L. duponcheli Stgr.	Македония	104	Тот же		
	L. duponcheli Stgr.	Турция	102, 103	de Lesse. 1960		
	L. duponcheli Stgr.	- A Paris	103	Lorković, 1966 in Robinson, 1971		
14	L. morsei Fent.	яинопЯ	54	Maeki, 1958a, b; 1959		
	L. morsei maior Grund.	Югославия	53, 54	Lorković 1941		

N₂N₂	Вид	Местность	Число хромосом (п)	Источник
15	L. sinapis L.	Финляндия	26—27, 28, 30—31	Federley, 1938
	L. sinapis L.	Югославия	28, 29, 30 31, 34, 35, 39	Lorković, 1941
	L. sinapis L. L. sinapis L.	Алтай Талыш	Около 44—45 28, 31, 32, 34	Данная работа Данная работа

Подсем. Pseudopontiinae Reuter, 1896

Pseudopontia Plötz

Нет данных

Подсем. Colladinae Swainson, 1827

	Триба (Colia dini Swa	inson, 1827	
16	Colias alexandra Edw.	С. Америка	31	Maeki, Remington, 1960; Maeki, 1961
17	C. aurorina HerrSchäff.	Иран	32	de Lesse, 1960
18	C. australis Verity	Франция	31	Тот же
19	C. chlorocoma Christ.	Турция	31	« «
20	C. croceus Fourc.	Югославия	32	Lorković, 1941
	C. croceus Fourc.	Азорские о-ва	31	Federley, 1942
21	C. dimera Doubl. et Hew.	Колумбия	31	de Lesse, 1967
22	C. erate nilagiriensis Feld.	Гималаи	31	Maeki, Ae, 1966
23	C. eurytheme Boisd.	С. Америка	31	Maeki, Remington, 1960; Maeki, 1961
24	C. fieldii Mén.	Гималаи	31	Maeki, Ae, 1966
	C. fieldii Mén.	Китай	31	Saitoh, Abe, 1981
	C. fieldii fieldii Mén.	Индия	31	Saitoh et al., 1986
25	C. hecla sulitelma Auriy.	Финляндия	31	Federley, 1938; 1942
26	C. hermina Butl.	Перу	31	de Lesse, 1967a
27	C. hyale L.	Югославия	31	Lorković, 1941
	C. hyale L.	Финляндия	31, 32	Federley, 1942
	C. hyale L.	Алтай	31	Данная работа
28	C. lesbia F.	Аргентина	31	de Lesse, 1967a
	C. lesbia F.	Эквадор	32	Тот же
29	C. meadii Edw.	С. Америка	31	Maeki, Remington, 1960; Maeki, 1961
30	C. myrmidone Esp.	Европа	31-32 (?)	Kernewitz, 1915
31	C. nastes werdandi Zett.		31	Federley, 1942
32	C. palaeno L.	Финляндия	31, 31 - 32	Federley, 1938, 1942
	C. palaeno sugitanii Esaki	Япония	31	Maeki, 1958b; 1959
33	C. phicomone Esp.	Пиренеи	30	de Lesse, 1960
34	C. philodice Godt.	С. Америка	31	Maeki, Remington, 1960; Maeki, 1961
12740	C. philodice Godt.	« «	31	Lorković, 1966 in Robinson, 1971
25	C. polyographus Motsch.	Япония	31	Maeki, 1958b; 1959
36	C. sagartia Led.	Иран	32	de Lesse, 1960
37	C. scudderi Reak.	С. Америка	31	Maeki, Remington, 1960; Maeki, 1961
38	C. stoliczkana miranda Fruhst.	Гималаи	31	Maeki, Ae, 1966
39	C. thisoa Mén.	Иран	3233	de Lesse, 1960
	C. thisoa Mén.	Армения	31	Данная работа
	C. thisoa Mén.	Алтай	31, 31+B, 32, 33, 34	Данная работа
40	C. vaulieri Guer.	Чили	31	de Lesse, 1967a
41	Zerene cesonia Stoll.	Мексика	31	Maeki, Remington, 1960; Maeki, 1961
42	Catopsila crocale Cram.	О. Тайвань	31	Maeki et al., 1965
	C. crocale Cram.	Гималаи	31	Maeki, Ae, 1966
	C. crocale Cram.	Малайзия	31	Saitoh, Kudoh, 1972

				
NºNº	Вид	Местность	Число хромосом (n)	Источник
43	C. florella F.	Сенегал	31	de Lesse, Condamin,
	C. florella F.	Уганда	31	de Lesse, 1968
	C. florella F.	Мадагаскар	31	de Lesse, 1972
44		Гималаи	31	Maeki, Ae, 1966
	C. pomona F.	Бангкок	31	Maeki, Ogata, 1970
	C. pomona F.	Австралия	31	Maeki, Ogata, 1971
	C. pomona F.	О. Тайвань	31	Maeki, Ae, 1968
45	C. pyranthe L.	Индия	31	Gupta, 1964
	C. pyranthe L.	Гималаи	31	Maeki, Ae, 1966
	C. pyranthe L.	Китай	31	Saitoh, Abe, 1981
46	Anteos clorinde Godt.	Мексика	31	Maeki, Remington,
	A. clorinde Godt.	Колумбия	31	1960; Maeki, 1961 de Lesse, 1967a
	12/20 who	Al 952		de Lesse, 1907a
47	Gonopteryx amintha formosana	Callidryini O Taŭpaut	31	Maaki Aa 1069
	Fruhst.			Maeki, Ae, 1968
48 49	G. farinosa Zell.	Турция	32	de Lesse, 1960
-50	G. machagura niphonica Verity G. rhamni L.		31	Maeki, 1958b; 1959
00	G. rhamni L.	Москва	31	Beliajeff, 1930
	G. rhamni L.	Финляндия	31—32	Federley, 1938
	G. rhamni L.	Югославия	31	Lorković, 1941
	G. rhamni maxima Butl.	Алтай	31, 31 + B	Данная работа
	G. rhamni major	Япония	. 31	Maeki, 1958b; 1959
	Dercas Doubl.	Китай	31	Saitoch, Abe, 1981
51	Phoebis argante F.	Нет данных Аргентина	31	de Lesse, 1967a
٠.	Ph. argante F.	Эквадор	31	Тот же
52	Ph.cipris F.	Аргентина	31	
53	Ph. eubule L.	Боливия	31	« «
00	Ph. eubule L.	Колумбия	31	« «
54	Ph. philea L.	Мексика	31	Maeki, Remington,
		-,		1960; Maeki, 1961; de Lesse, 1970a
55	Ph. sennae L.	Тобаго	31	Wesley, Emmel, 1975
56	Ph. (Aphrissa) statira Cram.	Колумбия	31	de Lesse, 1967a
57	Ph. (Rhabdodryas) trite L.	Аргентина	31	Тот же
58	Kricogonia lyside Godt.	Мексика	31	Maeki, Remington, 1960; Maeki, 1961
	Leucidia Boisd.	Нет данных		1000, Macki, 1901
	Gandaca Moore	Нет данных		
59	Eurema (Terias) andersoni	О. Тайвань	29	Maeki, Ae, 1968
60	godana Fruhst. E. (Terias) blanda arsakia	О. Тайвань	31	Тот же
61	Fruhst. E. (Terias) hecabe contudernalis			
01	Moore	3825 G	31	Maeki, Ae, 1966
	Тот же	Малайзия	31	Saitoh, Kudoh, 1972
	E. (Terias) hecabe mandarina de l'Orza	Япония	31	Maeki, Makino, 1953; Maeki, 1953b; 1958b; 1959
62	E. (Terias) senegalensis Boisd.	Сенегал	31	de Lesse, Condamin,
	Тот же	Габон	31	1962 Bernardi, de Lesse, 1964
	« «	Уганда	31	de Lesse, 1968
63	E. (Maiva) brigitta Cram.	Сенегал	12	de Lesse, Condamin,
	E. (Maiva) brigitta brigitta Cram.	Уганда	12	de Lesse, 1968
64	E. (Maiva) hapale Mab.	Уганда	31 (?)	Тот же

	L		1 4 0 11	n u a z (npoconscenae)
№№	Вид	Местность	Число хромосом (n)	Источник
65	E. (Nirmula) laeta bethesba Jans.	і Япония	29	Maeki, 1958b; 1959
66	E. (Eurema) albula Cram.	Колумбия	29	de Lesse, 1967a
	Тот же	Аргентина	28 (?)	Тот же
67	E. (Eurema) boisduvaliana Feld.	Мексика	31	de Lesse, 1970a
68	E. (Eurema) daira Godt.	Мексика	31	Тот же
69	E. (Eurema) deva Doubl.	Аргентина	31	de Lesse, 1967a
70	E. (Eurema) graduata Butl.	Боливия	31	Тот же
71	E. (Eurema) gratiosa Doub. et Hew.	Колумбия	31	« «
72	E. (Eurema) mexicana Boisd.	Мексика	31	Maeki, 1961
73	E. (Eurema) phiale Cram.	Боливия	31	de Lesse, 1967a
74	E. (Eurema) plataea Feld.	Аргентина	31 (?)	Тот же
75	E. (Eurema) reticulata Butl.	Эквадор	31	« «
76	E. (Eurema) salome Feld.	Боливия	31	« «
77	E. (Eurema) xanthochlora Koll.	Эквадор	31	« «
78	E. (Pyrisitia) calceolaria Butl.	Мексика	31	de Lesse, 1970a
	Тот же	Гватемала	31	Тот же
79	E. (Pyrisitia) leuce Boisd.	Тобаго	31	Wesley, Emmel, 1975
80	E. (Pyrisitia) limbia Feld.	Боливия	31—32	de Lesse, 1967a
81	E. (Pyrisitia) lisa Boisd. et Lec.	С. Америка	31	Maeki, Remington, 1960; Maeki, 1961
82	E. (Pyrisitia) nise Cram.	Боливия	31	de Lesse, 1967a
	E. (Pyrisitia) nise nelphe Feld.		31	de Lesse, 1970a
83	E. (Pyrisitia) proterpia F.	Мексика	31	Maeki, Remington, 1960; Maeki, 1961
	Тот же	Колумбия	31	de Lesse, 1967a
84	()	Тринидад	30	Wesley, Emmel, 1975
85		Мексика	31	Maeki, Remington, 1960; Maeki, 1961; de Lesse, 1970a
86	E. (Teriocolias) zelia Lucas	Аргентина	31	de Lesse, 1967a
87	Eurema esakii Shirozu	О. Тайвань	30	Maeki, Ae, 1968
88	Nathalis iole Boisd.	Флорида	31	Maeki, 1961
	Тот же	Мексика	31	de Lesse, 1970a
		Anthocharinae	Scudder, 1889	
90	Eroessa Doubleday	Нет данных	0.5	1 1 1000
89	Anthocharis cardamines L.	Франция	31	de Lesse, 1960
	Тот же	Франция	31	Lorković, 1960
	« «	Югославия Финляндия	31 31, 32	Тот же
	« «	Алтай	32, 30, 30 + B	Federley, 1938 Данная работа
	« «	Англия	30	Bigger, 1960; 1978
90	A. euphenoides Stgr.	Испания	31	de Lesse, 1970b
91	A. gruneri HerrSchäff.	1 Tollanin	24	Lorković, 1966 in Robinson, 1971
92	A. (Paramidea) scolymus Bitl.	RинопR	31	Maeki, Makino, 1953; Maeki, 1953b; 1958b; 1959
93	Zegris eupheme Esp.	Марокко	31	de Lesse, 1967b
	Z. eupheme menestho Mén.	Турция	31	Тот же
94	Euchloe ausonia Hübn.	Пиренеи	31	de Lesse, 1960
	E. ausonia melanochloros Röber	Марокко	31	de Lesse, 1967a
95	E. ausonides Bd.	С. Америка	31	Maeki, Remington,
96	34 31 34 C 35 25 X	2		1960; Maeki, 1961
96	E. crameri occidentalis Verity	Франция	31	Lorković, 1941
	E. crameri romana Calb.	Югославия	31	Тот же
97	E. (Elphinstonia) charlonia		30—32 (?)	Lorković, 1966 in
00	Donz.	Δ	0.1	Robinson, 1971
98	E. (Elphinstonia) tagis Hübn.	Франция	31	de Lesse, 1970b

NºNº	Вид	Местность	Число хромосом (n)	Источник
99	E. lessei	Иран	27—28	de Lesse, 1960
100	Hesperocharis marchalii Guer	Боливия	15	de Lesse, 1967a
101	H. costaricensis Bates	Мексика	15	de Lesse, 1970a
102	Pinacopteryx eriphia Godt.	Сенегал	13	de Lesse, Condamin 1962
	P. eriphia tritogenia Klug	Оман	13	Saitoh, 1982
	P. eriphia mabillei Auriv.	Мадагаскар	13	de Lesse, 1972
103	Hebomoia glaucippe L.	Гималаи	17	Maeki, Ae, 1966
	H. glaucippe formosana Fruhst. H. glaucippe shorizui	О. Тайвань Япония	17 17	Maeki et al., 1965 Maeki, 1958b; 1959
		Pierinae Dupono		94
	Триба Егог	riini Swinhoe i	n Moore, [1907]	
104	Eronia leda Boisd.	Уганда	1618	de Lesse, 1968
105	Nepheronia argia F.	Центрально- Африканская	18	de Lesse, 1966
106	N. thalassina Boisd.	Республика Уганда	18	de Lesse, 1968
	Триба	Teracolini R	euter, 1896	
107	Colotis antevippe zera Lucas	Уганда	28	de Lesse, 1968
	Тот же	Кения	28	Тот же
108		Уганда	-27	de Lesse, 1968
	C. aurora evarne Klug	Сенегал	5	de Lesse, Condamin, 1962
110	C. danae pseudacaste Butl.	Кения	28	de Lesse, 1968
111		Уганда	28	Тот же
	C. evanthe Boisd.	Мадагаскар	28	de Lesse, 1972
114	C. evippe complexivus Butl.	Уганда	28 .	de Lesse, 1968
115		Оман Сенегал	28 28	Saitoh, 1982 de Lesse, Condamin, 1962
116	C. puniceus Butl.	Кения	28	de Lesse, 1968
117		Мадагаскар	27	de Lesse, 1972
118	Gideona lucasi Grandidier	Мадагаскар	27 (?)	de Lesse, 1972
119	Ixias pyrene pyrene L.	Китай	28	Saitoh, Abe, 1981
	I. pyrene familiaris Butl.	Гималаи	28	Maeki, Ae, 1966
	I. pyrene insignis Butl.	О. Тайвань	28	Maeki et al., 1965
	Триба д	Appiadini Ku	isnezov, 1929	
120	Appias drusilla Cr.	Аргентина	32	de Lesse, 1967a
101	Тот же	Мексика	32	Maeki, Remington, 1960; Maeki, 1961
121	A. epaphia orbona Boisd.	Уганда	32	de Lesse, 1968
122	A. indra aristoxenus Fruhst.	О. Тайвань	32	Maeki, Ae, 1968
123	A. libythea libythea F.	Малайзия	32	Saitoh, Kudoh, 1972
125	A. lyncida formosana Wall A. melania F.	Формоза	32	Maeki et al., 1965
	A. (Glutophrissa) sabina Feld.	Австралия Габон	32 32	Maeki, Ogata, 1971 Bernardi, de Lesse, 1964
	A. (Glutophrissa) sabina confusa Butl.	Мадагаскар	32	de Lesse, 1972
	A. (Glutophrissa) sabina udei Suff.	Кения	32	de Lesse, 1968
	Udaiana Distant	Нет данных		
	Saletaria	Нет данных		
	Триба Р	ierini Dupono	hel, [1835]	
	201 Carlot Carlo			
	Eucheira Westwood	Нет данных		

	ATT VERNING			
₩₩	Вид	Местность	Число хромосом (n)	Источник
127	Catasticta albina Lathy et Rosenb.	Боливия	25	de Lesse, 1967a
128	C. flisa HerrSchäff. Тот же	Боливия Эквадор	25 (25—26) + (1—2) B	Тот же « «
100		Боливия	25	« «
129	TINE 10 10 10 10 10 10 10 10 10 10 10 10 10	Эквадор	(27-29)+(2-3) B	
130	C. reducta Butl. Тот же	Боливия	31(?)	« «
121		Боливия	25	« «
131	Archonias bellona hyrnetho Fruhst.	<u></u>		70 T 10 T
132	A. tereas Godt.	Бразилия	25	de Lesse, Brown, 1971
	A. tereas rosacea Butl.	Эквадор	26	de Lesse, 1967a
133	Aporia crataegi L.	Европа	25	Kernewitz, 1914; 1915
	Тот же	Югославия	26	Lorković, 1941
	« «	Финляндия	26	Federley, 1938
	« «	Москва	25	Beliajeff, 1930
	« «	Алтай	25	Данная работа
	A. crataegi adherbal Fruhst.	Япония	25	Маеки, 1953 а, б; Маекі, Макіпо, 1953; Маекі, 1958b
134	A. hippia japonica Mats.	Япония	25	Maeki, 1958b; 1959
	Metaporia Bult.	Нет данных	20	ласкі, 13000, 1303
135	Cepora coronis cibyra Fruhst.	О. Тайвань	23, 24, 25	Maeki, Ae, 1968
100	C. coronis phryne F.	Гималан	22-24	Maeki, Ae, 1966
136	C. nadina eunama Fruhst.	О. Тайвань	25	Maeki et al, 1965
137	Delias aglaia L.	Гималан	25	Maeki, Ae, 1966
137		О. Тайвань	25	Maeki et al., 1965
120	D. aglaia curasena Fruhst.		25	Kaur, 1988
138	D. belladonna belladonna F.	Индия	27—32	Maeki, Ae, 1966
139	D. descombesi Boisd.	Гималаи		
	D. hyparete diva Fruhst.	Малайзия	26, 27	
141	D. (Cathaemia) lucharis Dr.	Гималаи	25	Maeki, Ae, 1966
142	D. (Cathaemia) mysis F.	Австралия	25	Maeki, Ogata, 1971
143	Pereute swainsoni Gray	Бразилия	26-27	de Lesse, Brown, 1971
	Leodonta Butl.	Нет данных	05	de Lessa Condomin
144	Belenois aurota F.	Сенегал	25	de Lesse, Condamin, 1962
	Тот же	Кения	25	de Lasse, 1968
145	B. calypso Dr.	Габон	25	Bernardi, de Lesse, 1964
146	B. creona Cr.	Сенегал	25	de Lesse, Condamin, 1962
	B. creona infida Butl.	Уганда	25	de Lesse, 1968
	B. creona severina Stoll.	Кения	25	Тот же
	B. creona prorsus Talbot	Мадагаскар		de Lesse, 1972
147	B. crawshayi Butl.	Уганда	25	de Lesse, 1968
148	B. mesentina Cr.	Индия	25	Gupta, 1964
149	B. solilucis Butl.	Уганда	25	de Lesse, 1968
150	B. subeida instabilis Butl.	Уганда	25	Тот же
151	B. theora concolor Auriv.	Габон	25	de Lesse, Condamin, 1962
152	B. (Pseudanapheis) gidica Godt.	Сенегал	26	Bernardi, de Lesse, 1964
153	B. (Pseudanapheis) mabella Grose-Smith	Мадагаскар	25	de Lesse, 1972
154	Dixeia doxo lambertoni Le Cerf	Мадагаскар	25	Тот же
155	D. orbona Geyer	Сенегал	24	de Lesse, Condamin,
.00	Prioneris Wall.	Нет данных		1962
	Treater of Hall	and Administra		

