Biological Journal of the Linnean Society, 2007, **92**, 467–481. With 1 figure

Chromosomal evolution of South American frugivorous butterflies in the Satyroid clade (Nymphalidae: Charaxinae, Morphinae and Satyrinae)

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Received 7 September 2006; accepted for publication 20 December 2006

We describe the chromosome numbers of a monophyletic group of Satyroid subfamilies of primary fruit-attracted butterflies from South America: Charaxinae, Morphinae (including Brassolini) and Satyrinae. The charaxines do not have a distinct modal number. Their chromosome numbers are in the range $n = 6$–50, with $n = 7$–9, $n = 12$, $n = 16$, $n = 19$–21, $n = 26$, and $n = 28$–31 being the most common numbers. Within the Morphinae, the Morphini have a modal $n = 28$ and the Brassolini a modal $n = 29$, with few exceptions. The Neotropical satyrines, in particular the basal species, have a weak modal $n = 29$, which is a strong modal number in Palearctic satyrines. The African satyrines have an equally strong modal $n = 28$. Most Neotropical satyrines have, like charaxines, chromosome numbers lower than the weak modal $n = 29$, and often half this modal, but there are genera with stable numbers among the satyrines and charaxines. Evidently, the Neotropical satyroids descend from basal Nymphalidae with the typical lepidopteran modal number of $n = 31$, which have also given rise to the Heliconiini with modal $n = 31$ and 21 and Ithomiinae with modal numbers of $n = 14$–15. © 2007 The Linnean Society of London, *Biological Journal of the Linnean* Society, 2007, **92**, 467–481.

ADDITIONAL KEYWORDS: evolution – holokinetic – Lepidoptera – modal number – Neotropics.

INTRODUCTION

The order Lepidoptera is one of the groups of animals best known cytogenetically and the chromosome numbers of very many species have been determined (Robinson, 1971; White, 1978). The lepidopteran chromosomes are, however, small and uniform in size and lack primary constrictions. This has made cytogenetic mapping difficult. At the pachytene stage of meiosis, the chromosomes are much longer than mitotic ones and display a specific chromomere pattern (Traut, 1976). Progress in karyotype identification has been slow (cf. Yoshido *et al*., 2005).

Bauer (1967) showed with X-ray irradiation experiments that lepidopteran chromosomes (in the butterfly *Pieris* and the moth *Philosamia*) have a multiple kinetochore structure that allows them to survive fragmentation and translocations. The lepidopteran chromosomes are not holokinetic in the strict sense, however. Approximately 40% of the chromosome surface is covered with kinetochore plates (Gassner & Klemetson, 1974; but see Gus, Schifino & de Araujo, 1983). This kind of a chromosome is called nearly holokinetic. Phenomena associated with chromosome evolution, such as fission, fusion, and translocations, should nevertheless be relatively common in animals

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We dedicate this paper to the memory of late Dr Esko Suomalainen of the Department of Genetics of the University of Helsinki, Finland. He participated in the chromosome part of this study and checked almost all of the chromosome counts with the perspicuity that characterized his life and work. We hope that we succeed in expressing also his ideas in this contribution.

with nearly holokinetic chromosomes: all fragments with kinetochore activity can attach to spindle fibers at cell division.

In spite of these exceptional cytogenetic aspects, lepidopterans are characterized by remarkably stable chromosome numbers. To illustrate this stability, White (1978) provided a histogram of haploid chromosome numbers of 738 species of butterflies. He noted that the distribution of numbers was highly skewed, with most species having $n = 29$, 30 or 31, with the latter being the most common. There were relatively few species that had a higher number but a fair amount had a chromosome number below these three common numbers. Lepidopterans share the stability of chromosome number with their sister order: the trichopterans have $n = 30$ as the modal number (Suomalainen, 1969).