			ATOMOTAN	пци г (просолжение)
Nº №	Вид	Местность	Число хромосом (n)	Источник
156	Pieris (Pieris) brassicae L. P. (Pieris) brassicae L.		14—15 15	Henking, 1890 Doncaster, 1912a, b; Bauer, 1967; Rishi, 1977
	Тот же « «	Англия Германия	15 15	Bigger, 1960; 1975 Traut, Mosbacher,
	« «	Финляндия	15	1968 Federley, 1938
	« «	Югославия	15	Lorković, 1941
	« «	Москва	15	Beliajeff, 1930
	« «	Ленинград	15	Лухтанов, Кузне- цова, 1988
	« «	Талыш	15	Данная работа
	P (Pierie) benegiero erosionale	Индия	15	Kaur, 1988
	P. (Pieris) brassicae azoriensis Rebel P. (Pieris) brassicae azoriensis		15	Federley, 1942
	P. (Pieris) brassicae nepalensis Doubl.	1 ималаи	15	Maeki, Ae, 1966
	Тот же	Индия	15	Saitoh et al., 1986
157	P. (Pieris) brassicoides Guer.	Эфиопия	14	Saitoh, 1985
158	P. (Artogeia) canidia Sparr.	О. Тайвань	25	Maeki et al., 1965
	Tor we	Китай Гималаи	25, 26	Saitoh, Abe, 1981
	P. (Artogeia) canidia indica Evans	тималаи	25	Maeki, Ae, 1966
	Тот же	Индия	25	Saitoh et al., 1986
159	P. (Artogeia) krueperi Stgr.		24	Lorković, 1966 in Robinson, 1971
	Тот же	Турция	24	le Lesse, 1970b
160	P. (Artogeia) manni Mayer	Франция	25	Lorković, 1941
	Тот же	Югославия	25	Тот же
161	P. (Artogeia) ergane Hühn.	Турция Далмация	25 26	de Lesse, 1960 Lorković, 1941
101	Тот же	далмация	25 + (1-2) B	Lorković, 1968a
	« «	Нахичевань	25	Данная работа
162	P. (Artogeia) rapae L.	Англия	25, 25 + B	Bigger, 1960; 1976
	Тот же	Финляндия	26	Federley, 1938
	« «	Москва	25	Beliajeff, 1930
	« «	Югославия	25	Lorković, 1941
	« « « «	Алтай Китай	25, 26 25	Данная работа Saitoh, Abe, 1981
	« «	Корея	25, 26	Lee, Kim, 1976
	« «	Корея	25, 26, 27, 28	Park, Kim, 1977
	« «	США	25	Maeki, Remington, 1960; Maeki, 1961
	P. (Artogeia) rapae crucivora Bdv.	RинопR	25, 25+B	Maeki, 1953a, b; 1958b, c; Maeki, Makino, 1953
163	P. (Artogeia) dulcinea pseudo- napi Vty.	Япония	27, 27+B, 27+2B, 27+3B, 27+4B	Maeki, 1953a, b; 1958a; 1959; Maeki, Makino, 1953
164	P. (Artogeia) napi L.		25	Lorković, 1966 in Robinson, 1971
	Тот же	Англия	25, 25+B 25+2B	Bigger, 1960; 1976
	« «	Финляндия	25	Federley, 1938
	« «	Париж	25	Lorković, 1941
	« «	Югославия	25	Lorković, 1941; 1968;
	P. (Artogeia) napi mandarina P. (Artogeia) napi meridionalis	Китай	25 25	Saitoh, Abe, 1981 Lorković, 1966 in
	Heyne&Rühl	G	00	Robinson, 1971
	P. (Artogeia) napi japonica Shirozu	Япония	26	Maeki, 1986

	20		(inprovince)
Вид	Местность	Число хромосом (n)	Источник
P. (Artogeia) napi nesis Fruhst	. Япония	26	Maeki, 1953 a, b; 1958b; 1959
P. (Artogeia) segonzaki Le Cer	Япония f Марокко	25 25	Maeki, 1986 Suomalainen in Eitsch-
P. (Artogeia) macdunnoughii Rem.	С. Америка	25	berger, Ströhle, 1986 Maeki, Remington, 1960
P. (Artogeia) virginiensis Edv. P. (Artogeia) bryoniae O.	Массачусетс	$26 \\ 25-28$	Maeki, 1961 Lorković, 1966 in Robinson, 1971
Тот же « «	Альпы Альпы	25 25, 25+B,	Lorković, 1941 Lorković, 1968a
P. (Artogeia) bryoniae caucasica Lork.	Кавказ	25+2B 26	Lorković, 1972
P. (Artogeia) pseudorapae balcana Lork.	Югославия	25, 26, 27, 26+B, 26+2B, 26+3B, 27+B, 27+2B	Lorković, 1968b
P. (Artogeia) pseudorapae balcarica Wojt. et Nies.	Пятигорск	25, 25+B, 25+2B, 25+3B, 26+B, 26+2B	Тот же
Pontia daplidice L.	Югославия	26	Lorković, 1941
Тот же P. daplidice moorei Röb.	Алтай Гималаи	26	Данная работа
P. (Pontieuchloia) chloridice Esp.	Алтай	26 26	Маекі, Ае, 1966 Данная работа
P. (Synchloe) callidice Esp.		26	Lorković, 1966 in Robinson, 1971
Тот же P. (Synchloe) callidice ralora Moore	Франция Индия	26 24, 25, 26	de Lesse, 1960 Saitoh et al., 1986
P. (Synchloe) beskeri Edw.	С. Америка	26	Maeki, Remington, 1960; Maeki, 1961
P. (Synchloe) occidentalis Reak.		26	Тот же
P. (Synchloe) calyce Edw. (Synchloe) protidice Bdv.	С. Америка	26 26	Lorković, 1966 in Robinson, 1971
Talbotia Bernard Glennia Klots	Нет данных Нет данных	91	Robinson, 1971
Leptophobia aripa Boisd.	Боливия	26 (?)	de Lesse, 1967a
Тот же	Эквадор	26	Тот же
L. cleone Doubl et Hew. Тот же	Боливия Эквадор	26 26	« « « «
L. elensis Lucas	Эквадор	26	« «
L. philoma Hew.	Эквадор	26	« «
L. tovaria Feld. Leuciacria Roths. et Jord.	Эквадор Нет данных	26	« «
Elodina Feld.	Нет данных		
Theochila Field	Нет данных		
Tatochila autodice Hübn.	Аргентина	28	de Lesse, 1967a
T. mercedis Esch. T. microdice microdice Blansk	Аргентина	28 28	Тот же
T. microdice arctodice Stand	Аргентина Эквадор	28 28	« « « «
T. ortodice Weym.	Аргентина	27—28 (?)	« «
T. stigmadice Stand.	Аргентина	27-28 (?)	« «
T. sagittata Röb. T. theodice Boisd			« «
T. vanvolxemii Capr.			« «
Piercolias Grote		20	* *
Hypsochila Ureta	Нет данных		
Reliquia Ackery	Нет данных		
Baltia Moore			
T. sa T. th T. va Piero Hyps Reliq Phuli	gittata Röb. eodice Boisd. nvolxemii Capr. eolias Grote ochila Ureta uia Ackery ia HerrSchäff.	gittata Röb. Эквадор eodice Boisd. ЧИЛИ nnvolxemii Сарг. Аргентина eolias Grote. Нет данных ochila Ureta Нет данных uia Ackery Нет данных fa HerrSchäff. Нет данных	gittata Röb. Эквадор 27 eodice Boisd. ЧИЛИ 27 nnvolxemii Сарг. Аргентина 28 eolias Grote Нет данных ochila Ureta Нет данных uia Ackery Нет данных ia HerrSchäff. Нет данных

NºNº	Вид	Местность	Число хромосом (n)	Источник
190	Itaballia demophile centralis Joic. et Talb.	Мексика	25	de Lesse, 1970a
191	I. tithoreides Butl.	Эквадор	` 26	de Lesse, 1967a
192	I. (Pieriballia) viardi Boisd.	Гватемала	26	de Lesse, 1970a
193	Perrhybris pamela Stoll.	Бразилия	27, 28—29	de Lesse, Brown, 1971
	Aoa de Niceville	Нет данных		
194	Ascia monuste L.	Флорида	27	Maeki, Remington, 1960; Maeki, 1961
	Тот же	Мексика	27	Тот же
	« «	Аргентина	27	de Lesse, 1967a
195	Melete leucanthe Feld.	Эквадор	24	Тот же
196	M. lycimnia paulista Fruhst.	Бразилия	23	de Lesse, Brown, 1971
197	Mylothris rhodope F.	Габон	22—27	Bernardi, de Lesse, 1964
	M. rhodope uniformis Talb.	Уганда	22+(3-4)B	de Lesse, 1968
198	M. hilara Karsch.	Габон	22 (?)	Bernardi, de Lesse, 1964
199	M. oshracea Auriy.	Габон	25—26	Тот же
200	Leptosia alcesta Cr.	Сенегал	12	de Lesse, Condamin, 1962
	L. alcesta inalcesta Bdi	Кения	12	de Lesse, 1968
	L. alcesta sylvicola Boisd.	Мадагаскар	12	de Lesse, 1972
201	L. nupta Butl.	Уганда	12	de Lesse, 1968
202	L. wigginsi Dixey	Уганда	12	Тот же
203	L. nina niobe Wallace	О. Тайвань	19	Maeki, Ae, 1968; Maeki, 1981

бабочек рода Pieris, обработанных колхицином, наблюдаются центромероподобные перетяжки (Bigger, 1975). Самки гетерогаметны. Хромосомная система определения пола, по данным Биггера (Bigger, 1975), приведенным для Pieris, у самцов представлена двумя Z-хромосомами, у самок Z- и W-хромосомой (по другой системе обозначений XX и XY соответственно), причем Z относится к числу крупных (P. brassicae) или средних (P napi и P. rapae) хромосом, а W — к числу мелких. Хромосомы относительно мелкие. В MI биваленты имеют характерную гантелеобразную или крестообразную форму, что хорошо видно на рис. 2, b и 2, a. Чаще всего биваленты независимо от их числа по размерам составляют плавно убывающий ряд (рис. 1, 2).

Число хромосом у представителей семейства варьирует от n=12 до n=103-104 и часто является характерным для отдельных родов, триб и подсемейств. Многие группы, в том числе наиболее примитивные, имеют модальное число хромосом n=31. Это число наиболее широко распространено среди высших чешуекрылых (Robinson, 1971), встречается в самых примитивных семействах (Suomalainen, 1969) и, скорее всего, является анцестральным для всего отряда. Несомненно, что это число является исходным и для сем. Pieridae. Для многих видов семейства характерна внутри- и межпопуляционная изменчивость числа хромосом. Нами внутрипопуляционная изменчивость обнаружена у представителей всех четырех подсемейств белянок (табл. 1). Причиной подобной вариабельности числа хромосом бывает наличие дополнительных, так называемых B хромосом, обычно очень мелких и не образующих бивалента в мейозе (рис. $1, \partial$) или же изменение числа бивалентов (рис. 1, a и 1, a). Сведения о хромосомных числах белянок мировой фауны представлены в табл. 2.

Table 1. Summary of chromosome numbers in Tellervo and in the "primitive" radiation of Ithomiinae. Locality codes are shown at the end of Table 2. Localities in **bold** indicate places of origin of material for meiotic metaphases shown in Fig. 6 through 78.

Tribe	Genus	Species, subspecies	n =		No. f	ixed/counted
			_	Pop./ind.	Ind.	Localities
	Tellervo	zoilus zoilus	32	3/5	1	QA3 (EMMEL et al. 1974)
A	Aeria	o. olena	27	3/3	3	AR(a),ES,SP
		eurimedia (4 different)	°°38°°	10/16	7	AC3,CC3,RG3,RO
		elara (3 different)	°°°°80°°	8/28	8	AC,AN,DF,GO,MT,RG2,RO
	Elzunia	humboldt (4 different)	14	5/8	1	AN,CC,EE,TV,VC
		pavonii	°20	3/7	3	MP3
	Tithorea	harmonia (16 different, from salvadoris to caissara)	°14	22/45	25	AM2,AN(a),AR(a), BO ,CM,EB,EV, GO(d),HU,MP,MT2,MX(b),PA,RG, RO2,RR2,SP,TR(e)
		t. tarricina, franciscoi, parola	11	5/10	3	AN,CT2,VC2
В	Methona	m. megisto, new ssp.	14	3 /4	3	AM,MT,PA
		curvifascia	14	4/9	3	AC,EE2,HU
		g. grandior	14	2/4	4	AC,AM
		confusa (3 different)	14	11/20	18	AC,AM2,CM,EB,EE2,RO2,RR,TV
		themisto ssp. nov.	14	1/1	1	GO(d)
		singularis	13	2/4	1	PB,PE
С	Olyras	crathis (4 different)	8	5/15	12	CC,EV, RG 2,TV
	Eutresis	h. hypereia	20 + 19 - 20	2/6	4	EV,RG
	Athyrtis	mechanitis salvini	°50°	8/13	11	AC2,RO6
	Melinaea	mnasias (4 different)	$^{\circ\circ\circ}26^{\circ}$	5/7	5	AP,BA,CM,GY(c),RR
	(see details of this	l. ludovica	17-23	12/19	18	AM5,AP2,GY(c),PA,RO,RR2
	genus in Table 8)	paraiya; crameri	$^{\circ}23^{\circ}$	4/5	5	BA,RJ(d),SP,EV, BO
		i. idae, vespertina	13	4/4	4	AN,CC,CZ,WE
		maelus (8 different)	°15°°	10/23	18	AC2,AM2,EB3,EE,HU,RO
		lilis (6 different)	$^{\circ\circ}22^{\circ\circ}$	7/11	11	CC,CH,EV,MX,OX,RG,TR(e),TV
		ethra	°30	5/8	7	BA,ES,PE,RJ,SP
		mneme (3 different)	°17	5/21	18	AM,AP2,GY(c),RO
		menophilus (3 different)	$^{\circ}20^{\circ\circ}$	6/12	11	AC,EE(a),EE,RO3
		marsaeus (4 different)	$^{\circ}17^{\circ}$	9/16	15	AC2,PA,RO4,VV2
		phasiana, satevis	15	3 /4	4	AC2,EB
		maenius (6 different)	°°22°°°	10/18	17	AC,AP2,EE4,GY(c),RO,VV
D	Thyridia	psidii (6 different)	17	11/15	12	AC,CH2,EE2,ES,GO,MP,MT2,RO
	Sais	rosalia (6 different)	20	11/26	14	AC,ES,GO,MT,PA,RG,RO3,RR2
	Scada	z. zibia, xanthina, zeroca	$^{\circ}18^{\circ}$	4/6	2	CC3,CH
		batesi; batesi quotidiana	43	2/7	2	AC,EE
		reckia	28?	3/9	1	BA2,PE
		ethica (6 different)	°21°°	7/14	10	AC2,AM,EE,PA,RO,RR
		karschina	20	2/7	3	BA,ES
		kusa	21	2/5	1	MP2

al.

Table 1 (Continued)

Tribe	Genus	Species, subspecies	n =		No. f	ixed/counted
				Pop./ind.	Ind.	Localities
	Mechanitis	l. lysimnia	18-19	5/10	7	AR(a),BA,GO,RJ(d),SP
	(see details of this	nesaea, connectens	$16{-}17^{\circ}$	7/31	23	BA2;GO,MT2,PB,RO
	genus in Table 7)	menecles, ocona, acreana, elisa	15	7/26	15	CM,EB(a),EB2,EE,MT,RO
	,	macrinus (4 different)	22,23	4/8	5	CH,CZ,EV,RG
		polymnia (7, Transandean)	°18 ^{°°}	11/31	24	AN(a),CC,CZ,EV,GU(a),MX,RG, VC2,VV,WE
		(9, Amazonian to SE Brazil)	°15°	27/58	43	AM,AP3,CM,DF(d),EB,EE,GO,HU, MG,MP,MT5,PA3,RJ,RO3,RR3
		menapis (4 different)	$^{\circ\circ}24-25^{\circ\circ\circ}$	8/19	14	AN(a),CC3,EV,RG,VC2
		dariensis, mantineus	20	2/5	4	DA, WE(incl. a)
		mazaeus (6 different, Amazon Basin)	14,15	7/15	14	AC,AM2,EE,RO,VV2
		(4 from peripheries)	°°16	10/36	21	EE3,CM,GY(c),PA2,RO,VV2
	Forbestra	proceris	9 + 6 - 8	2/4	4	AC2
		olivencia (4 different)	9 + 1 - 6	5/11	10	AC2,AM,EB,EE
		equicola (4 different)	°°°63°°	5/11	11	AC,AM,AP,EE,RO
Е	Roswellia	acrisione(f), a. vitrala	32,34	2/4	2	EE(f), MP
	Athesis	clearista, c. colombiensis	24	5/11	8	AN,EV,RG2,VC
		,	28 + 10	1 /2	2	RG
	Patricia	d. dercyllidas	14	1 /2	2	VC
		d. demylus	14	1/1	1	EE(f)

Explanation of Tables: nomenclature follows Lamas (2004) with few exceptions (Results, footnote). Superscript dots before and after a number indicate variation, as much as 3–6 over or under the given figure, encountered infrequently, rarely in the same population.

Localities are grouped by region; a number at the end indicates more than one population sampled within this region; a letter in parentheses indicates previous work (a = de Lesse 1970a, c = de Lesse 1970b, d = de Lesse and Brown 1971, e = Wesley and Emmel 1975, f = Eliazar and Emmel, pers. comm., g = Maeki and Remington 1960, h = Maeki 1961).

Locality codes: AC = Acre (SW Brazil), AM = Amazonas (N Brazil), AN = NC Colombia, AP = Amapá (N Brazil), AR = N Argentina, AV = Amazonas (S Venezuela), BA = Bahia (Brazil), BO = Bolivar (SE Venezuela), CC = Chocó (W Colombia), CH = W Panama, CM = Chanchamayo (C Peru), CR = Costa Rica, CT = NW Venezuela, CZ = Canal Zone (Panama), DA = E Panama, DF = Brasília, DR = Dominican Republic, EB = E Bolivia, EE = E Ecuador, ES = Espírito Santo (Brazil), EV = NE Venezuela, GO = Goiás (C Brazil), GU = Guatemala, GY = Guianas, HU = Huallaga Valley (C Peru), JM = Jamaica, LO = NE Peru, MG = Minas Gerais (Brazil), MP = upper Río Marañón (NW Peru), MT = Mato Grosso (Brazil), MX = SE Mexico, OX = S Mexico, PA = Pará (Brazil), PB = Paraíba (NE Brazil), PE = Pernambuco (NE Brazil), PT = S Colombia, QA = N Queensland (Australia), RG = N Venezuela, RJ = Rio de Janeiro (Brazil), RO = Rondônia (SW Brazil), RR = Roraima (N Brazil), SC = Santa Catarina (S Brazil), SP = São Paulo (SE Brazil), TR = Trinidad, TV = Táchira (SW Venezuela), VC = Valle de Cauca (W Colombia), VV = Meta (E Colombia), WE = W Ecuador.