The nymphalid subfamily Satyrinae, the browns, constitutes a well-known and cosmopolitan group of butterflies. The study of Tinbergen *et al*. (1942) on the courtship behaviour of a European satyrine paved the way for further studies on animal ethology, and the work of Brussard & Ehrlich (1970a, b) on a North American satyrine contributed to a basic understanding of population sizes in the wild. The studies by Ford and colleagues (Ford, 1971) on *Maniola jurtina* in Britain represent a classic in ecological genetics. The chromosomal evolution of European satyrines has also been extensively studied. Lorković (1958) and later also de Lesse (covered in Lorković, 1990) described how change in chromosome number accompanies speciation in the Holarctic genus *Erebia.*

In the present study, we describe the chromosome numbers of a group of South American butterflies including the Charaxinae, the tribes Brassolini and Morphini of the Morphinae, and Satyrinae. The subfamily Satyrinae has a cosmopolitan distribution, the Charaxinae are pantropical, whereas the Morphinae are restricted to tropical America. They form a monophyletic 'satyroid' lineage (Harvey, 1991; Nijhout, 1991; Wahlberg, Weingartner & Nylin, 2003; Freitas & Brown, 2004; Peña *et al*., 2006; Wahlberg, 2006). These recent studies highlight the need to incorporate chromosomal data with the molecular and morphological data. We attempt to reveal evolutionary patterns in the chromosome number variation within and among these groups and try to identify mechanisms that maintain stability or give rise to change.

MATERIAL AND METHODS

Butterflies were collected by K. Brown in different parts of South America during the 1970s and 1980s; in a few especially interesting cases, we also include material collected in 2003 and 2004. The gonads of recently captured male butterflies were prepared as described by Brown *et al*. (1992) and stored for variable lengths of time until subjected to sectioning, staining and microscopy, also as described by Brown *et al*. (1992). The collecting localities are given in the Results section; several localities within a general area are often grouped together. Barbara von Schoultz performed the laboratory work and chromosome number determinations, which were independently checked by the late Dr Esko Suomalainen. Anja O. Saura and Anssi Saura put the material together with Keith Brown and André Freitas; most of the ecological and systematic data were provided by André Freitas. Anja O. Saura performed some *Taygetis* chromosome number counts at the Department of Cell and Molecular Biology of UNICAMP, Brazil, in 2003–2004 using the squash and smear method. Data on collection localities, dates and voucher specimens are stored at the Museu de História Natural of the Universidade Estadual de Campinas, Brazil, whereas the original laboratory notebooks and chromosome slides are available at the Finnish Museum of Natural History, University of Helsinki, Finland. To complement our chromosome number counts, we have included earlier counts obtained by Maeki & Remington (1960a, b), de Lesse (1967a, 1970a, b), de Lesse & Brown (1971) and Wesley & Emmel (1975). The names of subspecies, species, genera, subtribes, and tribes follow the checklist of Lamas *et al*. (2004). In the present study, the subfamily Satyrinae is an exception; we have used the new phylogenies put forward by Murray & Prowell (2005) and Peña *et al*. (2006) to give a provisional identification and relationships of tribes and subtribes.

RESULTS

Table 1 shows the haploid chromosome numbers for the South American representatives of the Nymphalid subfamily Charaxinae, the tribes Brassolini and Morphini of the subfamily Morphinae, and the subfamily Satyrinae. In the charaxines, the tribe Anaeini is usually characterized with high numbers, in the range $n = 6$–50, with the modal lepidopteran numbers $n = 28$–31 being common. The closely related genera *Siderone* and *Zaretis* together form an island of stability with $n = 21$ as modal, whereas the numbers of *Hypna clytemnestra* vary in the range $n = 6$–8 (i.e. there is sometimes variation within a recognized single species). The tribe Preponini has low numbers, with $n = 12$ being the most common single number.

Within the subfamily Morphinae, the taxa of the subtribe Morphina of the Morphini have $n = 28$ and the Brassolini a modal $n = 29$ (approximately two-thirds of the taxa). *Penetes* and *Selenophanes* of Brassolini have $n = 50$, and both Morphini and Brassolini show some variation from their modal numbers. An

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

Genus	Species, subspecies	*n*	Number of studied populations/ individuals	Locality
Subfamily CHARAXINAE				
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	*clytemnestra*	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
	g. nemesis	21	1/1	GO
Zaretis	*isidora*	21, 29	1/2	RO
	itys	21	4/7	AC, AN, GO, MT
	itys ssp.	21	1/2	MT
Anaea	*troglodyta*	30	1/3	Mexico (h)
Fountainea	*centaurus*	27	1/1	VC
	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, VC
	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 *acidalia*	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	26	1/1	CZ
	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