Tribe	Genus	Species, subspecies	n =		No	o. fixed/counted	
				Pop./ind.	Ind.	Localities	
F	Pagyris	cymothoe	30	3/9	4	RG,TV,VV	
	Placidina	euryanassa	28	2/2	2	BA,RJ(d)	
	Ithomia	iphianassa (5 different)	$^{\circ}11{-}12$	8/18	11	AN2,CC2,RG,VC,VV,WE	
		p. pellucida, ssp.	14	2/2	1	MP,TV	
		terra (4 different)	15-17	4/6	5	CC,CH,CM,EE	
		amarilla	15−16°°	1/9	3	EE	
		jucunda bolivari	16	2/2	1	CH2	
		diasia (3 different)	17	5/12	10	CC3,CH,WE	
		celemia plaginota	17-18	1/3	2	CH	
		agnosia (4 different)	°18°	7/18	17	GO,EE3,PE,RG,RJ	
		p. patilla, leila	18	3/3	3	CH, $GU(a)$, $MX(a)$	
		lichyi (3 different)	18	3/9	2	AC,BA,RJ(incl.d)	
		h. hyala, ssp.	19	2/5	2	CC,WE	
		lagusa theuda, linda	19	3/6	6	EE,VC2	
		avella	20	1/1	1	VC	
		drymo	20	2/4	4	ES,RJ(d)	
		ellara	20,21	1/2	2	CM	
		salapia (3 different)	34–35°°°	6/20	11	AC2,CM,EE3	
ŗ	Epityches	еиротре	17	2/4	2	BA ,RJ	
	Napeogenes	harbona domiduca	6	1/1	1	CM	
		verticilla	7	1/1	1	CM	
		gracilis	12	1/2	2	CM	
		pharo (4 different)	10,11,13	5/9	6	AC,PA,RO2,VV	
		aethra deucalion, ssp.	12,13,14	4/9	7	AC2,RO2	
		a. apulia, lycora	13	2/3	3	EE,VV	
		sylphis (4 different)	14°°	8/11	8	AM,AP,PA2,RO4	
		s. stella, opacella	°12,13,14	4/9	7	AN2(incl.a),CC2	
		(stella?) duessa, jamariensis	15	2/6	4	AC,RO	
		cranto ssp. nov.	18	1/1	1	WE	
		inachia johnsoni, pozziana (NW)	13,14	2/6	4	EE,VV	
		ssp. nov. (SW)	16,17,18	5/7	7	MT3,RO2	
		pyrois, 2 sspp. nov.(C)	22	3/5	2	AM2,PA	
		(inachia?) sulphurina, ssp. nov.	24,26,28	4/10	5	BA,PE3	
		cyrianassa (7, Amazon)	°32°	11/22	13	AM2,AP2,BO,PA,RO,3,RR2	
		rhezia, yanetta	35,37	4/9	5	BA2,ES2	
	Hyalyris	leptalina ssp. nov.	18	1/3	1	ES	
		c. cana	20	1/1	1	RG	
		oulita? oulita lurida?	26,28	2/8	2	CM,EB	
		o. ocna, adelinda	°43	2/2	3	EE,VV	
		coeno (4 different)	°48–49	4/23	12	MP,RG,TV,VV	

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Genus Tribe Species, subspecies n =No. fixed/counted Pop./ind. Ind. Localities excelsa ssp. nov 60 2 TV1/2 °66° antea flebilis, frater 2/7 6 CM.TV metella 98 - 1001/5 3 CMGarsauritis x. xanthostola, ssp. nov. 18.20 2/4 3 AM.AP 5 3/9 Rhodussa cantobrica nundina, ssp. nov 50 - 51RO3 5 Hypothyris thea, theatina, vestita 5 4/6 AM2,PA2 (fluonia?) rowena 9 1/3 2 VV °°15°° fluonia (4 Amazonian ssp.) 5/14 6 AC2.GO.MT.RO euclea (8 Amazonian and Atlantic 14° 18/42 32 AC,AM,AP2,BA,CM,EB2,EE3, ES, subspp.) GO,MT,RG,RO,TR,TV valora, philetaera °16° 4/10 7 AN,CC,CZ,VC °°16°° ninonia (9 Amazonian subspp.) 16/46 36 AC,AP2,AM5,BO,MT,PA2,RO2, RR2 daeta 18 - 194/9 8 BA,ES,MG(a),RJ(a) evanescens 21 - 233/10 9 BA2,PE °°17 8 semifulva (3 different) 5/10 AC2,RO3 v. vallonia, ssp. n. $^{\circ\circ}20^{\circ}$ 2/3 3 PA.RR d. daphnis, madeira °20 2/9 4 AM.RO leprieuri (4 different) °20 10/16 14 AC2.GY(c).MT3.RO4 anastasia (3 different) 17,20,21 3/6 3 AC2,RO mamercus (4 different) °24°° 7 6/13 AC, EE, RO4 °°°45° CC,EV,GU(b),RG,VC lycaste (5 different) 5/11 7 Η Hvposcada 12 1/2 2 CC(the genus *Oleria* is in sp. 12 1/2 1 AM Table 3) illinissa abida 12 1/3 2 CC attilodes? 13 2/2 2 EE2 zarepha 14 4 14 AP illinissa (4 different) 13.15 4/9 2 AM.EE.PT.RR v. virginiana, consobrina 15 2/2 2 AN.CC anchiala (3 different) 15 3/7 5 AC.EE.RO [like *makrena*] 19 1/1 EE Megoleria orestilla 35 1/4 1 EE(f) Ollantaya aegineta cleobulina 6? 1/1 CM canilla 14 1/3 2 CM I Callithomia hezia beronilla 11 1/1 1 CC alexirrhoe (5 different) 6/6 5 AM,GY(c),MT,PA2,RO 12 lenea (5 different) 12°° 12/19 11 BA,EB2,MT5,PA,RO,RR2 Dircenna loreta (4 different) °12 12/21 14 EE3,MT,PA,RG,RO4,VV2

14

14.15

4/8

14/44

7

20

EE2.RG.TV

MT,PE,SP,VV

AC,CM,EB2,EE,ES2,GO,MG2,

Table 2 (Continued)

(the genus *Pteronymia adina* (3 different)

dero (4 different)

is in Table 3)

Table 2 (Continued)

ribe	Genus Species, subspecies		n =		No	. fixed/counted
				Pop./ind.	Ind.	Localities
		"dero" euchytma (Transandean)	16,17	7/12	11	AN(a),CH2,RG2,VC2
		p. paradoxa, ssp.	17	2/3	3	VC,WE
		jemina (5 different)	°19°	5/14	11	CH,CM,EB,EV,RG
	(may be hybrids or	"dero celtina"	23	1/3	3	AR(a)
	contaminants)	"dero rhoeo, dark"	30,33	1/3	2	GO
	Hyalenna	sp. nov.	13	1/1	1	WE
		a. alidella	15	1/2	2	VC
		minna	22	1/2	2	CM
		pascua	43°	3/9	5	RJ,SP2
	Haenschia	derama	33	1/4	3	CM
	Episcada	hemixanthe	16	1/2	2	BA
	Брізсини	mira	17	3/5	3	AC,EE,VV
		c. clausina, striposis	°21°	3/5	4	EB,RJ(d),SP
		montanella	24	1/3	2	SP
		munda	26-27 + few	1/5	4	SP
		philoclea	28+many	3/6	4	RJ,SP2
		pnilociea polita	28°	5/6	4	AC2,CC,TV2
		sylpha	31	2/7	1	RG,TV
			°34°		_	
		s. salvinia, cabenis		5/7	5	MX,OX,VC3
	D 1 1 . 1	carcinia	60-62	3/5	2	BA,SP2
	Prittwitzia	hymenaea (4 different)	°15	7/12	10	AR(a),BA,DF,GO,MG(d),RJ,RG
	Ceratiscada	doto ssp.	12	1/1	1	BO
		canaria	24,27	2/7	3	BA,ES
	Ceratinia	iolaia	12,14,15	1/5	5	AN(incl.a)
		neso (7 different)	14	9/21	14	BO,CM,EE2,RG,RO2,RR,VV
		tutia (10 different)	°°17°°°	17/32	17	AC3,AN,CC,CM,EE4,RG3,RO, VC,V
		c. cayana, giparanaensis	19+1,23	2/2	2	RO,RR
	Talamancana	lonera	20	1/1	1	CH
	Velamysta	phengites	12	1/1	1	EE
		pupilla cruxifera	22	1/1	1	EE
		peninna ms. ssp.	38	1/3	2	CM
	Dygoris	d. dircenna, ssp. nov.	36	2/4	4	\mathbf{CM} , \mathbf{VV}
	Godyris	kedema (3 different)	13	3/9	4	EV,RG,VV
	-	nero	15	2/2	2	CH,OX
		crinippa ssp.	24	1/1	1	CM
		nepos hewitsoni, ssp. nov.	31,32	2/2	2	CM,EE
		panthyale ssp.	44	1/1	1	CM
		duillia	46,47	1/1	1	VV
		zavaleta (5 different)	····40·····	7/27	17	CM,EE,RO3,TV,VV
		zygia	75	2/3	3	CH2
		sappho	77	1/2	1	CM
		sappno gonussa, petersii, telesilla	98-120	5/11	9	AN,CC2,WE2

Table 2 (Continued)

ribe	Genus	Species, subspecies	n =	No. fixed/counted		
			-	Pop./ind.	Ind.	Localities
	Greta	p. polissena, umbrana	12	3/6	1	CH,WE2
		(andromica?) andania	°36°	2/8	5	CM,EE
		a. andromica, lyra	°42°	8/18	6	AN2(a),CC,CH,RG,TV,VC,WE
		morgane oto	°°47°	3/5	2	CH,MX(b),OX
		quisqueya	70	1/6	2 2	DR
		diaphanus	78	1/5	2	JM
		annette	73,80	4/4	2	CH.OX3
	Hypomenitis	cvrcilla?	24	1/1	1	CM
	JF · · · · · · · · ·	dercetis	27	4/7	2	EE2,RG,TV
		enigma	42	1/3	3	WE
		alphesiboea	60	2/2	1	EE,VV
		ortygia ssp.	68	1/1	1	CM
		ochretis	"very many"	2/2	1	AN,VC
		theudelinda	about 100	1/6	2	EE(f)
	Mcclungia	cymo (4 different)	°11	6/9	4	BO,GO2,MG2,MT
		fallens (3 different)	13	4/12	5	AC.RJ.RO
	Hypoleria s.1.	aelia pachiteae, plisthenes	8	14/28	11	AC3,BA,DF(d),GO2,MG,MT2, RO 3,S
	11) pore un on	orolina (5 different)	°15°	7/15	6	AC2,DF,GO,MT,RO,SP
	Hypoleria	ocalea (4 different)	10,11	6/15	9	AN2,MT2,RG,RO
	Пурочени	adasa (3 different)	20°	4/8	3	ES,GO,RJ(d),RR
		lavinia (4 different)	26.29-30	5/10	6	CC2,CZ,TV,WE
		alema (12 different)	36-38, 40-43	16/34	15	AC2,AP,BA,EE,ES,GO,MT4,PA,PE,
		aicma (12 different)	30 30, 10 13	10/51	13	RO2.VV
		sarepta virginia, +2 different	44,45	6/11	8	AC3,AM2,SP
	Pseudoscada	erruca	°30°	7/12	4	ES,MG4,RJ2
	1 seudoscudu	timna (5 different)	°31°	12/34	16	AC2,AN(a),CC2,CH,C-
		timia (5 different)	51	12/34	10	M,EE2,RG,VV,WE
		florula (4 different)	30-31	7/23	11	AC2,BA2,EE,ES,RJ
		acilla quadrifasciata, ssp.	31	5/16	13	GO(d),MT3,RO
	Heterosais	giulia (5 different)	°°31	15/31	20	AN(a),CH,CM,EB, E E,HU,MT3,
	neierosuis	giuiu (5 different)	31	13/31	20	RG,RO3,VV,WE
		edessa	30-31	4/7		PE,BA,ES2

Table 3. Chromosome numbers in two large, poorly resolved genera: Oleria and Pteronymia. Localities in **bold** indicate places of origin of meiotic metaphases shown in Fig. 54–59 and 66–69.

Tribe	Genus	Species, subspecies	n =	Pop./ind.	Ind.	Localities
Н	Oleria	victorine graziella	9	2/6	4	RG2
		deronda valida	10	1/1	1	CM
		fasciata	11	1/2	1	CM
		gunilla lota, lubilerda+2	10,11	5/15	5	AM2,EE2,VV
		amalda, a. modesta	12	3/8	3	CC2,WE
		olerioides	12	1/1	1	CM
		peruvicola	13	1/2	2	CM
		makrena?+2	°13°	7/16	6	CC,CH,CM,CZ,VC,WE2
		manora	14	2/5	4	RO,RJ(d)
		cyrene	14	1/6	5	CM
		aegle	14,15	1/2	2	AP
		ilerdina priscilla, quintina	°14°	6/25	18	AC2,CM,EB2,HU
		alexina didymaea+2	°°15	7/10	6	PA,RO,RR,EB
		a. astraea, burchelli, similigena	°15	5/25	12	AC2,AM,AP,BA3,EE,ES
		p. paula	16	2/3	3	MX2(b)
		phenomoe	18,19	3/8	2	RG,TV2
		onega crispinilla+1	°22	4/12	5	AC3,CH
		e. egra, divisa	23-24	3/11	2	AM2,AC
		e. estella	27-28	2/5	4	EE2
		padilla pseudmakrena+2	30	3/12	2	CM,RG,VV
		o. onega, ilerda, machadoi+1	30°	5/8	5	AP2,CM,EE,VV
		zelica (2 different)	32,29	2/7	7	VE,WE
		athalina	41	1/1	1	CM
		aquata (3 different)	°°43°°°	8/26	7	AC,BA2,ES,GO,MT2,RO
	Pteronymia	donella donata	10	1/1	1	DA
		alida	13	1/2	1	RG
		vestilla? (2 different)	14	3/6	5	AN,PA,VC
		sylvo	14	5/7	2	AR(a), GO , MG , $RJ(d)$, RO
		euritea	14	2/6	6	ES,RJ(d)
		cotytto	15	1/1	1	MX(b)
		são guntheri, ssp. nov. (Lamas)	15	2/3	1	AC,CM
		artena (3 different)	15	3/4	3	EE,TV,VV
		forsteri	16	1/1	1	AC
		latilla (3 different)	16	3/11	5	CC,RG,TV
		veia linzera+4	°°17°	7/10	9	CM,EE,HU,TV,VC2,WE
		o. oneida	20	1/1	1	EE
		granica?	23	1/1	1	EE
		oneida? asopo (2 different)	°24°°°	4/7	3	EE2,RG,TV
		zerlina nubivaga	26	1/2	1	RG
		aletta	26	4/10	3	AN,CC,RG,TV
		teresita thabena	38	1/10	2	EE(f)
		hara semonis?	54	1/2	1	VC

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Table 4. Chromosome numbers of the American Danainae. The taxonomic division follows Ackery and Vane-Wright (1984). The numbers n=29 for D. eresimus and (n=29-30) for D. gilippus come from Maeki (1961); the number for D. plexippus comes from a population kept at the University of Madras, India (RAO and MURTY 1975).

Tribe	Genus	Species, subspecies	n =	No. fixed/counted		
				Pop./ind.	Ind.	Localities
A	Anetia	thirza	31	1/2	1	OX
		briarea	31	1/5	2	DR
		pantheratus	31	1/2	1	DR
В	Lycorea	cleobaea (2 different)	30	2/2	2	AN(a),RJ(d)
	•	pasinuntia (3 different)	22	10/17	10	AC3,AM3,EV,GY(c),RO2
	(Ituna)	ilione (2 different)	30	3/5	4	EE2(incl. a),VV
C	Danaus	cleophile	30	1/2	1	DR
		plexippus	30	1/1	?	Madras, India
		erippus	30	1/2	2	SP
	(Anosia)	eresimus (5 different)	°30	6/8	5	CT,DR,DA,EV,MX(gh)
	,	plexaure	30 - 31	1/2	2	BA
		gilippus (2 different)	29°	3/6	3	BA,ES,MX(gh)

Not counted: Anetia jaegeri, A. cubana.

Table 5. Chromosome number comparisons in monophyletic sister-groups (within small genera, or between them and their closest relatives).

Tribe (Fig. 1)	Genus (most primitive or widespread species)	n/n	More advanced or restricted species, or putative sister-genus
A	Elzunia humboldt	14/20	Elzunia pavonii
	Tithorea harmonia	14/11	Tithorea tarricina
	Aeria olena	27/38, 80	Aeria eurimedia, A. elara
E	Athesis clearista	24/14	Patricia (2 spp.)
C	Olyras crathis	8/20+19-20 mc	Eutresis hypereia
	Melinaea (10 spp.)	13-30/50	Athyrtis mechanitis
D	Thyridia psidii	17/18-43	Sais rosalia, Scada spp.
	Mechanitis lysimnia	15-19/22-23	Mechanitis macrinus
	Forbestra olivencia	9+mc/63	Forbestra equicola
I	Callithomia (3 spp.)	11-12/12-38	Velamysta spp.
Н	Ollantaya canilla	14/6	Ollantaya aegineta cleobulina
	Hyposcada (11 spp.)	12–15/9–43, 35	Oleria (>20 spp.), Megoleria susiana
G	Epityches eupompe	17/6-37	Napeogenes spp.
F	Pagyris cymothoe	30/11-35	Ithomia spp.
G	Garsauritis xanthostola	18-20/50-51	Rhodussa cantobrica
I	Hyalenna sp. nov., H. alidella	13,15/22, 43	Hyalenna minna, H. pascua
	Ceratiscada doto	12/24-27	Ceratiscada canaria
	Prittwitzia hymenaea	15/17-62	Episcada spp.
J	Dygoris dircenna	36/13-120	Godyris spp.
	Mcclungia salonina	11/8-45	Hypoleria spp.
	Heterosais, Pseudoscada	31, 30-31/12-100	Greta, Hypomenitis

Table 6. Ithomiine species with appreciable geographic variation in their chromosome numbers, in different localities (see also Table 7–8). Asterisk (*) indicates variation within populations also.

Tribe	Genus	Species	Localities	n =	Comments
E	Athesis	clearista	Colombia, W Venezuela	24	Related Roswellia has 32, 34
			NE Venezuela	28 + 10 mc	
F	Ithomia	*iphianassa	C Colombia	10	Intergrade freely giving
		•	Venezuela, W Ecuador	12-13	n = 11,12
		terra	W Colombia	14	n = 16 also known
			Eastern Peru	17	in between these
G	Garsauritis	xanthostola	Amapá, N Brazil	20	
			Manaus, C Amazon	18	m1 10 11 0 1
	Napeogenes	*inachia	E Colombia	13–14	The conspecificity of these populations might be questioned
			Rondônia, SW Brazil	16-18	
		11.	Amapá-Para, N Brazil	22	
		sulphurina *stella	Pernambuco, Bahia Central Colombia	24,26,28 11–13	Almost supply off and
		stetta	W Colombia	12–14	Almost surely all are conspecific
	Hypothyris	*ninonia	Amazonian Brazil	15-18	Possibly not the same species
	11ypoiny is	*n. daeta	Eastern Brazil	18-23	ression not the same species
		vallonia	Roraima, N Brazil	24	Sister sp. (gemella)
			Pará, E. Brazil	20-21	has $n = 18-20$ in Roraima,
			SW Venezuela	22	Venezuela
		fluonia	E Colombia	9	Conspecificity is quite certain for
			E Ecuador	16–17	all these
		*euclea	S-C Brazil C America –	13 16–17	Intergrades in W Colombia,
		еистеи	W Colombia	10-17	n = 16-17
			Amazon to S Brazil	12-15	n = 10 - 17
		*lycaste	Guatemala	48	
		,	W Colombia	42-45	
			W Ecuador	50	
Н	Oleria	*aquata	SE Brazil	46	
			SW Brazil	43	
		zelica	W Colombia	29	Most species have the same
			W Ecuador	33	number in both
I	Dircenna	dero	C America to	16 - 17	
			W Ecuador	14 15	
	Ceratinia	*tutia	S Brazil-Argentina C America-	14–15 15–16	Almost surely these are
	Ceranna	iuita	W Colombia	13-10	conspecific with each other
			N Venezuela	19-20	conspecific with each other
			Acre, SW Brazil	15	
			Rondônia, SW Brazil	18	
	Ceratiscada	canaria	Bahia, E Brazil	24	
			Esp. Santo, E. Brazil	27	
J	Hypoleria	lavinia	Costa Rica to W	26	
			Colombia W. Fayadar	20	
		alema	W Ecuador SW Venezuela	29 30	
		aiema oreas	SW Brazil	36	
		orcus	NE Brazil	40-42	
			NW Brazil	38,40	
			E Colombia	37–38	

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Table 7. Chromosomes and systematics of Mechanitis species and subspecies.

Species	Subspecies examined	Localities	n =	Comments
lysimnia	menecles, ocona, acreana, elisa lysimnia	CM,E B ,EE,MT,RO AR,BA,RJ	15 18–19	no variation in these western sspp. Form "connectens" (GO,MT) has $n = 16-17$
	nesaea	BA,PB	17	Form "sulphurescens" has $n = 18$
macrinus	macrinus, utemaia, solaria, new ssp.	CH,CZ,EV,RG	22-24	Consistently higher n than <i>lysimnia</i> , for names see LAMAS (1988)
polymnia	lycidice, isthmia, veritabilis, werneri, caucaensis, kayei, chimborazona (Transandean)	AN,CC,CZ,EV,MX,VC,WE	17-19	Occasionally to $n = 20$ or more, especially in Sucre/Trinidad
	bolivarensis, dorissides, proceriformis, eurydice, polymnia, mauensis, new ssp., angustifascia, casabranca	MP,RR,VV,EE, CM,PA,AM,MT,CM, EB,HU,GO, MG,RJ	14–16	n = 16 seen very rarely, possibly due to non- pairing in an otherwise stable complement
menapis	menapis, occasiva, caribensis, new ssp.	DA,CC,VC,RG,EV	24-25	occasionally lower (22–23 in E Venezuela) or higher (28 in W Colombia)
mazaeus	dariensis, mantineus mazaeus, elevata, egaensis, pannifera, visenda, pothetoides, various forms	DA,WE GY,VV,EE,AM, RO,PA,AC	20 14–16	lowest numbers at extremes of range darker forms tend to lower numbers (14) in W Amazon and Andean foothills but most pops. have variable 14–16
	messenoides, deceptus	VV,EE,CM	15-16	very occasional counts of 14 seen

Table 8. Chromosomes and systematics of Melinaea.

Species	Subspecies examined	Localities	n =	Comments
mnasias	eratosthenes, rondonia, thera, comma, new ssp.	AP,CM,GY,RR, BA,PA,RO	23-27	Seems coherent and amply distinct; also includes 7–10 other ssp.
iudovica	ludovica (some populations)	AP,PA,RO,RR	17 - 19	Varies within populations or individuals
	ludovica, paraiya	AM,BA,GY	20-23	May be due to incomplete pairing at times
	crameri, paraiya	BA, BO ,EV,RJ,SP	23,24	Highest n at extremes of range
idea	idae, vespertina	AN,CC,CZ,WE	13	Separated from <i>ludovica</i> by chromosomes
ethra	(none)	BA,ES,PE,RJ,SP	29,30	E Brazil; separated from maelus/maeonis
maelus	zamora, maeonis, cydon,	AC,AM,CH,	14,15, 17	Consistent form of wing markings (FW
	tarapotensis, flavomaculata, mnemopsis, scylax	EB,EE,HU,TV		Cu, HW cell) and low number
	lamasi, new ssp.	AC,RO	14 - 17	higher numbers can be seen in this region
lilis	imitata, parallelis, lilis, dodona	CH,CC,MX,OX RG	21-24	Variable within and between populations, includes also 7 more Transandean ssp.
	sola, lateapicalis	EV,TR,TV	20-21	Lowest n at NE, S extremes of range
mneme	mneme, mauensis, new ssp.	AM,AP,GY,RO	16,17	Consistent in pattern and number
menophilus	menophilus, orestes, zaneka	AC,EE,RO	19-22	Consistent E to E Pará
marsaeus	messenina, mothone, clara,	AC,EE,TV,VV	16-18	Also includes marsaeus, macaria, rileyi;
	pothete	RO,PA	1.5	sympatric with maelus, menophilus, maenius
	phasiana, satevis	AC,EB	15	lowest numbers in SW, satevis was in ludovica
maenius	mediatrix, isocomma, simulator,	GY,AP,VV,EE,	20 - 23	Up to $n = 25$ in some areas; often hard to
	cocana, egesta, juruaensis	RO,AC		separate superficially from <i>marsaeus</i>

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Table 1. Haploid chromosome numbers for South American Nymphalidae. The taxon name used in the original reference is in parentheses. A comma between chromosome numbers shows that the numbers come from different individuals. Localities are grouped by region; a number at the end of locality codes indicates the number of populations sampled within a region. A lower case letter in parentheses indicates previous work (a = DE LESSE 1967a, b = DE LESSE 1970a, c = DE LESSE 1970b, d = DE LESSE and Brown 1971, e = Francini 1989, f = Maeki and Remington 1960, g = Wesley and Emmel 1975, h = Emmel and Eliazar, unpubl.). Locality codes: AC = Acre (extreme western Brazil), AM = Amazonas (northwestern Brazil), AN = Andes of north-central Colombia, AV = Amazonas (southern Venezuela), BA = Bahia (eastern Brazil), BO = Bolivar (southern Venezuela), CC = Chocó (western Colombia), DF = Brasília (central Brazil), DR = Dominican Republic, EE = eastern Ecuador, ES = Espírito Santo (eastern Brazil), MG = Minas Gerais (central Brazil), MT = Mato Grosso (central Brazil), OX = Oaxaca (southern Mexico), PA = Pará (northern Brazil), RJ = Rio de Janeiro (southeastern Brazil), RO = Rondônia (western Brazil), TV = Táchira (southwestern Venezuela), VC = Valle de Cauca (western Colombia), VV = Villavicencio, Meta (eastern Colombia).

Genus	Species, subspecies	n =	No. studied pop./ind.	Locality
Family NYMPHALIDAE				
Subfamily LIBYTHEINA	E			
Libytheana	carinenta	31+2 small	1/1	Mexico(b)
Libytheana	carinenta bachmanii (L. b.)	31	1/7	Mexico(f)
Subfamily DANAINAE; I	Brown et al. (2004)			
Tribe Danaini; Brown et	al. (2004)	~30		
Tribe Ithomiini; Brown e		\sim 14–15-variable		
Subfamily CHARAXINA		variable		
Subfamily SATYRINAE;	Brown et al. (2007)	\sim 29-variable		
Subfamily CYRESTINAE	3			
Marpesia	berania	32	1/1	Colombia(a)
Marpesia	corinna	33	1/2	Bolivia(a)
Marpesia	petreus	32	1/2	Argentina(a)
Marpesia	zerynthia (coresia)	32	1/2, 1/1	Bolivia(a), Ecuador(a)
Subfamily BIBLIDINAE				
Tribe Biblidini				
Biblis	hyperia	28	1/2, 1/5	Argentina(a), Mexico(f)
Mestra	dorcas apicalis (M. a.)	31	1/1	Bolivia(a)
Mestra	dorcas hersilia	31	1/1	Tobago(g)
	(M. hypermestra cana)			
Mestra	dorcas semifulva (M. s.)	33	1/1	Colombia(a)
Vila	sp.	15	1/1	RO
Tribe Epicaliini				
Catonephele	antinoe	14	1/2	Guyane(c)
Catonephele	chromis	15	1/1	TV
Catonephele	numilia	15	1/1	Mexico(b)
Catonephele	nyctimus	23	1/1	OX
Catonephele	orites	21	1/1	TV
Catonephele	salambria	15	1/1	TV
Cybdelis	phaesyla (phaesila)	23	1/2	Bolivia(a)
Eunica	alcmena flora	30	1/2	MT
Eunica	bechina 	28	1/1	DF(d)
Eunica (Libythina)	cuvierii	31	1/1	DF(d)
Eunica (Evonyme)	eburnea	30	1/2	Argentina(a)
Eunica	ingens	30	2/4	MT, RO(h)
Eunica	macris	16	1/1	RO(h)
Eunica Eunica	malvina monima	14, 31 31	1/1, 1/1 2/2	MT2 MT, RO
Eunica Eunica		31	1/3	MT, KO
Eunica Eunica	mygdonia nr eurota	30	1/3	TV
Eunica Eunica	nr <i>orphise</i>	29	1/1	ES
Eunica Eunica (Evonyme)	tatila	26	1/3	Argentina(a)
Eunica (Evonyme) Eunica	sp.	15	1/1	RO(h)
Eunica	sp.	29-30	1/1	MT
_mmca	~P·		-/ -	*** *

Table 1 (Continued)

Genus	Species, subspecies	n =	No. studied pop./ind.	Locality
Eunica	sp.	31	1/1	AN
Eunica	sp.	31	1/1	RO(h)
Myscelia	orsis	24	1/1	RJ(d)
Nessaea	batesii	11	1/1	Guyane(c)
Nessaea	hewitsonii	7	1/1	La Macarena, Colombia(h)
Nessaea	obrinus	7	1/2	AM(h)
Nessaea	obrinus	8	1/1	BO
		-	-, -	
Tribe Ageroniini	1:: 1	1.6	1/1	AM
Ectima	lirides	16	1/1	
Hamadryas	amphinome	31	1/1	Colombia(a)
Hamadryas	arinome	31	1/1	Colombia(a)
Hamadryas	epinome	31	1/2	Argentina(a)
Hamadryas	feronia '	31	1/1	Guyane(c)
Hamadryas	glauconome	31	1/2	Mexico(f)
Hamadryas	guatemalena	31	1/1	Mexico(b)
Hamadryas	laodamia (Peridroma	31	1/2	Guatemala(b)
	arethusa)	20	4.14	7.0
Hamadryas	sp.	30	1/1	RO
Panacea	procilla	31	1/1	VC
Panacea	sp.	31	1/3	CC
Tribe Epiphilini				
Asterope	sp. nr <i>markii</i>	10	1/1	AC
Asterope	sp.	10	1/1	AV
Epiphile	adrasta	29	2/2	Guatemala(b), Mexico(b)
Epiphile	hubneri (huebneri)	32	1/1	MG(d)
Epiphile	orea	32	1/1	DF
Epiphile Epiphile	orea	32, 34	1/2	Argentina(a)
Nica (Pseudonica)	flavilla	54	1/2	Guatemala(b)
Peria	lamis	23	1/1	EE
Pyrrhogyra	neaerea ophni	29	1/1	ES
		31	1/1	BA
Pyrrhogyra	neaerea ophni	30		
Pyrrhogyra	otolais (nasica)		1/1	Colombia(a)
Pyrrhogyra	sp.	30	1/1	EE MT(1)
Temenis	laothoe	11	1/1	MT(h)
Temenis	laothoe	12	2/3	DF, RO
Temenis	laothoe	13	3/5	Argentina(a), MG, PA
Temenis	laothoe (dark)	14	1/1	EE
Temenis	laothoe	14	1/1	VV
Temenis	laothoe bahiana	13 (2 small)	1/3	BA
Temenis	pulchra	27	2/3	VC, VV
Temenis	sp. nr <i>huebneri</i>	7	1/1	EE
Tribe Eubagini				
Dynamine	agacles	ca 29	1/1	Argentina(a)
Dynamine	arene	30	1/1	Tobago(g)
Dynamine	athemon	29	1/4	Argentina(a)
Dynamine	coenus	30	1/1	Argentina(a)
Dynamine Dynamine	myrrhina	29	1/1	Argentina(a)
Dynamine	postverta (myllita)	28	1/2	Guatemala(b)
Dynamine Dynamine	postverta (myllita)	29	2/4	Argentina(a), Guatemala(b)
Dynamine Dynamine	tithia	30	1/1	Argentina(a), Guatemaia(b)
Dynamine Dynamine	tithia salpensa (D. s.)	30	1/1	Bolivia(a)
-	uma saipensa (D. s.)	50	1/4	Donvia(a)
Tribe Callicorini				
Callicore	hydaspes	30	1/2	Argentina(a)
Callicore	hydaspes	30 - 31	1/1	Argentina(a)
Callicore	lyca	31	1/1	Ecuador(a)
Callicore	tolima	21	1/1	Ecuador(a)
Diaethria	anna (annua)	31	1/1	Mexico(b)
			1/5	
Diaethria	candrena	31	1/3	Argentina(a)

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Table 1 (Continued)

Genus	Species, subspecies	n =	No. studied pop./ind.	Locality
Diaethria	clymena marchalii (D. m.)	31	1/3	Colombia(a)
Haematera (Callidula)	pyrame	30	1/2	Argentina(a)
Haematera	pyrame	30 - 31	1/1	RJ(h)
Mesotaenia (Perisama)	vaninka	31	1/3	Bolivia(a)
Orophila (Perisama)	cardases	31	1/1	Ecuador(a)
Perisama	bomplandii	31	1/3	Ecuador(a)
Perisama	humboldtii	31	1/1	Ecuador(a)
Perisama	lebasii hilara (P. h.)	31 - 32	1/1	Bolivia(a)
Perisama Perisama	morona oppelii	31 31	1/2 1/1	Bolivia(a) Ecuador(a)
Subfamily APATURINAE				
Asterocampa	leilia	31	1/1	Mexico(f)
Doxocopa	cyane	32 - 33	1/1	Ecuador(a)
Doxocopa	elis	31	1/1	Bolivia(a)
Doxocopa	laurentia (seraphina)	31	1/1	Argentina(a)
Doxocopa	linda	32	1/1	Argentina(a)
Doxocopa	pavon	33-34	1/1	Mexico(b)
Doxocopa	sp. nr agathina	31	1/1	EE
Subfamily NYMPHALINA Tribe Coeini	Æ			
Baeotus	deucalion	15	2/2	EE, RO(h)
Baeotus	sp.	14	1/1	CC
Historis (Coea)	acheronta	31	1/1	Ecuador(a)
Tribe Nymphalini		2.1	1.10	P.7(1)
Colobura	dirce	31	1/2	RJ(d)
Hypanartia	bella	31	1/3	Argentina(a)
Hypanartia	dione	31	1/1	Bolivia(a)
Hypanartia	kefersteini	31	1/1	Bolivia(a)
Hypanartia	lethe	31	2/3	Argentina(a), Ecuador(a)
Smyrna	blomfildia	31	1/2	MG
Tigridia	acesta latifascia	30	1/1	DF(d)
Vanessa	carye	31 31	1/1 1/1	Argentina(a)
Vanessa	virginiensis	31	1/1	Argentina(a)
Tribe Victorinini				
Anartia	amathea	30-31	1/1	Argentina(a)
Anartia	amathea	31	3/10	Argentina(a), Trinidad2(g)
Anartia	amathea	32	1/1	Argentina(a)
Anartia	fatima	31	1/2	Mexico(f)
Anartia	jatrophae	31	6/8	Bolivia(a), Colombia(a), Guyane(c), Mexico(f), Trinidad2(g)
Metamorpha	elissa (sulpicia)	31	1/3	Ecuador(a)
Siproeta	epaphus	31	1/3	Ecuador(a)
Siproeta (Metamorpha)	stelenes	31	3/4	Colombia(a), Ecuador(a), Mexico(f)
Tribe Junoniini				.,
Junonia	coenia	31	1/1	Mexico(f)
Junonia	evarete	31	2/4	Ecuador(a), RJ
Junonia (Precis)	evarete zonalis (lavina z.)	31	3/3	Mexico(f), Trinidad2(g)
Junonia	vestina	31	1/1	Argentina(a)
Junonia	vestina livia	31	1/1	Ecuador(a)
Tribe Melitaeini				
Anthanassa (Phyciodes)	frisia hermas	31	1/1	Argentina(a)
Castilia (Phyciodes)	eranites	31	1/1	Colombia(a)
Chlosyne	gaudialis	31	1/1	Mexico(b)
Chlosyne	hippodrome	31	1/1	Mexico(b)
Chlosyne	janais	31	2/4	Mexico2(b)
Chlosyne	lacinia adjutrix	31	1/1	Mexico(b)

Table 1 (Continued)

Genus	Species, subspecies	n =	No. studied pop./ind.	Locality
Chlosyne	lacinia lacinia	31	1/1	Mexico(b)
Chlosyne	narva	ca 31	1/1	Colombia(a)
Eresia	datis moesta (Phyciodes m.)	32	1/3	Ecuador(a)
Eresia	datis moesta (Phyciodes m.)	33, 33–34	1/2	Ecuador(a)
Eresia	datis margaretha (Phyciodes m.)	ca 34-35	1/1	Colombia(a)
Eresia (Phyciodes)	emerantia	31	1/1	Colombia(a)
Eresia (Phyciodes)	lansdorfi	31	2/2	Argentina(a), MG(d)
Ortilia (Phyciodes)	ithra	31	1/1	Argentina(a)
Telenassa (Phyciodes)	teletusa	31	1/1	Argentina(a)
Subfamily LIMENITIDIN	AE			5 ()
Adelpha	alala	42, 45	1/2	Bolivia(a)
Adelpha	cocala	27	1/1	Ecuador(a)
Adelpha	c. cocala (c. urraca)	15, 16	1/2	MT
Adelpha	cocala didia (c. riola)	30	1/1	RJ(d)
Adelpha	cytherea	30	1/2	Colombia(a)
Adelpha	epione	33	1/1	VC
Adelpha	epione ssp.	32-33	1/1	EE
Adelpha	justina valentina (A. v.)	30	1/1	Ecuador(a)
Adelpha	lycorias lara (A. lara)	30	1/1	Ecuador(a)
Adelpha	malea goyama (A. g.)	30	1/1	Argentina(a)
Adelpha	mesentina	30	1/2	AM
Adelpha	mythra	30	1/1	RJ(d)
Adelpha	saundersii	30	1/1	Bolivia(a)
Adelpha	serpa	11	1/2	ES ES
Adelpha	svma	29	1/1	MG(d)
Adelpha	thessalia indefecta	30	1/2	Argentina(a)
Айсірій	(A. mincia)	30	1/2	Aigentina(a)
Subfamily HELICONIINA	ΔE			
Tribe Argynnini		2.1	2.12	D # 1 () 34 () (0
Euptoieta	hegesia	31	2/3	Bolivia(a), Mexico(f)
Euptoieta	hortensia	31	1/2	Argentina(a)
Yramea	cytheris	31	2/4	Argentina(a), Chile(a)
Yramea	lathonioides	31	1/1	Chile(a)
Tribe Acraeini		1.50	1./1	P 11 1 ()
Abananote (Actinote)	erinome	ca 150	1/1	Bolivia(a)
Actinote	carycina	31	several	SP(e)
Actinote	melanisans	31	several	SP(e)
Actinote	parapheles	31	several	SP(e)
Actinote	pellenea	31	several	SP(e)
Actinote	thalia pyrrha (A. p.)	31	several	SP(e)
Altinote (Actinote)	alcione corduba	14	1/1	Bolivia(a)
Tribe Heliconiini; SUOMAL Brown et al. (1992)	AINEN and Brown (1984),	31 →21		

2004). The two tribes of Charaxinae have quite different distributions of numbers (Brown et al. 2007). The Anaeini have a peak at n = 31, followed by a descending series with many numbers in n = 26 through 30 and a minor peak at n = 21, all the way to n = 6, while the Preponini have a peak at n = 12 with a single number above n = 19.