Table 1. *Continued*

Genus	Species, subspecies	*n*	Number of studied populations/ individuals	Locality
	sp. nr *moruus*	28	1/1	AN
	sp. nr *nenia* a	26	1/1	AC
	sp. nr *nenia* 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				
Noreppa	*chromus*	16	2/2	Bolivia (a), VC
Archaeoprepona	*amphimachus*	9	4/5	DF, MT2, TV
	a. pseudomeander	9	1/1	RJ
	amphimachus (dark)	14	2/2	ES2
	demophon	16	3/6	DF (e), Mexico (c), PE
	d. thalpius	16	1/1	MT
	demophoon andicola	15	3/5	DF, ES, PE,
	d. antimache	15	2/3	DR, PR
	meander	9	1/1	TV
Prepona	*d. deiphile*	12	2/3	ES, RJ
	laertes demodice	19	2/2	DF, PE
	l. laertes	19 (?)	1/1	PE
	l. laertes ssp.	19, 25	1/1, 1/1	AN, AM
	sp. nr *laertes*	18	1/1	AC
	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 ferdinandi*	12	1/1	PE
	amydon ssp.	12	1/1	AM
	narcissus tapajonus	12	1/2	AM
Subfamily MORPHINAE				
Tribe Morphini				
Subtribe Antirrheina				
Antirrhea	*archaea*	13	1/2	RJ (e)
	phasiana	25	1/1	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 Morphina				
Morpho	*achilles*	27 or 28	1/1	RO
	achilles ssp. (much blue)	28	1/1	EB

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 (g), RG
	h. pindarus	28	2/5	EB, MT
	h. rugitaeniatus	28	1/1	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 Brassolini				
Subtribe Brassolina				
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	AM
	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	*amphirhoe*	29	1/1	RJ (e)
Dynastor	*darius*	28	2/4	MT, RJ
Eryphanis	*automedon amphimedon*	29	1/1	MT
	reevesii	31	1/1	ES

Table 1. *Continued*

Genus	Species, subspecies	*n*	Number of studied populations/ individuals	Locality
Opoptera	*aorsa*	29	1/1	ES
	syme	29	1/2	RJ
Opsiphanes	*boisduvallii*	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
	cyllabarus	31	1/1	VV
	cyllastros	28?, 29	2/2	ES, RJ (e)
	panniculus	29	1/1	MT
Subfamily SATYRINAE (nomenclature according to Peña *et al*., 2006; Fig. 1)				
Tribe Melanitini				
Manataria	*hercyna*	28	1/1	Argentina (a)
	h. hyrnethia	28	1/1	MT
Tribe Haeterini				
Cithaerias	*pireta*	25	1/1	Colombia (a)
	p. aurora	12	2/3	AM, EE
Haetera	*macleannania*	24, 25	2/2	VC2
	piera	25	2/2	PA, VV
	sp. (blue-spot)	25	1/2	EB
Pierella	*helvina*	30	1/1	VC
	lamia	20	1/1	PE
	lamia	29, 26–30, 28–30	3/3	BA, VV, PA
	l. chalybaea	29	1/1	MT
	sp. nr *helvina*	30	1/2	CC
	lena	27	1/2	PA
	luna	29	1/2	Colombia (a)
	l. rubecula	29	1/1	Mexico (c)
Hypocystina *sensu* Miller				
Oressinoma	*typhla*	28–29	1/1	RG
Subtribe Pronophilina, clade 1				
Corades	*enyo*	29	1/5	Ecuador (a)
	iduna	29	1/1	Bolivia (a)
	i. procellaria	29	1/2	Argentina (a)
Oxeoschistus	*puerta simplex*	29	1/2	Colombia (a)
	sp.	28	1/1	EE
	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*

Genus	Species, subspecies	*n*	Number of studied populations/ individuals	Locality
Pronophila	*cordillera*	8?	1/1	Bolivia (a)
	cordillera	29	1/1	Bolivia (a)
	intercidona thelebina	29	1/1	Colombia (a)
	timanthes	29	1/1	Ecuador (a)
Subtribe Pronophilina, clade 2				
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	*boisduvalii*	*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 Euptychiina				
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 *palladia*	105	1/1	TV
	sp. nr *penelope*	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	*albofasciata*	50	1/3	Ecuador (a)
	griphe	25	2/3	Colombia (a), Ecuador (a)
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)
	soter	24	1/1	ES (i)

Table 1. *Continued*

Genus	Species, subspecies	*n*	Number of studied populations/ individuals	Locality
Pareuptychia	*metaleuca*	17	1/1	Mexico (c)
	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
Paryphthimoides	*poltys*	13	1/1	RJ (i)
Pharneuptychia	*pharnaces*	25	1/1	ES
Praefaunula	*armilla*	*c*. 12	1/1	GO (e)
Splendeuptychia	*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.

interesting feature of this variation is that it is either slight, one or two steps up or down from the modal one, or extensive, one-half or almost double the modal number, down to $n = 13$ or up to $n = 46$–50.

The most common chromosome numbers of satyrines are $n = 29$, $n = 25$, and $n = 13$ with a rather even distribution among the numbers inbetween, extending to a low of $n = 6$. Remarkably, only four species have the two other modal lepidopteran $n = 30$–31 (three of the four also show $n = 29$ or a higher number). The tribe Haeterini has variation in the range $n = 20$–30 with a single $n = 12$; $n = 29$ is common in the genus *Pierella*. All five genera of the first clade of the subtribe Pronophilina appear to be fixed for $n = 29$. The Euptychiini range from $n = 6$ up to approximately $n = 105$, with many numbers being around $n = 11$–18, $n = 21$–30, and only 12 being higher than $n = 30$. An interesting feature is variation within a species. The most variable genus *Taygetis*, and genera closely related to it, are presented separately (Table 2).

DISCUSSION

Patterns in chromosome numbers

A modal number, such as the $n = 29$–31 of lepidopterans, is evidently an ancestral condition to the whole order. The Papilionidae with $n = 30$ (Emmel *et al*., 1995) and many families and tribes of the Nymphalidae (Maeki & Remington, 1960b), such as the basal genera of Heliconiinae with $n = 31$ (Brown *et al*., 1992) and the Danainae with $n = 30$ (Brown, von Schoultz & Suomalainen, 2004), conform to the modal numbers, as do the rest of the Nymphalinae (Brown *et al.*, 2007). Our results show that the Morphini have $n = 28$ and the Brassolini have $n = 29$ established as modal numbers. The number 29 is one (albeit the least common) of the general lepidopteran modal numbers but $n = 28$ is not one of the recognized modal ones. Nevertheless, the large genus *Heliconius* has a derived modal $n = 21$ (Brown *et al*., 1992), the family Lycaenidae has a modal $n = 24$ (White, 1978), whereas $n = 14$–15 are the most common numbers within the large subfamily Ithomiinae (Brown *et al*., 2004).

Halving the modal number is a chromosome number change that evidently has arisen independently in many different and unrelated lineages of butterflies. Beliajeff (1930) showed that each chromosome joins with another of similar size resulting in a set of chromosomes again all with similar size. Fusion in lepidopteran chromosomes appears to leave traces of former telomeres along the fusion products (Rego & Marec, 2003), and that it may become possible to study the course of evolution through fusions. The process of fragmentation to high numbers results in very many small chromosomes, such that often only a single large pair (i.e. probably the sex chromosomes) is left intact. It may lead to an apparently runaway process up to very high numbers, such as in the satyrine genus *Cissia* that has numbers in the range $n = 9$–105. White (1973) argued that the mechanism of cell division equalizes the size of chromosomes (i.e. the dimensions of the spindle apparatus impose limits to the size and number of chromosomes).

Even though the Satyrinae are polyphyletic, the Neotropical taxa included in the present study belong to a monophyletic assemblage (Peña *et al*., 2006). Relatives of some Neotropical satyrines (e.g. *Manataria* and *Oressinoma*) may have repeatedly invaded other continents through dispersal jumps (Peña *et al*., 2006). *Manataria* has $n = 28$ and *Oressinoma* and all taxa of the first clade of Pronophilina have $n = 29$, which can be taken to be the modal number for Neotropical satyrines.

Biological aspects

Some general details about biological characteristics of the satyroids are provided in DeVries (1987). The charaxines are strong fliers but they are also territorial. Comstock (1961), Rydon (1971), Owen (1971), and Henning (1989) have described many aspects of the biology of charaxines.