Among Satyrinae (Brown et al. 2007), the Morphini have a peak at n = 28, while the Brassolini have an equally distinctive peak at n = 29. The other tribes of Satyrinae have a weak modal of n = 29 (Brown

et al. 2007), starting with the basal groups with n=29 relatively common, followed with the first clade of Pronophilina (Peña et al. 2006) which has n=29 fixed, followed by the second clade that has an uneven distribution resembling the one of Euptychiina that has all numbers between n=6 and n=31 present at least once, with n=13 as the most common one but without any clear modal number.

The next clade is made up of Heliconiinae (including Argynnini, Heliconiini and Acraeini) and Limenitidinae. The samples for Argynnini and Acraeini are

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Table 1. Haploid chromosome numbers for species and recognized additional subspecies of South American riodinids. The taxon name used in the original reference is in parentheses. A comma between chromosome numbers indicates different individuals, a dash indicates uncertain alternative numbers within an individual.

*** 1				No. studied	T 11.
Voucher code	Genus	Species	n =	pop./ind.	Locality
Subfamily EUSELASIINA	AE				
Tribe Euselasiini					
314	Euselasia	clesa	29	1/1	ES
335		eucerus	28	1/1	ES
260		eusepus	29	1/1	ES
304		fervida	29	1/1	ES
1117		gelanor	28	1/1	EB
419		melaphaea	12	1/1	MT
476		mys cytis	28	1/1	MT
399		praeclara	29	1/1	MT
252		thucydides	27	1/1	ES
316		utica	17	1/1	ES
1452	Hades	noctula	20	1/1	CC
Subfamily RIODININAE					
Tribe Mesosemiini					
Subtribe Mesosemiina					
428, 438, 455	Mesosemia	bella	21, 23	1/1, 2/2	MT; MT2
Wesley and Emmel 1975 (TR-118)		lamachus (methion)	18	1/1	Trinidad
189		melpia	20	1/2	DF
464		melpia vaporosa (?)	ca 46	1/1	MT
577		metope	26	1/1	PB
951, 866		mevania mimallonis	43, 45	1/1, 1/2	VC, VV
Subtribe Napaeina		mevanta nuntationis	15, 15	1/1, 1/2	v e, v v
261	Cremna	alector	24	1/1	ES
414	Cremna	cuyabaensis	43	1/1	MT
158	Eucorna	sanarita	13	1/1	RJ
310	Napaea	eucharila	22	1/1	ES
298	тириси	orpheus	26	1/2	ES
Tribe Eurybiini		orpheus	20	1/2	LS
1146	Alesa	nroma	21	1/1	MG
1120, 1042	Eurybia	prema dardus	14	2/2	EB, EE
442, 400, 445, 751, 907	Ешубій	dardus annulata			
974		franciscana ssp.	28, 29, 32 14	1/1, 2/3, 1/1 1/1	MT; MT, PA; VV WE
974 1541		halimede	29	1/1	BA
de Lesse and Brown 1971			29	1/1, 1/1	DF, MG
		halimede passercula (elvina tephrias)			
de Lesse and Brown 1971		misellivestis (dardus misellivestis)	13	1/2	MG
de Lesse and Brown 1971		molochina hyacinthina	30	1/1, 1/1	RJ
743, 1059		nicaeus	29	1/1, 1/1	EE, PA
de Lesse and Brown 1971		nicaeus (f. paula)	14	1/1	DF
1250		nicaeus ssp. (violet HW)	29	1/1	RO
Tribe Riodinini					
380, 454	Amarynthis	meneria	20	2/3	MT2
307	Ancyluris	aulestes pandama	27	1/2	ES
1229		meliboeus	27	1/1	RO
311	Baeotis	hisbon	28	1/1	ES
267		melanis (?)	15	1/2	ES
de Lesse 1967	Barbicornis	basilis mona	30	1/2	Argentina
529	Calephelis	aymaran	9	1/1	BA

(Continued)

Table 1. (Continued).

Voucher code	Genus	Species	n =	No. studied pop./ind.	Locality
de Lesse 1967		candiope (Charmona c.)	23	1/2	Colombia
de Lesse 1967		nilus	10	1/1	Bolivia
Maeki and Remington 1961		virginiensis	45	1/1	Florida
270	Chalodeta	chelonis	16	1/1	ES
de Lesse 1967		theodora	15	1/1	Argentina
708	Charis	cadytis	27–28	1/1	MG
175, 456	Chorinea	amazon	21, 27	1/1, 1/1	MG, MT
519		octauius	20	1/3	MT
de Lesse and Brown 1971	Detritivora	zama [Charis (gynaea?) zama]	20	1/1	DF
562	Isapis	agyrtus	27	1/1	PE
450	Lasaia	agesilas	22 (?)	1/2	MT
452	Lyropteryx	apollonia	25	1/1	MT
de Lesse 1967	Melanis	aegates aegates (Lymnas a.)	16	1/2	Argentina
241, 447, 440, 427		aegates albugo	20, 21, 27	1/1, 1/1; 1/1; 1/1	MG, MT; MT; MT
1188		aegates/hillapana	21	1/1	MT
224, 829		electron electron	19, 21	1/2, 1/1	MG, RG
422		marathon	34	1/3	MT
569, 443		smithiae	16, 31	1/1, 1/2	PE, MT
437		xenia ambryllis	31	1/2	MT
179	Metacharis	lucius	11	1/1	GO
1471a, 1471b	Necyria	bellona	21, 27	1/1, 1/3	EE
de Lesse and Brown 1971	Panara	jarbas (thisbe)	15, 16	1/1, 1/1	MG
239		ovifera	26	1/1	RJ
de Lesse and Brown 1971, 423	Rhetus	periander (arthuriana)	15	1/1, 1/2, 1/1	GO, MT
477, 792	Riodina	lysippus	14	1/3, 1/2	MT, RR
de Lesse 1967	Siseme	neurodes	17	1/1	Bolivia
295	Syrmatia	nyx	21	1/1	ES
Tribe Symmachiini					
439	Mesene	monostigma	24	1/1	MT
563		phareus	27	1/1	PE
793	Phaenochitonia	cingulus	8–10	1/1	RR
513		rufilinea	10	1/3	MT
de Lesse and Brown 1971	Pirascca	sagaris satnius (Phaenochitonia s. s.)	20	1/1	GO
1595	Symmachia	accusatrix	22	1/1, 1/1	ES
319		menetas	27	1/1	ES
Tribe Helicopini					
812, 3317	Helicopis	cupido	20	2/2	GY, AV
1028		gnidus	16	1/1	EE
Tribe INCERTAE SEDIS	α 1 1	1	40	1 /1	EG
1366	Calydna	lusca	40	1/1	ES DE MT
583, 1187	F olas 1	thersander	33, 64	1/1, 1/1	PE, MT
1118	Echydna	chaseba (?)	26	1/1	EB
de Lesse 1967	Emesis	angularis	ca 34	1/1	Bolivia
de Lesse 1967		cypria	17	1/1	Ecuador
463 910		lucinda lucinda	29 25	1/1 1/1	MT VV
		lucinda ssp.			
425a,b,c		mandana	11, 21, 27	1/1, 1/1, 1/1	MT

(Continued)

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Table 1. (Continued).

				No. studied	
Voucher code	Genus	Species	n =	pop./ind.	Locality
1446		ocypore ssp.	15	1/1	CC
654		tenedia	14	1/1	SC
de Lesse 1967	Imelda	mycea glaucosmia	21	1/1	Ecuador
Tribe Nymphidiini					
Subtribe Aricorina					
de Lesse 1967	Aricoris	chilensis (Hamearis c.)	31	1/1	Argentina
de Lesse 1967, 797		epulus (Hamearis e.)	29, 28–30	1/1, 1/1	Argentina, RR
1181		middletoni	34 (?)	1/1	MT
Subtribe Lemoniadina					
750	Juditha	azan majorana	13	1/1	PA
479		azan?	31	1/1	MT
1265, 673	Lemonias	zygia	24, 25	1/1, 1/1	RO, RJ
726	Synargis	abaris?	24	1/2	PA
1161		brennus	ca 20	1/1	DF
de Lesse and Brown 1971; 659		calyce	17	1/1, 1/1	GO
796		orestessa (?)	18	1/2	RR
1577		phliasus	17	1/1	SP
802		pittheus	27	1/1	RR
de Lesse and Brown 1971	Thisbe	irenea	ca 15	1/1	RJ
Subtribe Nymphidiina					
1004	Adelotypa	huebneri	20	1/1	EE
300		leucophaea	30	1/2	ES
744	Calospila	lucianus ssp.	ca 30	1/1	PA
655, 672	Menander	menander nitida	28–29, 29	1/1, 1/1	SC, RJ
619	Nymphidium	acherois	31	1/1	PE
421		caricae	31	2/2	MT
de Lesse and Brown 1971		leucosia	31	1/1	DF
481		mantus	31	1/2	MT
1598		molpe (?)	31	1/1	BA
Subtribe Theopina					
497	Theope	acosma	16	1/3	MT
605	_	foliorum	29	1/1	PE
1551		foliorum (?)	32	1/1	BA
Tribe Stalachtini					
Rio 10	Stalachtis	magdalena	19	1/1	VC
de Lesse and Brown 1971		phlegia	28	1/2	DF
de Lesse and Brown 1971		phlegia susanna	36	1/1	RJ

Localities are grouped by region; a number at the end of the locality code indicates that more than one population has been sampled within this region. Locality codes: AM = Amazonas (northwestern Brazil), AV = Amazonas, (southern Venezuela), BA = Bahia (eastern Brazil), CC = Chocó (western Colombia), DA = Darien (southern Panama), DF = Brasília (central Brazil), EB = eastern Bolivia, EE = eastern Ecuador, ES = Espírito Santo (eastern Brazil), GO = Goiás (central Brazil), GY = French Guyana, MG = Minas Gerais (central Brazil), MT = Mato Grosso (central Brazil), OX = Oaxaca (southern Mexico), PA = Pará (northern Brazil), PB = Paraíba (northeastern Brazil), PE = Pernambuco (northeastern Brazil), PT = Putumayo (southern Colombia), RG = Aragua (northern Venezuela), RJ = Rio de Janeiro (southeastern Brazil), RO = Rondônia (western Brazil), RR = Roraima (northern Brazil), SC = Santa Catarina (southern Brazil), SP = São Paulo (southeastern Brazil), TV = Táchira (western Venezuela), VC = Valle de Cauca (western Colombia), VV = Villavicencio, Meta (eastern Colombia), WE = western Ecuador.

In addition, certain details on fore or hind wings are abbreviated as FW or HW.

We also give the chromosome numbers for 17 Neotropical lycaenids (Theclinae and Polyommatinae) for comparison in Table 3. The names of species follow the checklist of ROBBINS and LAMAS (2004). Among

the theclines, *Eumaeus minyas* has both n = 24 and n = ca 45. With three exceptions the Neotropical Lycaenidae have n = 24, characteristic for this family elsewhere.

Table 2. Chromosome numbers for riodinids that have not been reliably assigned to species. Certain details on fore or hind wings are abbreviated as FW or HW. Otherwise as in Table 1.

Voucher code	Genus	Species	n =	No. studied pop./ind.	Locality
Subfamily EUSELASIINAE					
Tribe Euselasiini					
970	Euselasia	sp. nr <i>eusepus</i>	29	1/2	WE
1278	Busciusiu	sp. nr <i>cafusa</i>	28	1/1	RO
1210		sp. (large)	18	1/1	MT
Tribe Mesosemiini		sp. (large)	10	1/1	141 1
Subtribe Mesosemiina					
1517	Mesosemia	co or maturara	26	1/1	EE
1023, 1514	Mesosemia	sp. nr metuana	44	2/2	EE2
1143		sp. nr mevania		1/1	
778		sp. (blue-lined, light)	11 25	1/1	RO AM
		sp. (like large <i>metope</i>)			
1119		sp.	26	1/1	EB
1283		sp. (white HW border)	27	1/1	MT
3263		sp.	41	1/1	RR
1397		sp. (large, very blue)	43–44	1/1	VC
785		sp. (blue lines)	ca 110 (two large chr.)	1/1	AM
Subtribe Napaeina					
1052	Ithomiola	sp.	25	1/2	EE
Tribe Eurybiini					
1021	Alesa	sp. (blue-black)	19	11	EE
846	Eurybia	franciscana (?)	17	1/1	TV
1082a	•	sp. (small)	14	1/2	EE
1082b		sp. (small)	26	1/1	EE
1444		sp. (large, yellow on HW)	29	1/1	CC
1526		sp. (eye, violet HW)	29	1/1	WE
1213		sp. (violet HW)	29–30	1/1	MT
Tribe Riodinini		·F. ()		-, -	
1440	Ancyluris	sp. (narrow shorter band)	27	1/1	CC
1382	11110 / 1111 15	sp.	28	1/1	EE
1496		sp.	28	1/1	EE
1230		sp. (straight caudal red)	31	1/1	RO
1015	Caria	sp. (red under FW)	16	1/1	EE
914	Charis	sp. (dark)	16	1/1	PT
652a	Charis		18	1/1	SC
652b		sp.	25	1/1	SC
		sp.		1/1	
1266	C	sp. (blue ventrally)	29		RO
1064	Crocozona	sp.	23	1/1	EE
1038	Ithomeis	sp. (large, orange-tipped)	18 (?)	1/1	EE
475	Melanis	sp. ('white spot')	12	1/2	MT
697		sp. (albugo?)	20	1/2	ES
1466		sp. (orange HW border)	33	1/1	EE
554		sp.	38	1/2	PE
634		sp.	15	1/2	BA
606		sp.	25	1/1	PE
1476	Rhetus	sp. (white lines under)	15	1/1	EE
1380		sp.	15	1/1	EE
Tribe Symmachiini					
404	Mesene	sp. (two-dot)	15	1/1	MT
441	Symmachia	sp.	14	1/1	MT
651		sp. (dark)	18	1/1	SC
Tribe INCERTAE SEDIS					
327	Argyro-grammana	sp. (red)	16	1/1	ES

(Continued)

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Table 2. (Continued).

Voucher code	Genus	Species	n =	No. studied pop./ind.	Locality
302		sp.	30	1/1	ES
689	Emesis	sp.	45	1/1	RJ
Tribe Nymphidiini		_			
Subtribe Lemoniadina					
564	Synargis	sp. nr <i>phliasus</i>	20	1/1	PE
1436		sp. (orange half HW)	15	1/1	CC
Subtribe Nymphidiina					
781	Adelotypa	sp. (russet FW, white HW)	21	1/1	AM
1112		sp. (dark)	ca. 30	1/1	EB
1435	Calospila	?sp. (small pattern)	30	1/1	CC
763	Menander	sp. (very blue)	18	1/1	AM
518		sp.	18	1/4	MT
779	Nymphidium	sp. nr <i>cahcrus</i>	21	1/1	AM
733		sp. (light orange on borders)	31	1/1	PA
515		sp.	31	1/2	MT
Subtribe Theopina					
1149	Theope	sp. (blue and grey)	16	1/1	MG
UNKNOWN					
1361	Riodinid	like Callicore (Orimba?)	27	1/1	EE
1467		sp. (small, blue, short white band)	27	1/1	EE

DISCUSSION

The results show that the riodinids have widely variable chromosome numbers, while the Neotropical lycaenids largely conform to the modal n=24 that characterizes the family (White 1978). The riodinids do not appear to have a distinct modal number. Very few (six at most in this study) have the n=23 or 24 that characterize the lycaenids (Fig. 1).

The most common numbers among riodinids are n=27, 29 and 31. The latter two belong to the modal n=29-31 of butterflies (White 1978; Brown et al. 2007a, 2007b). The distribution of these numbers is, however, uneven and it is difficult to discern a pattern at all. Nevertheless, the most primitive Euselasiinae have n=28-29, while the highly advanced genus *Nymphidium* is nearly stabilized at n=31. Maeki and Ae (1968a, 1968b) give chromosome numbers for three representatives of the small Old World subfamily Hamerarinae (Nemeobiinae): *Abisara burnii etymander* (from Taiwan) has n=30, *Abisara echerius echerius* (from Hong Kong) n=31, *Zemeros flegyas flegyas* (from Hong Kong) n=31.

The over-all distribution of riodinid chromosome numbers with no modal one is unique among the Lepidoptera. The nymphalids are the sister group of the evidently monophyletic Lycaenidae and Riodinidae (Campbell et al. 2000). The satyroids have a weak modal n = 29 with many numbers lower than that and

rather few higher than the modal numbers (Brown et al. 2007a) but even they include many groups with stable chromosome numbers. Ithomiinae, another variable nymphalid subfamily, seem to have originated from a lineage that already has had the nymphaline modal, n=31 (Brown et al. 2007b) divided by two through what appears to have been pairwise fusions of all chromosomes, with about n=14 as a predominant number.

If the Ithomiinae have had their chromosome number halved, then such a process runs riot among the riodinids. They, and *Eumaeus* among the theclines, show clear evidence for near-even multiples of a chromosome number, either up or down or both within a species or within a genus. So, in addition to the examples mentioned in the results section, *Melanis smithiae* has n = 16 and n = 31, *Emesis mandana* n = 11, 21 and 27. This implies that once one chromosome is either divided into two or fuses with another to form a larger chromosome, then the other follow suit until again a set of chromosomes of about equal size is again attained. Such a concerted evolution of lepidopteran chromosomes was described by Beliajeff (1930) and discussed e.g. by Lorković (1990).

Our riodinid sample sizes are limited, so that it is difficult to say much about the nature of the variation within a species. Several samples from a locality or samples from several localities may have either the same or quite different chromosome numbers.

Table 3. Haploid chromosome numbers for 17 neotropical lycaenids (Theclinae and Polyommatinae). The genus and species names used in earlier publications are in parentheses.

Voucher code	Genus	Species	n =	No studied pop./ind.	Locality
Subfamily THECLINAE					
Tribe Eumaeini					
Eumaeus section					
Maeki and Remington 1960, Lyc 11	Eumaeus	childrenae (debora)	24	2/2	Mexico, OX
de Lesse 1970, M 7		minyas	24, ca 45	1/1, 1/1	Mexico, AM
Lyc 1		minyas ssp.	23	1/1	DA
Brangas section					
de Lesse 1967	Evenus (Thecla)	coronata	24	1/2	Ecuador
1367		regalis	24	1/1	ES
646		satyroides	24	1/1	BA
Atlides section					
Lyc 10		mavors	24	1/1	TV
297		triquetra	24	1/3	ES
Thereus section					
Wesley and Emmel 1975 (TR-202)	Arawacus	aetolus (linus)	22-24 (22,23,24)	1/1	Trinidad
de Lesse 1967	Contrafacia (Thecla)	francis	24	1/1	Argentina
Strymon section					
de Lesse 1967	Strymon (Thecla)	Astiocha (faunalia)	24	1/1	Argentina
de Lesse 1967	Strymon (Thecla)	eurytulus	24	1/3	Argentina
Subfamily POLYOMMATINAE					
de Lesse 1967	Hemiargus	hanno	14	1/1	Argentina
de Lesse 1967	Itylos	sp. probably titicaca (?)	ca 23–24	1/1	Argentina
de Lesse 1967	Leptotes	andicola	24, 24–25	1/3	Ecuador
de Lesse 1967	-	callanga	24	1/1	Peru
de Lesse 1967		cassius	18	1/1	Argentina

The authors who write about riodinids (Brown 1993a, 1993b; DEVRIES 1997) stress that there are undescribed species in each major genus and that the genera are in need of revision. We have included in our lists several undescribed species and feel that much of the variation within what we think is a species at a locality may, in fact, be explained through sibling species, each with a different chromosome number. DE LESSE (1967) who had studied the relationship of chromosome change and speciation of lycaenids in detail (WHITE 1978; WIEMERS 2003) argued that whenever one sees sympatric populations of what seems to be a single species with different chromosome numbers, one must suspect a pair of sibling species with probably, in part, overlapping distributions. On the other hand, species having the same chromosome number may lack an obstacle for interbreeding. Gompert et al. (2006) and Mavárez et al. (2006) have not only shown that hybrid speciation is not only possible but that it has contributed to lepidopteran speciation. It may be argued to be a factor that has stabilized chromosome numbers in two groups with

exceptionally stable chromosome numbers: lycaenids and the genus *Heliconius*. Such phenomena are, however, evidently rare. Maeki and Ae (summarized in Ae 1995) have shown that between species crosses involving papilionids with n=30 show gross chromosome pairing disturbances at meiosis.