Through a somewhat forced argument, the tribe Anaeini shows what can be seen as a trend from the modal $n = 29$–31 to mostly lower numbers, with many intermediates between $n = 50$ and $n = 9$. The Preponini have apparently originated from forms that have had the original modal number already halved.

de Lesse and colleagues (de Lesse & Condamin, 1965; de Lesse, 1966, 1967b, c, 1968) reported chromosome numbers for 27 species or subspecies of African charaxines. The numbers are in the range $n = 13$–58, with a peak at $n = 25$–26 and a lesser one at $n = 13$. de Lesse (1966) points out that $n = 13$ is just one-half of what he calls charaxine modal (i.e. $n = 25$–26). In comparison with this rather limited sample, we may note that the distribution of Neotropical charaxine numbers is closer to the lepidopteran mode of $n = 29$–31 and that there is certainly neither a peak at $n = 13$, nor at $n = 25$.

In the Morphini, *Antirrhea* are night fliers, whereas the large *Morpho* fly during the day, often high in the canopy. In general, almost all Brassolini are crepuscular; almost all males perch whereas a few exhibit diurnal patrolling. Males in both tribes can be strongly territorial. The tribe Haeterini, the basal group of satyrines, originates from a group related to the ancestors of morphines, brassolines, and charaxines. The genus *Pierella* of Haeterini has $n = 29$ as the most common number and species of the first clade of the subtribe Pronophilina are fixed for this.

Table 2. The haploid chromosome numbers for *Taygetis*, the most variable genus of Satyrines, and its closest relatives

Genus	Species	*n*	Number of studied populations/individuals	Locality
Posttaygetis	*penelea*	14	1/2	DF
Pseudodebis	*dubiosa*	11	1/1	MT (i)
	euptychidia	9	2/2	GO, MT
	zimri	16	1/2	Guatemala (c)
Taygetis	*araguaia*	9 + 1 small	1/1	MT
	cleopatra	19	1/1	VV (i)
	echo	10	1/1	DF
	kena	12	*	*
	kerea	23	2/3	GO, Guyane (d)
	sp. nr *kerea*	26	1/2	MT
	laches	*c*. 13	1/1	Guyane (d)
	laches	17	1/1	Ecuador (a)
	laches	20	1/1	Colombia (a)
	larua	40	1/1	GO (i)
	leuctra	11	1/1	RG
	mermeria	14	1/1	MT
	mermeria	15	1/1, 1/1, 1/4	CM, DF, MT
	mermeria	16	2/2	EE, MT
	sosis	12	2/3	MT2
	sosis	14	1/1	BA
	sosis	17–18	1/1	PA
	thamyra	8, 9, 13, 14	1/1	WE
	thamyra	12	3/3	MG, MT2
	thamyra	12–13	1/1	PE
	thamyra	13	1/1	EE
	thamyra	14	1/1	MG
	thamyra	15	1/1	MG
	thamyra	21, 22	1/2, 1/1	CZ
	thamyra	26	1/1	CT
	sp. nr *thamyra*	16	1/1	EE
	tripunctata	15	1/2	MT
	virgilia	12, 13	1/1, 1/1	MT (i), PA (i)
	virgilia	8 + 1	1/1	Guatemala (c)
	virgilia	13	1/1	CZ
	virgilia	14	2/2	DF, SP
	virgilia	15	1/2	PE
	virgilia	16	2/3	DF, VC
	virgilia	17	1/1	PE
	ypthima	31	1/1	Argentina (a)
	ypthima	39	1/7	SP
Taygetomorpha	*celia*	18	1/1	CZ
	celia	20	2/3	MT2

For an explanation of symbols, abbreviations and locality codes, see footnote to Table 1.

The remaining satyrines are characterized by extensive variation in chromosome numbers. The best way to understand this variation is to project it against the phylogeny and historical biogeography of the subfamily (Fig. 1). Viloria (2003) has argued that the tropical satyrine tribes are of Gondwanan origin and have reached their present distributions through continental drift. Peña *et al*. (2006) and Wahlberg (2006) present strong evidence against Viloria's hypothesis, however. There is an overall trend from a basal $n = 29$ towards low numbers in the entire subfamily. This trend is already seen in the Haeterini, where *Cithaerias* has $n = 12$ but it is most prevalent in the subtribe Euptychiina with very many genera.

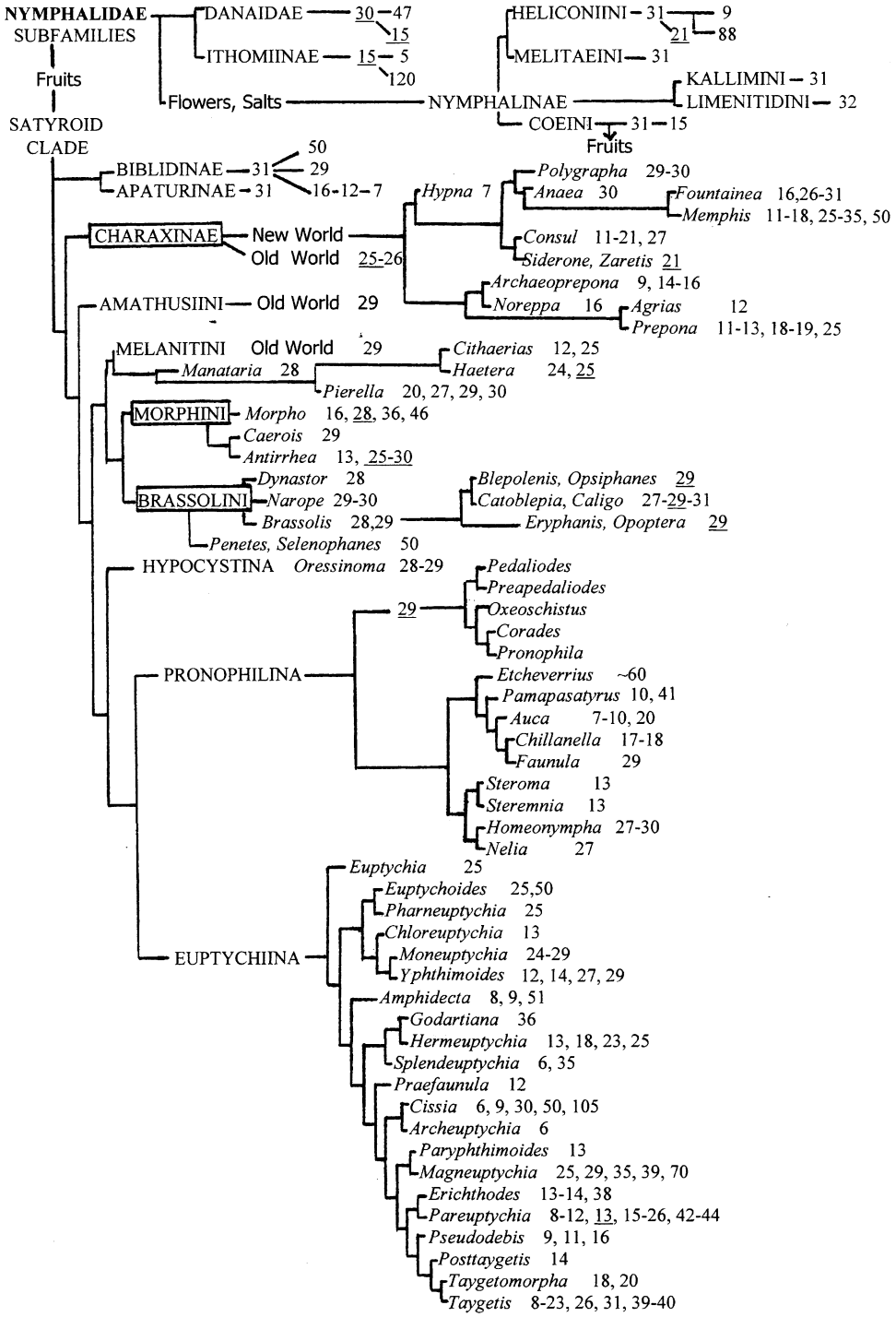

Figure 1. The Satyrines are characterized by extensive variation in chromosome numbers. One way to understand this variation is to project it against the phylogeny and historical biogeography of the subfamily.

de Lesse (1967b, 1968; de Lesse & Condamin, 1962, 1965) has given chromosome numbers for 23 African satyrine taxa. They have a strong modal $n = 28$ (15 out of 23) with one case being half that ($n = 14$); the rest are three $n = 29$, two $n = 26$ and $n = 24$. Lorković (1990) presented a histogram of the chromosome numbers of Palearctic satyrines. Like in Africa but unlike in the Neotropics, there is little variation, with a strong modal $n = 29$, followed by a rapidly descending series down to $n = 24$. Lorković (1990) had,

however, taken out the large Holarctic genus *Erebia* that has a range $n = 7–51$, with about every number between $n = 7$ and $n = 29$ being represented at least once, without any indication of a modal number. Nevertheless, the extent of known variation in other parts of the world is clearly lower than that in the Neotropics.