Ecology

A coevolutionary process is thought to accelerate the rate of evolution. The riodinids show several kinds of coevolution. They have a potential arms race with their host plants; the larvae of Eurybiini, Lemoniadina and Nymphidiina associate with ants; the representatives of some 16 genera participate in mimicry rings of heliconians, ithomiines, arctiids, dioptids and other lepidopterans (Brown 1993a). In addition to nectar, adults feed on damp sand and mud ('puddling') and carrion (Hall and Willmott 2000). Most riodinid subfamilies and tribes have diverse host plants representing a wide range of both monocots and dicots; in addition the adults

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
Subfa	mily 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
Subfa	mily Euschemoninae no chromosomal	data available		
Subfa	mily 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
Subfar	nily Pyrginae			
	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
	Celaenorrhinini	7 22		1
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
	C. voeimus Neverain, 1913	20-40	naly	de Lesse 1900

		Haploid chromosome Country		Reference	
#	Species				
52	C. dravira (Moore, 1874)	number 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 A	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 I	7 8				
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	<i>Pyrgus aladaghensis</i> 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	
Subfan	nily Heteropterinae	1			
113	Butleria quilla Evans, 1939	29	Chile	de Lesse 1967a	
Subfan	nily Trapezitinae	.			
114	Trapezites eliena Hewitson, 1868	31	Australia	Maeki and Ogata 1971	
	nily Hesperiinae	31	2 tustrana	Iviacki and Ogata 1971	
	eromachini	-			
		24	Mexico	Freeman 1969	
115	Aegiale hesperiaris (Walker, 1856) Agathymus alliae	24	Iviexico	rreeman 1969	
116	(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	

C. Felder et R. Felder, 1867 129	Lesse 1967a Lesse 1968 and Brown 1971 and Kumagai 1974 Lesse 1967a teman 1969 teman 1969 teman 1969 teman 1969
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130	nd Kumagai 1974 Lesse 1967a reman 1969 reman 1969 reman 1969
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138 Stallingsia maculosus (Freeman, 1955) 50 USA (Texas) Maeki	eeman 1969
(Freeman, 1955) 50 USA (Texas)	Lesse 1968
120 C (F.1.:. 1700) 22 T: 3.5.1.	1961, Freeman 1969
139 Suastus gremius (Fabricius, 1798) 23 Taiwan Maeki	and Ae 1968b
140 Thoressa varia (Murray, 1875) 31 (2n=62) Japan Abo	e et al. 2006
141 <i>T. varia</i> (Murray, 1875) 31 Japan M	Iaeki 1953
Tribe Baorini	
142 Gegenes gambica (Mabille, 1878) 41 Yemen Sa	aitoh 1984
41 Turkey de	Lesse 1960
41 Lebanon La	arsen 1982
143 Gegenes nostrodamus (Fabricius, 1793) 15 Egypt La	arsen 1982
	979, Larsen 1982
Gegenes pumilio (Hoffmansegg, 1804) 24 France de	Lesse 1960
145 Parnara guttata 16 Japan Maeki I	Lesse 1967b
	953, Maeki and
Pelopidas conjucta conjucta	
147 <i>P. jansonis</i> (Butler, 1878) 16 (2n=32) Japan Abo	1953, Maeki and akino 1953

#	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 T	aractrocerini			
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	<i>T. ohara formosana</i> Fruhstorfer, 1911	29 (2n=58)	Taiwan	Abe et al. 2006
Tribe T	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 C	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 A	Anthoptini no chromosomal data avail	able		
Tribe N	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 Kumagai et al. 2010	
178	Enosis immaculata immaculata (Hewitson, 1868)	29	Ecuador		
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 I	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	

Table 1. The haploid chromosome numbers for the South American representatives of the Nymphalid subfamilies Charaxinae, Morphinae (including Brassolini) and Satyrinae. Question marks indicate uncertain data

	Species,		Number of studied populations/		
Genus	subspecies	n	individuals	Locality	
Subfamily CHARA	XINAE				
Tribe Anaeini					
Consul	electra	20	1/1	OX	
	fabius	21 + 1 - 2 small	1/1	AN	
	fabius	27	1/1	RG	
	$f.\ albinotatus$	19–20	1/1	Colombia (a)	
	fabius ssp.	19-20	1/1	EE	
	panariste	11	1/1	VC	
Hypna	cly temnestra	7	2/2	EE, PA	
	$c.\ clytemnestra$	7	1/1	AM	
	c. corumbaensis	8	1/1	MT	
	$c.\ forbesi$	7	1/2	BA	
	c. huebneri	6	1/1	RJ (e)	
Polygrapha	suprema	29, 30	1/1, 1/1	SP2	
Siderone	galanthis	21	2/2	DF, MG	
2140.0.10	g. nemesis	21	1/1	GO	
Zaretis	isidora	21, 29	1/2	RO	
Zarens	itys	21, 23	4/7	AC, AN, GO, MT	
	itys ssp.	21	1/2	MT	
Anaea	troglodyta	30	1/3	Mexico (h)	
Fountainea		27	1/1	VC	
rountainea	centaurus				
	eurypyle confusa	31	2/2	Mexico2 (c)	
	glycerium	31	1/1	TV	
	g. cratais	30	1/1	GO	
	halice evelina	31	1/2	AC	
	$h.\ moretta$	31	1/2	BA	
	nessus	16	4/4	Ecuador (a), EE2, Vo	
	nobilis titan	26	1/1	AN	
	ryphea phidile	31	2/3	ES,MG	
	r. ryphea	31	2/2	Argentina (a), CC	
Memphis	acidalia ssp.	28	1/2	MT	
	sp. nr <i>acidalia</i>	18	1/1	VC	
	anna	36	1/1	EE	
	appias	30, 30–31	2/3, 1/1	BA, ES, BA	
	arginussa (?)	31	1/1	VV	
	sp. nr arginussa	35	1/1	TV	
	cleomestra	15	1/1	AN	
	sp. falcate FW	12	1/2	CM	
	glauce	11	1/1	VV	
	glauce	16	1/1	RO	
	g. felderi	50	1/1	PT	
	sp. nr glauce	12	1/1	VV	
	laertes	28	1/2	AM	
	laertes var. laertes	24, 27	1/1	AM	
	laura	26	1/1	VC	
	laura balboa		1/1	$^{ m VC}$	
		26			
	leonida	29	1/1	RJ	
	leonida editha	29	1/1	RJ	
	lineata	29	1/1	EE	
	lyceus	14	1/1	VC	
	moruus	26, 27, 28	1/1, 1/1, 3/3	VC, AC, AC, DF, VV	
	$m.\ stheno$	28, 29	2/2, 1/1	DF, MT, ES	

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Table 1. Continued

	Species,		Number of studied populations/		
Genus	subspecies	n	individuals	Locality	
	sp. nr <i>moruus</i>	28	1/1	AN	
	sp. nr <i>nenia</i> a	26	1/1	AC	
	sp. nr <i>nenia</i> b	31	1/1	VV	
	offa	26	*	*	
	otrere	29	3/4	ES, RJ, SP	
	perenna austrina	30	1/1	TV	
	polycarmes	14	1/1	AM	
	pseudiphis	25	1/1	VC	
	xenocles	33	1/1	AM	
	sp. nr xenocles	30	1/1	TV	
Anaeini	sp.	9	1/2	VV	
Anaeini	sp.	26	1/1	EE	
Anaeini	sp.	26	1/2	VV	
Tribe Preponini	sp.	20	1/2	* *	
Noreppa	chromus	16	2/2	Bolivia (a), VC	
Archaeoprepona		9	4/5	DF, MT2, TV	
Archaeoprepona	a. pseudomeander	9	1/1	RJ	
	amphimachus (dark)	14	2/2	ES2	
	demophon	16	3/6	DF (e), Mexico (c), PI	
	d. thalpius	16	1/1	MT	
	demophoon	15	3/5	DF, ES, PE,	
	andicola	10	9/9	DF, ES, 1 E,	
	$d.\ antimache$	15	2/3	DR, PR	
	meander	9	1/1	TV	
Prepona	d. deiphile	12	2/3	ES, RJ	
Ттеропа	laertes demodice	19	2/2	DF, PE	
	l. laertes	19 (?)	1/1	PE	
		19, 25	1/1, 1/1	AN, AM	
	l. laertes ssp.			AIV, AIVI AC	
	sp. nr <i>laertes</i>	18	1/1		
	pheridamas	11–13	1/1	MT	
	pylene bahiana	12	1/1	ES	
	pylene eugenes	12	1/1	AM	
	'pylene laertides'	11	1/1	DF	
Agrias	amydon	12	1/1	PE	
	ferdinandi				
	amydon ssp.	12	1/1	AM	
	narcissus	12	1/2	AM	
	tapajonus				
Subfamily MORPH	INAE				
Tribe Morphini					
Subtribe Antirr					
Antirrhea	archaea	13	1/2	RJ (e)	
	phasiana	25	1/1	$_{-}^{\mathrm{CM}}$	
	philoctetes	29–30?	1/1	EE	
	p. avernus	30	1/1	AM	
	p. lindigii	29	2/2	CC, Colombia (a)	
	taygetina	25	1/1	AC	
Caerois	chorinaeus	29	1/1	CC	
Subtribe Morph					
Morpho	achilles	27 or 28	1/1	RO	
	achilles ssp.	28	1/1	EB	
	(much blue)				

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Table 1. Continued

Genus	Species, subspecies	n	Number of studied populations/ individuals	Locality
	achilles ssp.	28	1/1	EE
	anaxibia	28	1/1	ES
	athena	31	1/1	SP
	athena	28	1/1	DF
	athena	c. 30	1/1	RJ
	athena	34	1/1	RJ
	cisseis	28, 46	1/1, 1/1	PA
	epistrophus	28	2/2	RJ (e), RJ
	hecuba	28	1/1	AM (i)
	helenor	28	1/1	Guyane (d)
	h. achillaena	28	3/7	DF, MG, RJ
	h. achillides	28	2/2	Argentina (a), VV
	$h.\ anakreon$	28	2/4	PE2
	h. helenor	28	2/2	PA, RO
	h. insularis	28	1/1	Trinidad (f)
	h. leontius	28	1/2	Bolivia (a)
	h. peleides	28	3/7	Colombia (a), Mexico (a)
	h. pindarus	28	2/5	EB, MT
	h. rugitaeniatus	28	1/1	$\overline{\mathrm{VC}}$
	h. violaceus	28	1/1	SC (a)
	menelaus	27, 46	2/3, 1/1	EE, RJ, RJ
	$m.\ amathonte$	27	1/1	Colombia (a)
	m. coeruleus	30	1/1	DF (e)
	m. menelaus	28	2/2	Guyane (d), RO
Tribe Brassolin	i			
Subtribe Bra	ssolina			
Blepolenis	batea	29, 30	1/2, 1/1	ES
Brassolis	astyra	28	1/1	RJ
	sophorae	29	1/1	BA
Caligo	atreus	29	3/3	Colombia (a), TV, WE
	beltrao	29	1/1	RJ (e)
	euphorbus	27	1/1	$\mathbf{A}\mathbf{M}$
	sp. nr euphorbus?	29	1/1	AC
	brasiliensis	29	1/2	RJ (e)
	idomeneus	29	1/1	VV
	illioneus	29	1/1	Ecuador (a)
	$i.\ illioneus$	29	1/1	DF (e)
	teucer	28	1/2	RG
	teucer	29	2/2	AN, PE
	teucer	c. 30–31, 30, 31	3/3	Colombia (a), MT2
	$t.\ japetus$	30	1/2	MT
	teucer ssp.	28	1/1	EE
	sp. nr teucer	29	1/1	EE
	sp. nr teucer	30	1/1	VC
	zeuxippus	29	1/2	VC
	sp.	29	1/1	VC
	sp. (yellow band)	29	1/1	VC
Catoblepia	•	29	1/1	RJ (e)
Dynastor	darius	28	2/4	MT, RJ
Eryphanis	$automedon \ amphimedon$	29	1/1	MT
	reevesii	31	1/1	ES

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Table 1. Continued

	Species,		Number of studied populations/	
Genus	subspecies	n	individuals	Locality
Opoptera	aorsa	29	1/1	ES
	syme	29	1/2	RJ
Opsiphanes	bois duvallii	29	1/2	OX
	cassiae crameri	29	1/1	ES
	$c.\ strophios$	29	1/1	VV
	invirae	29	1/1	Argentina (a)
	i. remoliatus	29	1/1	DF (e)
	quiteria	31	1/2	RO
	q. meridionalis	29	1/2	DF (e)
	tamarindi	29	2/2	OX, VC
Penetes	pamphanis	50	1/1	PN
Selenophanes	cassiope	50	1/1	RO
Subtribe Naropina				
Narope	cyllarus	29	1/1	MT
2.0.000	cyllabarus	31	1/1	VV
	cyllastros	28?, 29	2/2	ES, RJ (e)
	panniculus	29., 23	1/1	MT
Culafornila CATVIDIA	=			1111
Tribe Melanitini	NAE (nomenclature ac	coruing to rena et a	ı., 2000, rig. 1)	
Manataria	hercyna	28	1/1	Argentina (a)
manataria		28	1/1	MT
Tribe Haeterini	h. hyrnethia	28	1/1	WII
	. ,	0.5	1/1	0.1 1: ()
Cithaerias	pireta	25	1/1	Colombia (a)
77 .	p. aurora	12	2/3	AM, EE
Haetera	macleannania	24, 25	2/2	VC2
	piera	25	2/2	PA, VV
D: 11	sp. (blue-spot)	25	1/2	EB
Pierella	helvina	30	1/1	VC
	lamia	20	1/1	PE
	lamia	29, 26–30,	3/3	BA, VV, PA
	1 . 1 . 1 . 1	28–30	1/1	MT
	l. chalybaea	29	1/1	
	sp. nr <i>helvina</i>	30	1/2	CC
	lena	27	1/2	PA
	luna	29	1/2	Colombia (a)
TT	l. rubecula	29	1/1	Mexico (c)
Hypocystina ser		00 00	1/1	DC.
Oressinoma	typhla	28–29	1/1	RG
Subtribe Pronoph		00	1/5	E d ()
Corades	enyo	29	1/5	Ecuador (a)
	iduna	29	1/1	Bolivia (a)
0 1::	i. procellaria	29	1/2	Argentina (a)
Oxeoschistus	puerta simplex	29	1/2	Colombia (a)
	sp.	28	1/1	EE
n	sp.	28	1/1	VV
Pedaliodes	palaepolis	29	1/1	Peru (a)
	pisonia	29	1/1	Ecuador (a)
	sp.	29	1/1	Bolivia (a)
	sp.	29	1/1	Ecuador (a)
Praepedaliodes	phanias	29	2/2	Argentina2 (a)

Table 1. Continued

	~ .		Number of		
	Species,		studied populations/		
Genus	subspecies	n	individuals	Locality	
Pronophila	cordillera	8?	1/1	Bolivia (a)	
•	cordillera	29	1/1	Bolivia (a)	
	intercidona	29	1/1	Colombia (a)	
	thelebina				
	timanthes	29	1/1	Ecuador (a)	
Subtribe Pronophi					
Auca	coctei	20	1/1	Chile (a)	
	nycteropus	7	1/2	Chile (a)	
	nycteropus	7–8, 8	1/2	Chile (a)	
	nycteropus	9–10	1/1	Chile (a)	
Chillanella	stelligera	17	1/1	Argentina (a)	
	stelligera	17–18	1/1	Chile (a)	
Etcheverrius	chiliensis	c. 60	1/1	Chile (a)	
Faunula	leucoglene	29	1/7	Argentina (a)	
Homoeonympha		c. 29-30	1/2	Argentina (a)	
	schajovskoii	27	1/4	Argentina (a)	
Nelia	nemyroides	27	1/4	Chile (a)	
Pampasatyrus	nilesi	c. 41	1/1	Argentina (a)	
	ocelloides	10	1/1	GO (e)	
Steroma	bega	13	1/1	Bolivia (a)	
	bega andensis	c. 12-13	1/1	Bolivia (a)	
	modesta	13	1/2	Bolivia (a)	
Steremnia	pronophila	13	1/1	Colombia (a)	
Subtribe Euptychi	ina				
Amphidecta	calliomma	8	1/1	MT	
	calliomma	9	1/2	MG	
	pignerator	9	1/1	MT	
	reynoldsi	c. 50, 51	2/2	MT, GO	
Archeuptychia	cluena	6	2/3	RJ (e)	
Chloreuptychia	arnaca	13	1/1	CC	
Cissia	occypede	9	1/1	RJ (i)	
	penelope	30, 36, 50-51	1/1, 1/1, 1/1	RO, Trinidad (f), WE	
	sp. nr <i>palladia</i>	105	1/1	TV	
	sp. nr <i>penelope</i>	16	1/1	CZ (i)	
	sp.	6	1/1	MT	
Erichthodes	antonina	c. 13–14	1/1	Bolivia (a)	
	s.l. arius	38	1/1	Bolivia (a)	
Euptychia	jesia	25	1/1	AM (i)	
Euptychoides	albo fasciata	50	1/3	Ecuador (a)	
1 0	griphe	25	2/3	Colombia (a), Ecuador (
Godartiana	muscosa	36	1/1	MG	
Harjesia	sp.	13	1/1	GO (i)	
Hermeuptychia	hermes	13	1/1	Trinidad (f)	
	hermes	18, 23, 25	1/1, 1/1, 1/2	Tobago (f)	
Magneuptychia	libye	25–26	1/1	Mexico (c)	
	libye	29	1/1	WE	
	libye	35	1/1	CC	
	libye	39	1/1	Guatemala (c)	
	sp.	c. 70	1/1	RO	
Moneyptychia	paeon	25–29	1/1	RJ (i)	
2.120100 Jpt y Citta	soter	24	1/1	ES (i)	

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Table 1. Continued

Genus	Species, subspecies	n	Number of studied populations/ individuals	Locality
Pareuptychia	metaleuca	17	1/1	Mexico (c)
1 0	ocirrhoe	12	1/1	MT
	ocirrhoe	13	4/5	DF (e), MT, PA, RJ (e)
	ocirrhoe	18	2/2	RG, Trinidad (f)
	ocirrhoe	23	1/1	Mexico (c)
	ocirrhoe	24	1/1, 6/15	Guatemala (c), Mexico (c)
	ocirrhoe	26	1/1	BA
	$ocirrhoe\ s.l.$	13	1/3	Argentina (a)
	$ocirrhoe\ s.l.$	15	1/1	Argentina (a)
	$ocirrhoe\ s.l.$	21	1/1	Ecuador (a)
	$ocirrhoe\ s.l.$	24	1/1	Colombia (a)
	$ocirrhoe\ s.l.$	42-43	1/1	Ecuador (a)
	$ocirrhoe\ s.l.$	44	1/2	Ecuador (a)
	sp.	8	*	*
	sp.	12	2/2	CM, CZ
	sp.	13	1/1	EE
	`ocirrhoe'	13	2/4	DF, ES
	summandosa	15	1/1	MT
Paryphthimoide	es poltys	13	1/1	RJ (i)
Pharneuptychio	pharnaces	25	1/1	ES
Prae faunula	armilla	c. 12	1/1	GO (e)
Splendeuptychi	$a\ cosmophila$	35	1/1	ES
	sp.	6	1/1	MG
	sp. (dark)	7	1/1	AM (i)
Yphthimoides	celmis	12	1/1	MG (i)
	celmis	27	2/2	Argentina (a), Peru (b)
	renata	27	1/1	CZ (i)
	sp.	14	1/1	WE
Yphthimoides?	sp. nov.	29	1/1	MT

The nomenclature follows the list of Lamas *et al.* (2004), except for the tribal and subtribal division of the Satyrinae, where we follow Peña *et al.* (2006); note that the species names used in some original publications may differ from the names used here. A comma between chromosome numbers shows that the numbers come from different individuals and a dash indicates variation within individuals. In a few cases, a single individual had different chromosome numbers in different cells; in these cases, the chromosome numbers have been separated with a semicolon. Additional data: voucher codes, the name of the specimen in the original reference and an exact reference to the locality are given in http://www.fmnh.helsinki.fi/english/zoology/entomology/research/satyroid-clade/.

Localities are grouped by region; a number at the end of locality codes indicates the number of populations sampled within a region. A letter in parentheses indicates previous work (a, de Lesse, 1967a; b, de Lesse, 1967d; c, de Lesse, 1970a; d, de Lesse, 1970b; e, de Lesse & Brown, 1971; f, Wesley & Emmel, 1975; g, Maeki & Remington, 1960a; h, Maeki & Remington, 1960b; i, T. C. Emmel, pers. comm.). Numbers with an asterisk without locality and number of individuals are derived from the unpublished notes left by the late Dr H. de Lesse.

Locality codes: AC, Acre (extreme western Brazil); AM, Amazonas (north-western Brazil); AN, Andes of north-central Colombia; BA, Bahia (eastern Brazil); CC, Chocó (western Colombia); CM, Chanchamayo (central Peru); CT, Catatumbo (north-western Venezuela); CZ, Canal Zone (central Panamá); DF, Brasília (central Brazil); DR, Dominican Republic; EB, eastern Bolivia; EE, eastern Ecuador; ES, Espírito Santo (eastern Brazil); GO, Goiás (central Brazil); MG, Minas Gerais (central Brazil); MT, Mato Grosso (central Brazil); OX, Oaxaca (southern Mexico); PA, Pará (northern Brazil); PE, Pernambuco (extreme eastern Brazil); PN, Paraná (southern Brazil); PR, Puerto Rico; PT, Putumayo (southern Colombia); RG, Aragua, northern Venezuela; RJ, Rio de Janeiro (south-eastern Brazil); RO, Rondônia (western Brazil); SC, Santa Catarina (southern Brazil); SP, São Paulo (south-eastern Brazil); TV, Táchira (south-western Venezuela); VC, Valle de Cauca (western Colombia); VV, Villavicencio, Meta (eastern Colombia); WE, western Ecuador.

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Table 1. Summary of chromosome numbers in the Heliconiini

Genus	Species	n =	No. s recog	sp. n/fixed		Localities	Testis sizes	Testis colors
Philaethria	pygmalion wernickei dido	29 •29 •88•	l 1 4	1 1 4	6/11 14/22 38/106	MT/PA/AM RJ4/SP5/ES/BA/SC AM10/MT2/PA5/ RO6/AC/PE/PB/ EE/AV/DA2/CH/ CZ3/AC/CC	m/ms m/ms m/ms/s	R/r/dR R/Rr R/Rr/r
	diatonica	72· ·67-68·	2 4+	2 4	3/17 9/149	OX/TV2 ES4/SP/RJ/BA/ PE/PA/OX/TV	m/ms	R/Rr/r/G/yG
	constantinoi	62	1	l	1/1	CC	ms	G
	sp. nov.? ostara?	··52··· ·21···	$\frac{3+}{2+}$	3	7/25 3/6	ES/PA2/TV2 TR/TV/ES	m/ms	R/Rr/r Rr
	sp. nov.?	12 + 19 - 25mc	2+	2 2	8/17	PA6/BO	ms s/ms/m	R/r
Podotricha	telesiphe	28-29	2	2	2/16	EE2	ml/m/ms	R/Rr/G
	•	26-27	1	1	1/2	CP	m	dR
	euchroia	.9.	4	3	7/25	VC2/CC/WE/EE2	ml/ms	R/dR/Rr
Dione	juno	31	5	5	12/23	WP/CV/WE2/MX/DF/ EB/EE/TR/CR/MT	m/ml/l	B/RB
	moneta glycera	"31 31	3	3 1	4/5 4/4	SP/MX/OX CP/VC	l/m l/ml	B/dB B/RB
Commedia		31	8	7		,	m/ml/l	
Agraulis	vanillae	31	0	,	13/28	MX2/TR/EE/AR/ CB2/WE/WP/C12	111/1111/1	B/RB/R
Dryadula	phaetusa	·31	1	1	6/9	CR/TR/AR/ES	ml	R
Dryas	iulia	31	12	4	14/17	MX2/CR2/C13/ TX/EE/AN/TR/ GY/AR/WE	m/l	R
Eueides	vihilia	•31	6	3	9/15	ES/GO/VV/RR/ TV/RD/PA/AM	m/ms/s	R/Rr
	pavana	31	1	l	1.1	RJ	m	r R/Rr
	lineata procula	31-32 31	4 7	1 2	1/2 6/13	AN RG/VC/EE	s/ms m/ms/s	R/Rr R/Rr
	lampeto	31	10	ī	1/1	AM	ms	r
	eanes	31	5	1	1/4	AC OVERNOOD ACCOUNT	ms	R
	isabella lyhia	31.	17 6	5 5	5/23 12/34	OX/AN/TR/MG/WE CT/CR/CZ/CC/ GY/VV/PA/AM/	m/ms m/ms/s	R/Rr/G Rr/R
	tales	·31·	13	7	12/30	MT/GO/TV VV/TV3/AM/PA/ RO/AM/AN	m/ms/ s/vs	Rr/r/ cr/OR/y/lr
	aliphera	37 31	3	2	1/1 7/10	AM EE/CR/CZ/TR/AR	s/ms/m	R/Rr/r
Neruda	metharme	·31·	3	3	3/10	RO2/AC	m/ml/l	R/Rr/r/cr/dR
	godmani	$^{\circ}26-27+2-4$ mc $21-22^{\circ}+5-10$ mc	1	1	7/12 3/14	AM/RR/RO2/AV/AC CC	ms/m/ml	R/dR/RB
	aoede	·21· + 1 - 5mc	11	8	29,56	AP/AM6/RR2/PA7/ RO5/GY/EE/MT3	m/mi/l	R/r/rB/ RB/dR/Or
Laparus	doris	···2527···	8	8	59/154	PA10/CR/RO6/ CZ3/WE/CH/AN/RG/ EV/AB/BO/AM8/TR/ PA/VV/EE2/MT3/LP/ AC/TV2/AP2/CP/CC2	l/ml/vl	R/Rr/r/cr/rB
		20, 24–27 21, 25 22 24–30, 38 24, 30			1/1 1/1 1/3 1/25 1/3	CR RO RG TR RO		
Heliconius	hierax hecuha	21, 22 22–24	2 7	2	3,3 2/2	VV/EE VV	m/ml/l l	r/Rr dR
xanthocles- -wallacei	xanthocles	·21 -22·	14	6	15/26	RO3/PA/MT/EE3/ VV/AV/AM	ms/m/ml	R/Rr/r/c
group	egeria	21	4	2	4,4	PA/AM2	ms/m/ml	R/Rr
	astraea	21	2	ì	4/6	AM/RO3	ml/l/vl	Rr/r
	hurneyi	24-25 21·	7	5	1/1 12/23	RO AV2/AM2/RO2/	m/ml/l	Y/G/cr/Rr
	wallacei	21.	5	4	8/17	EB/PA2 TR/GY/VV/EE/	m/ml	R/Rr/r/cOr

(Table 1, continued)

Genus	Species	n =	No. reco		No. fixed pops/inds	Localities	Testis sizes	Testis colors
silvaniform	nattereri	21.	1	1	2/15	ES/BA	ms/m/ml	Rr/R/r/G/W
group	numata	···21	25	14	26/52	RO3/VV/EE/EB/MT/ RJ/PA/AM2/AC/RR/ MP/TV/ES/BA2	ms/m/ml	Rr/R/r
	ismenius	21	7	4	7/14	OX/AN/DA/CT	m/ml	R/r
	pardalinus	21.	10	5	6/19	LP/AC/VV/AM3	m/ml	R/Rr/r
	hecale	-21	29	14	19/35	CZ/CH/AN/VV/WE/ EE/BO/CT/RO2/ AC/RR/PA4	m/ml/l/vl	R/Rr/r
		21 + 3mc			1/1	RO		
	ethilla	·21	22	11	19/28	VV/TR/MT/DF/RJ2/ HU/AM/TV/RO/PA3	m/ml/l	R/Rr/r/RB
	atthis	21	1	1	2/9	WE	ml	R
cydno-	besckei	21	1	1	4/7	DF/MG/RJ/SP	ml	R/r/dR
-melpomene	elevatus	21	8	4	6/8	GY/RO3/PA/AM	m/ml/l	R/Rr/r
group	luciana	21	2	2	4/10	AV2/RR2	m/ml	R/dR
	timareta	21	2	2	2/7	EE2	1	R/Rr
	heurippa	21	l	1	1/5	VV	m/l	R
	(cydno) pachinus	21	1	1	1/11	CR	ml/l	r
	cydno	21	11	6	8/19	CZ/AN/WE2/CV/ PT/TV	m/ml	R/r
	cydno × melpomene	21		(-)	4/4	AN/TV2	m/ml/l	R/Rr/r/lr
	melpomene	··21	29	13	22/45	CR/AN2/WE/TR2/ VV/EE/AV/GY/RR/ DA/RG/RO/AM2/PA2	m/ml/l	R/Rr/r/dR
erato-	charitonia	21	9	3	6/15	CI/WE/EE/WP/AN2	ms/s	R/Rr
group	hermathena	21	6	2	2/3	PA/AM	ms	R/r/dR
	hecalesia	21	6	3	3/6	CH/TV	m/ms	R/r
	clysonymus	21	4	2	5/10	EE/CC/WE2	ml/l	R/r
	hortense	21	I	1	3/4	MX/OX	m	R
	telesiphe	21	4	2	4/11	EE4	m/ml	R/dR
	erato	·21	28	17	23/43	MX/OX/GU/AN/TR/ EE/WE/GY2/EB/AR DF/RR2/MP2/HU/RO	m/ms/s	R/Rr/r/dR/RB
sara-	ricini	21.	. 1	1	4/6	TR2/RO	ms	r/cr
-sapho	demeter	21	10	4	10/18	AM2/RO3/EB/PA	ms/s	R/Rr/r/cr/eY
group	leucadia	21.	2	1	7/9	EE/MT/AM/RO2/ AC/PA	ms	R/Rr/r
	sara	··21	7	5	15/31	CZ/AN/WE2/VV/TR2/ GY/DF/CC/RJ/EE/RO	s/ms/m/ml	R/cr/Rr/cY/Or/r
		29			1/1	TR		
	hewitsoni	21	1	1	2/2	CR	m	R
	antiochus	21.	6	5	18/32	RG2/VV/RR/RO/AM/ PA3/LP/GO/BO/TV		R/r/G/Y/Or
	congener	33	3	2	3/16	EE2/VV	m/ms	R/Rr/r/cr
	eleuchia	·37	1	1	3/5	CZ/AN/VC	m/ms	r/G
	eleusinus	·59-60··	2	2	5/18	CC3/WE2	m/ms/s	R/r/cr/ly/G
	sapho	·56-57	4	4	6/26	OX/CC/AN/CZ/WE2	m/ms/s	Rr/r/cr

Chromosome number: A comma between numbers indicates different individuals; a dash, variation within individuals. Superscript dots before and after a number indicate variation in the number, as much as 3 over or under the given figure, infrequent but regular

Localities: Localities grouped by region; the number following indicates more than one population fixed within the region. Codes: AC = Acre, AM = Amazonas (Brazil), AN = north-central Colombia, AP = Amapá (Brazil), AR = northern Argentina, AV = Amazonas (Venezuela), BA = Bahia (Brazil), BO = Bolivar (Venezuela), CC = Chocó (W. Colombia), CH = W. Panamá, CI = Caribbean islands, CH = Chanchamayo (Peru), CR = Costa Rica, CT = N.W. Venezuela, CZ = Canal Zone, DA = E. Panamá, DF-Brasília (Brazil), EB = E. Bolivia, EE = E. Ecuador, ES = Espírito Santo (Brazil), EV = E. Venezuela, GO = Goiás (Brazil), GU = Guatemala, GY = Guianas, HU = Huallaga valley (Peru), LO = N.E. Peru, MG = Minas Gerais (Brazil), MP = upper Rio Marañón (Peru), MT = Mato Grosso (Brazil), MX = eastern Mexico, OX = S. Mexico, PA = Pará (Brazil), PB = Paraiba (Brazil), PE = Pernambuco (Brazil), PT = South Colombia, RG = N. Venezuela, RJ = Rio de Janeiro (Brazil), RO = Rondônia (Brazil), RR = Roraima (Brazil), SC = Santa Catarina (Brazil), SP = São Paulo (Brazil), TR = Trinidad, TV = Táchira (Venezuela), TX = S. Texas, VC = Valle de Cauca, W. Colombia, VV = Meta, E. Colombia, WE = West Ecuador, WP = western Peru

Testis sizes: vs = very small (less than 0.4 mm), s = small (0.4-0.7 mm), ms = medium small (0.7-1.0 mm), m = medium (1.0-1.0 mm) 1.3 mm), ml = medium large (1.3-1.6 mm), 1 = large (1.6-2.0 mm), vl = very large (2.0-3.0 mm) in fresh material

Testis colors: B = brown, cOr = clear orange, cr = clear rose, cY = clear yellow, DB = dark brown, dR = dark red, G = green, Ir = light rose, ly = light yellow, Or = orange, R = red, r = rose, RB = red brown, rB = rose brown, Rr = rose red, W = white, y = yellow

Table 1. Karyotype numbers (2n) in Tortricidae.

Tribe	Species ^a	2n	Reference(s)
Subfamily Tortricina	ae		
Archipini	Adoxophyles orana	60	[5,23]
	Aphelia paleana	60	[24]
	Archips breviplicanus	60	[5,23]
	Archips cerasivorana ^b	60	[5,23,25]
	Archips crataegana	60	[27]
	Archips fervidana	60	[25]
	Archips fuscocupreanus	60	[5,23]
	Choristoneura biennis	60	[25,28]
	Choristoneura conflictana	60	[25]
	Choristoneura fumiferana	60	[5,25,28]
	Choristoneura lambertiana	60	[28]
	Choristoneura occidentalis	60	[25,28]
	Choristoneura orae	60	[28]
	Choristoneura pinus	60	[5,25,28]
	Choristoneura retiniana	60	[28]
	Clepsis senecionana	58	[24]
	Homona coffearia ^c	60	[5]
	Homona magnanima	60	[5,23]
	Lozotaenia forsterana	60	[24]
	Pandemis heparana	60	[5,23]
Cochylini	Eupoecilia ambiguella	60	this study
Sparganothini	Cenopis penitana	60	[25]
	Sparganothis directana	60	[25]
Tortricini	Acleris forsskaleana	60	[24]
	Acleris variana	60	[25]
	Tortrix viridana	60	[26]
Subfamily Olethreu	rtinae		
Bactrini	Bactra furfurana	33/32 ⁱ	[30]
	Bactra lacteana	31/30 ⁱ	[30]
	Bactra robustana	46	[30]
Eucosmini	Blastesthia tessulatana ^d	56	[26]
	Epinotia radicana ^e	58	[25]
	Epinotia solandriana	56	[25]
	Gypsonoma haimbachiana	50	[25]
	Retinia albicapitana ^f	54	[25]
	Rhyacionia buoliana	56	[25]
	Zeiraphera canadensis	56	[25]
	Zeiraphera fortunana	56	[25]
	Zeiraphera griseana ^g	56	[31]
Grapholitini	Cydia pomonella	56	[26,32]
	Grapholita funebrana	56	this study
	Grapholita molesta	56	this study
Olethreutini	Lobesia botrana	56	this study

Table 1. Cont.

Tribe	Species ^a	2n	Reference(s)
	Phiaris mori	44	[29]
	Pseudosciaphila duplex ^h	56	[25]

^aSpecies names are used according to [19];

syn. Choristoneura cerasivorana;

^csvn. Homona menciana:

^dsyn. *Pseudococcyx tessulatana*;

esyn. Epinotia (Griselda) radicana;

^fsyn. Petrova albicapitana;

^gZeiraphera diniana,

^hSciaphila duplex;

species with multiple sex chromosomes W_1W_2Z/ZZ (female/male).

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located in the originally autosomal part of the neo-sex chromosomes [53]. However, the sex-chromosome location of rDNA in other insects seems to be rather common as shown, for example, in tiger beetles of the genus Cicindela [54], bushcrickets of the genus Odontura [55], and Triatominae bugs [56]. In dipteran insects, the association of rDNA with sex chromosomes even seems to be an ancestral character for the whole order [57–60]. The rare occurrence on the sex chromosomes in Lepidoptera suggests that the sex-linkage of rDNA is not favorable, possibly due to the inactivation of the W chromosome in somatic nuclei of females [44].

The sex chromosomes of tortricids examined here showed some common features in addition to their large size. Similar to codling moth, the W chromosomes were largely composed of heterochromatin, and in CGH experiments they were differentiated by both the female and male genomic DNA probes, with slight preference for the female probes. These results suggest preponderance of common repetitive sequences and transposons and a low amount of W-specific sequences on the W chromosome (cf. [32,37,40]). However, a detailed analysis carried out in this study revealed considerable between-species differences in the formation of W chromatin bodies in the highly polyploid somatic nuclei of females (see Results), in the level of W-chromosome heterochromatinization, and in the pattern of molecular differentiation of the W and Z chromosomes. Only the codling moth W chromosome showed a conspicuous heterochromatinization and uniform CGH pattern along the entire W thread of the pachytene WZ bivalents ([32]; this study), unlike the indistinctive and scattered pattern of the W chromosome in the closely related G. molesta.