The genus *Taygetis* and the related genera can be taken as an example for chromosome number variation among and within populations. They constitute a strong clade with the internal relationships still not being clear (Peña *et al*., 2006). Within species variability has been observed using paraffin sectioning (de Lesse, 1967a) and the squash technique (Wesley & Emmel, 1975). de Lesse (1967a) discussed this and illustrated it with fine drawings in the context of '*Euptychia*' (= *Hermeuptychia*). He pointed out that, in many cases, different chromosome numbers were observed in geographically separated populations (cf. Brown *et al*., 2004, who made a similar observation in Ithomiinae). de Lesse failed to see a consistent morphological difference. Wesley & Emmel (1975) left open the question of the nature of this variability. To reveal whether there is chromosome number variation within a single species living at a single locality, we sampled repeatedly a population of *Taygetis ypthima*: all individuals had $n = 39$. One might think that when all chromosomes are rather small, as in this case, there is no more easily discernible fragmentation similar to that seen in a single individual of *Taygetis thamyra*. We venture to suggest that the variation within a species reflects incipient speciation and reproductive isolation that deserves to be studied further. To understand it, one should seek an answer in the mate recognition system and population structure.

Satyrine populations are often extensive and the butterflies engage in complex territorial and courtship behaviour (Tinbergen *et al*., 1942; Brussard & Ehrlich, 1970a, b). Although data on temperate species of Satyrinae are relatively abundant, population data of Neotropical species are less known (Emmel, 1970; Young, 1972; Whittaker, 1983). The available data suggest that, for example, *T. ypthima* and *Paruptychia ocirrohoe interjecta* have large sparse populations throughout their habitat (M. Uehara-Prado & M. A. R. Andrade, pers. comm.).

As for nonforest species of urban areas (H. P. Dutra & A. V. L. Freitas, data not shown) demonstrated that *Yphthimoides affinis* has a patchy distribution whereas *Hermeuptychia hermes* and *Paryphthimoides phronius* have large dispersed populations that percolate through all the anthropic environments of the region, as also demonstrated by enzyme gene variation (R. Fernandes, A. V. L. Freitas & V. N. Solferini, data not shown).

All species of *Pierella* studied (Whittaker, 1983; Ramos & Freitas, 1999) show relatively low vagility but some individuals can move very far (Whittaker, 1983) and the populations appear to be large and stable (A. V. L. Freitas, data not shown) whereas *Cithaerias*, and probably *Haetera* and related genera, have widespread low density populations (Young, 1972; Whittaker, 1983).

Lorković (1958), and later Lorković and de Lesse, as summarized in Lorković (1990), showed that the process leading to speciation in the Holarctic satyrine genus *Erebia* involves chromosome number change. Each number is peculiar to a species, accompanied by a set of behavioural and mechanical isolation attributes. Hybrid sterility is most pronounced between geographically overlapping species. There is no evidence of hybrids in nature. Two species having the same chromosome number do not coexist at any locality. Sexual isolation is not the primary condition but, once it had arisen it was, in the opinion of Lorković (1958), strengthened through natural selection and hybrid breakdown. Kandul *et al*. (2004) and Lukhtanov *et al*. (2005) have shown how this kind of reinforcement operates in the genus *Agrodiaetus* (Lycaenidae).

Chromosome number change is thought to occur in small, isolated, and inbred populations, such as envisioned by Lorković (1958). An individual with a newly arisen variant will be heterozygous for it. It will have problems at chromosome disjunction in meiosis, with reduced fertility as a result. The conditions under which a karyotypic change can be established are therefore severely limited. A chromosome number change is very unlikely to become fixed in a large, outbreeding population. The novel karyotype must somehow land in a small population, with an effective size of a few individuals. This small population must remain reproductively isolated from other members of the species for a long enough period, at least for two generations. The novel karyotype can then become fixed in individuals homozygous for it through inbreeding. If the new karyotype confers increased fitness to its bearers, it will start to spread. Prezygotic isolating mechanisms will be built up through selection in addition to the postzygotic one effected through the karyotype change, and a new species is born. Its future will depend on the environment and geographical attributes. Chromosomal changes need not be a factor driving speciation; rather, they may intensify the reproductive isolation between species that has arisen by other mechanisms (Coghlan *et al*., 2005).