On the contrary, the CGH patterns in *L. botrana* and *E. ambiguella* suggest that their W chromosomes are composed of two parts, the highly differentiated and poorly differentiated parts. The latter finding strongly suggests that not only the Z chromosome (see above) but also the tortricid W chromosome had originated by fusion between an ancestral W chromosome (the highly differentiated part) and an autosome (the weakly differentiated part), most probably also corresponding to the *B. mori* chromosome 15 (see [41]). Following the W chromosome-autosome fusion event, the complete absence of meiotic recombination in lepidopteran females resulted in independent molecular degeneration of the autosomal part of the neo-W

Виды		Число хромосом		площадь полога, мкм²	Средняя суммарная плошадь гаплоид- ного набора на стадии максимальной спирализации хромосом, мкм ²	
			минимальная	максимальная	N	$x \pm S. E.$
	Надсем. Gelechioidea					
1.	Sitotroga cerealella Надсем. Yponomeutoidea	30	0.29 ±0.017	0.50 ±0.028	9	10.0 ±0.20
2.	Yponomeuta malinellus Hagcem. Tortricoidea	31	0.42 ±0.026	0.69 ±0.029	8	15.3 ±0.34
	Archips crataegana Tortrix viridana	30 30	$0.40\pm0.036 \\ 0.34\pm0.21$	1.06 ±0.069 0.61 ±0.053	8	13.2 ± 0.42 12.1 ± 0.53
	Надсем. Zygaenoidea					
6.	Zygaena doricnii Zygaena carniolica Zygaena filipendulae	30 30 30	0.32 ± 0.017 0.33 ± 0.028 0.30 ± 0.027	0.61 ±0.030 0.46 ±0.020 0.39 +0.015	6 12 12	10.6 ±0.33 11.2 ±0.33 9.9 ±0.18
	Надсем. Pyraloidea			0.00 ±0.010		0.0 ±0.10
	Galleria mellonella Plodia interpunctella	30 31	$0.54 \pm 0.024 \\ 0.51 \pm 0.028$	1.01 ±0.046 0.95 ±0.059	5 6	18.7 ±0.80 18.6 ±0.91
	Надсем. Noctuoidea					\$1000 XX 000 ALL PRINCES
11.	Mamestra brassicae Acronicta rumicis Olene fascelina caucasica	31 31 16	0.34 ± 0.024 0.25 ± 0.016 0.78 ± 0.065	0.85 ± 0.038 0.65 ± 0.032 1.29 ± 0.162	10 14 11	16.9 ±1.24 11.5 ±0.44 14.3 ±0.31
	Надсем. Bombycoidea					155561
13.	Bombyx mori	28	0.36 ± 0.016	0.54 ± 0.023	13	11.7 ±0.34
	Надсем. Papilionoidea					
	Pieris brassicae Melitaea didyma	15 27	$0.48\pm0.040\ 0.59\pm0.027$	0.98 ±0.067 1.06 ±0.058	<u>6</u>	10.0±0.58

Примечание. N — число измеренных пластинок.

ставители сем. Noctuidae, даже относящиеся к одному роду, существенно отличаются по абсолютным размерам хромосом. Автор исследовала этот признак у 20 видов совок и обнаружила, что средние суммарные длины метафазных хромосом в их кариотипах варьируют от 0.66 до 1.00 мкм, что соответствует примерно 5-кратным различиям в объемах хромосом. Также и по нашим данным, два вида совок из разных родов — Mamestra brassicae и Acronicta rumicis — резко различаются по абсолютным площадям хромосом (табл. 1, рис. 3, а и б). Следует, правда, иметь в виду, что роды Mamestra и Acronycta относятся к разным подсемействам Noctuidae.

Таким образом, имеющиеся данные весьма противоречивы. В целом приходится признать, что количество видов, у которых известны абсолютные размеры хромосом, в настоящее время еще ничтожно и не позволяет прийти к какимлибо выводам.

Мы специально исследовали вопрос о возможности использования признака «суммарные размеры хромосом» для систематики близких форм бабочек. Оказалось, что по этому признаку между видами одного рода — $Zygaena\ carniolica\ u\ Z.\ filipendulae$ — имеются статистически значимые различия (P < 0.01). Эти данные, а также упомянутые выше данные Вернер (Werner, 1975), свидетельствуют о том, что в процессе видообразования у бабочек происходят изменения абсолютных размеров хромосом.

Природа изменений размеров хромосом без изменения их числа неизвестна. Они могут быть связаны с различными способами упаковки ДНК или с изме-



RESEARCH ARTICLE

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Dynamic karyotype evolution and unique sex determination systems in *Leptidea* wood white butterflies

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Abstract

Background: Chromosomal rearrangements have the potential to limit the rate and pattern of gene flow within and between species and thus play a direct role in promoting and maintaining speciation. Wood white butterflies of the genus *Leptidea* are excellent models to study the role of chromosome rearrangements in speciation because they show karyotype variability not only among but also within species. In this work, we investigated genome architecture of three cryptic *Leptidea* species (*L. juvernica*, *L. sinapis* and *L. reali*) by standard and molecular cytogenetic techniques in order to reveal causes of the karyotype variability.

Results: Chromosome numbers ranged from 2n = 85 to 91 in *L. juvernica* and 2n = 69 to 73 in *L. sinapis* (both from Czech populations) to 2n = 51 to 55 in *L. reali* (Spanish population). We observed significant differences in chromosome numbers and localization of cytogenetic markers (rDNA and H3 histone genes) within the offspring of individual females. Using FISH with the (TTAGG)_n telomeric probe we also documented the presence of multiple chromosome fusions and/or fissions and other complex rearrangements. Thus, the intraspecific karyotype variability is likely due to irregular chromosome segregation of multivalent meiotic configurations. The analysis of female meiotic chromosomes by GISH and CGH revealed multiple sex chromosomes: $W_1W_2W_3Z_1Z_2Z_3Z_4$ in *L. juvernica*, $W_1W_2W_3Z_1Z_2Z_3$ in *L. sinapis* and $W_1W_2W_3W_4Z_1Z_2Z_3Z_4$ in *L. reali*.

Conclusions: Our results suggest a dynamic karyotype evolution and point to the role of chromosomal rearrangements in the speciation of *Leptidea* butterflies. Moreover, our study revealed a curious sex determination system with 3–4 W and 3–4 Z chromosomes, which is unique in the Lepidoptera and which could also have played a role in the speciation process of the three *Leptidea* species.

Keywords: Lepidoptera, Wood white butterflies, Karyotype variability, Fluorescence *in situ* hybridization Chromosome fusion and fission, Multiple sex chromosomes, Speciation

Background

Speciation, *i.e.* the origin of new species, is a complex evolutionary process which leads to the formation of barriers preventing gene flow between emerging species. Defining the factors that generate such barriers is a central goal for evolutionary biologists. Among animals, moths and butterflies (insect order Lepidoptera) represent an ideal model group for the study of various

aspects of speciation. This is mainly due to the immense diversity of Lepidoptera, which include nearly 160,000 species and belong to the most speciose groups of animals [1]. Moreover, the study of moths and butterflies provides a number of practical advantages. Many species can be easily collected in the field, reared and hybridized in laboratory conditions and experiments can be replicated fairly often due to the relatively short generation time of many species.

Among traditional models, the *Heliconius* butterflies have been the subject of a high number of evolutionary studies showing that various wing patterns, resulting from predator-induced selection through Müllerian mimicry, ultimately lead to divergence and speciation

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Table 1. Haploid chromosome numbers for species and recognized additional subspecies of South American Hesperiidae and Pieridae. A comma between chromosome numbers indicates different individuals, a dash indicates uncertain alternative numbers within an individual. A voucher code is given for each new chromosome number. The identity of species which is uncertain is marked as "sp". Localities are grouped by region; lower case letters in parentheses indicate previous work (a = de lesse 1967, b = de lesse 1970a, c = de lesse 1970b, d = de lesse and Brown 1971, e = Maeki and Remington 1960a, f = Wesley and Emmel 1975). Locality codes: AM = Amazonas (northwestern Brazil), CC = Chocó (western Colombia), DF = Brasília (central Brazil), EE = eastern Ecuador, ES = Espírito Santo (eastern Brazil), GO = Goiás (central Brazil), MG = Minas Gerais (central Brazil), MT = Mato Grosso (central Brazil), PA = Pará (northern Brazil), PE = Pernambuco (northeastern Brazil), RG = Aragua (northern Venezuela), RJ = Rio de Janeiro (southeastern Brazil), RO = Rondônia (western Brazil), SP = São Paulo (southeastern Brazil), VC = Valle de Cauca (western Colombia), WE = western Ecuador.

Genus	Species	n =	No. studied pop./ind.	Locality
Family HESPERIIDAE				
Subfamily Pyrginae				
Tribe Pyrrhopygini				
Elbella	lamprus	40(39+1 s)	1/1	DF(d)
Jemadia?	sp. (blue/white) 1261	32?	1/1	RO
Mimoniades	montana 1574	27	1/3	SP
	nurscia	28	1/1	Ecuador(a)
	nurscia malis Hesp 3	28	1/2	CC
	versicolor	28	1/1	DF(d)
	sp. 948	21	1/1	VC
	sp. 948	28	1/1	VC
Pyrrhopyge	charybdis 1571	14?	1/1	SP
7 170	pelota	28	1/1	Argentina(a)
	sp. (UNH white at base) 1279	15	1/1	RO
Sarbia	sp. (narrow black on HW) 1583	30	1/1	SP
Tribe Pyrgini	•			
Achlyodes	pallida (selva)	15	1/1, 1/1	Bolivia(a), Mexico(b)
Anisocharia	sublimbata	31	1/1	Argentina(a)
Antigonus	erosus	31	1/1	Mexico(b)
	liborius	31	1/1	Argentina(a)
Chiomara	asychis georgina	31	1/1	Mexico(b)
	sp.	31	1/1	Trinidad(f)
Ebrietas	anacreon	31	1/1	Argentina(a)
	osyris	31	1/1	Argentina(a)
Erynnis	funeralis (E. zarucco f.)	31	1/2	Argentina(a)
Gesta	gesta	32	1/1	Tobago(f)
Grais	stigmaticus	31	1/2	Mexico(e)
Heliopetes	arsalte	30	1/1, 1/1	Bolivia(a), Mexico(b)
<i>p</i>	omrina	30	1/1	Argentina(a)
Heliopyrgus	americanus (Pyrgus a.)	30	1/1	Chile(a)
Oechydrus	chersis	31	1/1	Bolivia(a)
Paches	l. loxus (P. l. zonula)	31	1/2	Guatemala(b)
Pyrgus	bocchoris	30	1/2	Argentina(a)
- 7.0	fides	30	1/1	Chile(a)
Theagenes	albiplaga	31	1/2	Bolivia(a)
Trina	g. geometrina	31	1/1	RJ(d)
Zera	z. zera	34	1/1	RJ(d)
Subfamily Eudaminae				
Achalarus	toxeus	16(15+1s)	1/1	Mexico(e)
Astraptes	anaphus	31	1/1	Bolivia(a)
	naxos 1563	31	1/1	SP
	phalaecus	25	1/1	Guatemala(b)

(Continued)

Table 1. (Continued)

Genus	Species	n =	No. studied pop./ind.	Locality
Chioides	catillus	31	1/1	Mexico(e)
	albofasciatus	31	1/1	Mexico(b)
	(C. catillus albofasciata)			
Entheus	priassus pralina 602	22	1/1	PE
Epargyreus	barisses	31	1/4	Argentina(a)
	clavicornis tenda	ca 29–30	1/1	Guatemala(b)
Phocides	polybius phanias 662	16	1/2	RJ
Tarsoctenus	praecia plutia Hesp 1	15	1/2	AM
Udranomia	spitzi	29	1/1	DF(d)
Urbanus	d. dorantes	31	1/1	Mexico(b)
	proteus	31	1/1, 1/1	Bolivia(a), Mexico(b)
	simplicius	31	1/1	Argentina(a)
	teleus	31	1/2, 1/1	Argentina(a), Bolivia(a)
Subfamily Heteropteri	nae			
Butleria	quilla	29	1/1	Chile(a)
Subfamily Hesperiinae				
Alera	vulpina	ca 27	1/1	Ecuador(a)
Arotis	derasa (Euphyes d.)	28	1/1	RJ(d)
Cymaenes	sp.	31	1/1	Tobago(f)
Cynea	iquita	29	1/1	Argentina(a)
Ebusus	ebusus	29	1/1	Mexico(b)
Euphyes	leptosema	ca 28	1/1	Argentina(a)
Hylephila	fasciolata	29	1/1	Argentina(a)
J F	phyleus	29	1/1	Argentia(a)
	signata	29	1/1	Chile(a)
Lychnuchus	celsus	30	1/1	RJ(d)
Polites	vibex catilina	29	1/2	Argentina(a)
Thargella	caura	25	1/1	RJ(d)
Vettius	coryna	31, ca 32	1/2	Ecuador(a)
	phyllus prona	26	1/1	RJ(d)
Wallengrenia	premnas	27	1/1	Argentina(a)
Family PIERIDAE				
Subfamily Dismorphiin				
Dismorphia	amphione astynome 191	31	1/1, 1/1	GO, MG
	a. broomeae 823	30	1/1	RG
	a. praxinoe	30	1/1	Mexico(b)
	astyocha 325	16	1/1	ES
	c. crisia 134, c. crisia (D. critomedia)	13, 31	1/1, 1/1	RG, Bolivia(a)
	crisia foedora (D. critomedia foedora)	31	1/1	Colombia(a)
	hyposticta	48	1/1	Colombia(a)
	spio Pr 4	30	1/3	Puerto Rico
	thermesia 161, thermesia	19, 31	1/2, 1/1	RJ, Df(d)
	theucharila	18	1/1	Colombia(a)
	theucharila vitrea (theonoë melanina)	ca $14 + 1$ s	1/1	Guyane(c)
	theucharila? ssp. M 2, Pr 1	26	1/1, 1/1	PA, RO
	zathoe demeter 971	31	1/1	WE
	sp. (like <i>Oleria zelica</i>) 1393	21	1/2	WE
	sp. (yellow) 959	22	1/1	WE
	sp. (yellow) 959	24	1/1	WE

(Continued)

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Table 1. (Continued)

Subfamily Dismorphii	nae			
Subtuining Dismorphia	sp. (like <i>Oleria zelica</i>) 1523	24	1/1	WE
	sp. 1090	30-31	1/3	EE
	sp. (yellow) M 1	31	1/2	PA
Enantia	jethys (Dismorphia j.)	31	1/6	Mexico(b)
27000000	lina psamathe (Dismorphia p.)	23, 24	1/1, 1/5	Argentina(a)
	lina galanthis 1168, 523	30	1/2, 1/2	GO, MT
	sp. nr <i>melite</i> 1473	31	1/2, 1/2	EE
Lieinix	nemesis (Dismorphia n.)	31	1/10	Bolivia(a)
Moschoneura		17	1/10	Guyane(c)
Woschoneura	pinthous (Dismorphia p.) sp. PI 8	15	1/1	VC
Patia	orise M 3	53	1/1	PA
Pseudopieris	nehemia	23	1/3	Argentina(a)
	viridula (P. nehemia v.)	23	1/1	Ecuador(a)
Subfamily Coliadinae				
Abaeis	nicippe (Eurema n.)	31	1/1, 1/2	Mexico(b), Mexico(e)
Anteos	clorinde	31	1/2, 1/5	Colombia(a), Mexico(e)
Aphrissa	statira (Phoebis s.)	31	1/2	Colombia(a)
Colias	dimera	31	1/4	Colombia(a)
	euxanthe hermina (C. hermina)	31	1/3	Peru(a)
	lesbia	31, 32	1/3, 1/1	Argentina(a), Ecuador(a)
	lesbia vautherii (C. vautherii)	31	1/2	Chile(a)
Eurema	albula	ca 28, 29	1/1, 1/1	Argentina(a), Colombia(a)
	arbela boisduvaliana (E. boisduvaliana)	31	1/1	Mexico(b)
	arbela graduata (E. graduata)	31	1/2	Bolivia(a)
	arbela gratiosa (E. gratiosa)	31	1/1	Colombia(a)
	daira	31	1/1, 1/1	Mexico(b)
	deva	31	1/2	Argentina(a)
	elathea platescens (E. plataea)	ca 31	1/1	Argentina(a)
	mexicana or E. boisduvaliana	31	1/1	Mexico(e)
	phiale	31	1/1	Bolivia(a)
	reticulata	31	1/2	Ecuador(a)
	salome	31	1/2	Bolivia(a)
	xantochlora	31	1/1	Ecuador(a)
Kricogonia	lyside	31	1/7	Mexico(e)
_		31		
Nathalis Phoebis	iole argante	31	1/1 1/1, 1/1	Mexico(b) Argentina(a),
	n naconnis (D cinnis)	21	1/3, 1/1	Ecuador(a)
	n. neocypris (P. cipris)	31		Argentina(a)
	philea	31	1/1, 1/7	Mexico(b), Mexico(e)
	sennae	31	1/3	Trinidad(f)
~	s. sennae (P. eubule)	31	1/1, 1/4	Bolivia(a), Colombia(a)
Pyrisitia	dina (Eurema leuce d.)	ca 31	1/1	Argentina(a)
	dina westwoodi (Eurema calceolaria)	31	1/1, 1/1	Guatemala(b), Mexico(b)
	leuce (Eurema l.)	31	1/1	Tobago(f)
	nise (Eurema n.)	31	1/2	Bolivia(a)
	nise nelphe (Eurema n. n.)	31	1/1	Guatemala(b)
	proterpia	31	1/3, 1/2	Colmbia(a), Mexico(e)
	venusta (Eurema v.)	30	1/1	Trinidad(f)
	v. venusta (Eurema limbia)	31–32	1/2	Bolivia(a)

(Continued)

Subfamily Coliadinae				
Rhabdodryas	trite (Phoebis t.)	31	1/1	Argentina(a)
Teriocolias	zelia (Eurema z.)	31	1/3	Argentina(a)
Zerene	cesonia	31	1/1	Mexico(e)
Subfamily Pierinae Tribe Anthocharidini				
Cunizza	hirlanda Pi 7, Pr 6	15	1/1, 1/1	ES
Currica	hirlanda ssp. 1277	15	1/1	RO
Hesperocharis	costaricensis	15	1/1	Mexico(b)
resperoenaris	erota 1572	16	1/1	SP
	marchalii	15	1/2	Bolivia(a)
Tribe Pierini				
Archonias	brassolis negrina (A. bellona hyrnetho)	25	1/1	Bolivia(a)
	brassolis rosacea (A. tereas r.)	26	1/1	Ecuador(a)
	brassolis tereas (A. tereas)	25	1/1	DF(d)
Ascia	monuste	27	1/4, 1/2	Argentina(a), Mexico(e)
	monuste suasa	27	1/2	Bolivia(a)
Catasticta	ctemene alma (C. albina)	25	1/1	Bolivia(a)
	flisa	25, 26–28	1/1, 1/3	Bolivia(a), Ecuador(a)
	pieris	25	1/3	Bolivia(a)
	reducta	29-31, ca 31	1/1, 1/1	Ecuador(a), Bolivia(a
Glutophrissa	drusilla (Appias d.)	32	1/2, 1/6	Argentina(a), Mexico(e)
Hypsophila	microdice (Tatochila m. m.)	28	1/1	Argentina(a)
Itaballia	demophile centralis	25	1/1	Mexico(b)
Leptophobia	aripa	ca 26, 26	1/1, 1/1	Bolivia(a), Ecuador(a
	eleone	26	1/2, 1/4	Ecuador(a), Bolivia(a
	eleusis	26	1/1	Ecuador(a)
	philoma pastaza (L. subargentea pastaza, L. philoma)	26	1/1	Ecuador(a)
	tovaria	26	1/4	Ecuador(a)
Melete	leucanthe	24	1/1	Ecuador(a)
Melete	lycimnia 1374	24	1/1	EE
	lycimnia paulista	23	1/2	MG(d)
Pieriballia	viardi	26	1/1	Guatemala(b)
	viardi tithoreides (Itaballia tithoreides)	26	1/1	Ecuador(a)
Pereute	swainsoni	ca 26–27	1/1	MG(d)
Perrhybris	pamela eieidias	27, 28–29	1/1, 1/2	RJ(d)
	pamela flava Pie 10	28	1/2	ES
Perrhybris (?)	sp. yellow 1521	26 (?)	1/1	WE
Tatochila	autodice	28	1/1, 1/1	Argentina(a), Bolivia(a)
	mercedis	28	1/2	Argentina(b)
	mercedis arctodice (microdice a.)	28	1/1	Ecuador(a)
	orthodice (or stigmadice)	27 (or 28)	1/1 (or 1/3)	Argentina(a)
	sagittata	27	1/1	Ecuador(a)
	stigmadice (or orthodice)	28 (or 27)	1/3 (or 1/1)	Argentina(a)
	theodice	27	1/5	Chile(a)