Gilbert (2003) has explained the deviating chromosome numbers of derived *Heliconius* species reported by Brown *et al*. (1992) through social structuring and small population sizes. Gilbert (2003) points out that

the derived *Heliconius* form a clade that allows developing an argument on the role of sexual selection. Males of these species guard female pupae and mate with the female as she emerges from the pupa (Deinert, 2003); the females mate only once in their lifetime. This excludes any female choice of her mate; accordingly, there is no sexual selection.

We feel that many aspects of chromosome number variation observed in a single population of satyrines are difficult to explain through phenomena occurring in small populations. All the available evidence indicates that most populations are large and continuous. Similar observations have been made earlier by de Lesse (1967a), de Lesse & Brown (1971) and Wesley & Emmel (1975). Mate choice can then be invoked as a factor speeding up evolution. Carson (2003) has shown that nonrandom mating will give rise to reduced effective population size, inbreeding, and low gene flow. This process can be observed and has been studied in numerous animal groups, from insects to large carnivores.

The chromosome numbers of lepidopterans resist change. The first demonstration that karyotype differences in animals give rise to hybrid sterility was performed with lepidopterans (Federley, 1913). Butterflies have been crossed extensively (Lorković, 1990; Ae, 1995) and there is little doubt, notwithstanding the nearly holokinetic chromosomes, that hybrids between differing karyotypes have reduced fitness. Evidently, the taxon-specific numbers are old.

Butterflies have complicated mate choice systems (Wiklund, 2003) extending from complex behaviours, such as first observed by Tinbergen *et al*. (1942) for a satyrine, to a total absence of female choice in pupal mating *Heliconius* (Deinert, 2003). Mate choice is in general polygenically controlled (Carson, 2003). Mate choice may involve assortative mating among individuals that differ in chromosome number within sympatric and extensive butterfly populations, such as we have seen in the present study. The alternative is a population composed of reproductively isolated forms that now live in sympatry but that have originated elsewhere. Lukhtanov *et al*. (2005) have shown that the alternatives can be tested using the standard tools of evolutionary and molecular biology. The high butterfly diversity of South America together with the ecological richness offers an excellent possibility of studying the process of karyotype evolution in relation to ecology and speciation.

ACKNOWLEDGEMENTS

K. S. Brown is grateful to BIOTA-FAPESP (98/05101-8) for laboratory supplies and field support, and the Brazilian CNPq for research fellowships and for help in travel. This study has been conducted as a part of the Post-Doctoral project on Satyrine ecology and systematics of André Freitas. He acknowledges the FAPESP grants 00/01484-1 and 04/05269-9 and the BIOTA-FAPESP program (98/05101-8), the Brazilian CNPq (fellowship 300315/2005-8) and the National Science Foundation grant DEB-0316505. The late Dr Esko Suomalainen of the Department of Genetics of the University of Helsinki encouraged and participated in the early part of the study and checked the slides made by Barbara von Schoultz. This part of the work has been supported by grants from the Finnish Natural Science Research Council. Anja O. Saura and Anssi Saura put the material together in collaboration with Drs Brown and Freitas. They thank the Departamento de Biologia Celular, UNICAMP, for working facilities in 2003–04 (we especially thank Drs Shirlei Maria Recco Pimentel, Odair Aguiar Junior, Ana Cristina Prado Veiga Menoncello, and Clélia Aparecida de Carvalho of the Departamento de Biologia Celular). Their work has been supported financially in part by the Finnish Cultural Foundation (A.S. and A.O.S.), the University of Helsinki Research Funds, the Jenny and Antti Wihuri Foundation and the Betty Väänänen Foundation (A.O.S.), and the Royal Physiographic Society of Lund, Sweden (A.S.). We wish to thank Drs Carlos Peña and Niklas Wahlberg for comments and advice.

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