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The Chromosomes of Neotropical Butterflies from Trinidad and Tobago[1]

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ABSTRACT

Chromosome numbers and karyotypic observations are reported for 27 species of neotropical Lepidoptera in 8 families (Satyridae, Ithomiidae, Nymphalidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae, and Hesperiidae). Characteristic haploid numbers for certain genera are found: *Parides* (N=30 or 31), *Phoebis* (N=31), *Eurema* (N=28, 29, 30, or 31), *Dynamine* (N=29 or 30), *Mestra* (N=31 or 33), *Anartia* (N=31) and *Agraulis* (N=31). Two genera showing widely varying chromosome numbers are *Heliconius* (N=19, 20, 21, 22, 24, 25, 26, 27, 28, 29, 30, 33, 38, and 56) and *Mechanitis* with (N=16, 17, 18, 19, 21, 24). The butterflies in these genera are involved in extensive mimicry complexes. The occurrence of fragmentation in *Heliconius* and *Mechanitis* may play a role in promoting ease of genetic recombination, which in turn could increase the diversity of phenotypes in the population and influence effects of natural selection.

THE ISLANDS OF TRINIDAD AND TOBAGO, 10 miles off the east coast of Venezuela, provide a varied series of tropical lowland and montane habitats for some 617 species of butterflies (Barcant 1970). Numerous studies on the behavior and genetics of several lepidopteran groups have been carried out at the Arima Station of New York Zoological Society (e.g., Crane 1955). However, little information is available on the karyotypes of these species. De Lesse (1967, 1970) has published chromosome counts on species from Central America and northern South America, which include a few subspecies of species also found on the islands of Trinidad and Tobago. Suomalainen *et al.* (1972) give haploid numbers for 14 heliconiine butterflies found in Trinidad. The purpose of this paper is to report chromosome numbers and karyotypic observations for 27 species of eight butterfly families (Satyridae, Ithomiidae, Nymphalidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae, and Hesperiidae) from Trinidad and Tobago.

MATERIALS AND METHODS

All material studied in this report was collected by the authors on the islands of Trinidad and Tobago during the month of September 1970. Testes of live, wild-caught males were removed with fine dissecting forceps and fixed in vials containing 3:1 alcohol:acetic acid (Emmel 1969). Upon returning from the field the vials containing the testes were stored at –20°F until processing in the Gainesville laboratory. For microscopic observation, testes were stained with lacto-aceto-orcein, and squashed under a press until the testicular material was approximately one cell layer thick. Preparations were examined with a Carl Zeiss Research Microscope Standard WL fitted with 25x, 40x, and 100x planapochromatic flatfield objectives and automatic camera (refer to Emmel 1969 for further details). All uniformly spread metaphase plates of each individual were counted in order to verify the count and determine any variance within a particular specimen. Additional observations were made under phase contrast using a Watson Photoautomatic Phase Contrast Microscope Hilux 70 pH fitted with 40x Planpara and 90x Fluorite phase contrast objectives and automatic camera. It may be noted that many examined specimens lacked dividing cells. In some species, spermatogenesis may be largely completed in most of the individuals at the time of eclosion, therefore making it difficult to observe divisions in a wild-caught adult unless caught and preserved immediately upon emergence. Alternately, some of the butterflies of these islands may be seasonal in gamete production. *Heliconius,* for instance, are known to have a life span of up to six months (Benson 1972; Benson and Emmel 1973; Ehrlich and Gilbert 1973). It would be possible, therefore, that certain species were not undergoing meiotic divisions at the time of capture since collections were made only in the middle of the wet season.

RESULTS

A. SATYRIDAE:

1. *Euptychia penelope* (Fabricius) N=36

The count was made in one nucleus in the testes of one male (TR-141) taken at the William Beebe Tropical Field Station of the New York Zoological

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Society at Simla, Arima Valley, Trinidad on 8 September 1970. All chromosomes appeared to be of the same size and extremely small and compact in relation to other species. Many more cells were observed in prophase.

2. *Euptychia hermes* (Fabricius) N=13, 18, 23, 25

Counts of N=13 were in 17 nuclei in the testes of one male (TR-100) taken 1 mile west of Blanchisseuse, northwest Trinidad, on 4 September. Five chromosomes were notably larger than the others. Counts of N=18, N=23, and N=25 were all discovered in the same population 1 mile southwest of Moriah, western Tobago on 6 and 7 September. Three nuclei in the testes of one individual (TO-527) were N=18. Three of the chromosomes were distinctly larger than the other 15. Eighteen nuclei in the testes of one individual (TO-511) were N=23. Three of the chromosomes were larger than the remainder. A total of eight nuclei in the testes of two different individuals (TO-507 and TO-511) gave a count of N=25. Three chromosomes were noticeably larger than the others.

This butterfly is the smallest *Euptychia* found on Trinidad and Tobago and occurs throughout the Neotropics and north into eastern North America. Great variability in karyotype exists elsewhere in its range (Emmel, unpublished). De Lesse (*in litt.* before his death) had found similar geographic and local variability in haploid number for this butterfly, but thought these numbers perhaps represented sibling species and withheld publication of any *E. hermes* counts.

3. *Euptychia occirhoe* (Fabricius) N=18

Counts were made in five nuclei in the testes of a male (TR-139) collected at the Beebe Station at Simla, Arima Valley, Trinidad, on 8 September. Six chromosomes appeared larger than the others.

B. ITHOMIIDAE:

1. *Mechanitis ishmia kayei* (Fox) N=21

Counts were made in five good nuclei in the testes of a male (TR-126) collected at the Beebe Station at Simla, Trinidad, on 8 September. All chromosomes were of equal size. All dividing cells were found in one section of a testis. A very abundant butterfly on Trinidad and Tobago, this species ranges from Mexico to central Peru and into Venezuela.

2. *Tithorea harmonia megara* (Latreille) N=14

Counts were made in three nuclei in the testes of one male specimen (TR-198) collected at the Texaco Forest Preserve, Perrylands Road, near Cochrane, southwest Trinidad, on 9 September. All of the chromosomes were of equal size. This is a common species in Trinidad and has a widespread neotropical distribution, ranging from Mexico to Brazil.

C. HELICONIIDAE:

1. *Heliconius doris* (Linnaeus)

N=24, 25, 26, 27, 28, 29, 30, and 38

A total of 275 cells were counted in 25 individuals all from the same population in the Texaco Forest Reserve, Perrylands Road Number 2, near Cochrane, southwest Trinidad, on 9 September. The chromosome number varied not only between individuals but also within the same individual. A summary of the data for 25 male specimens shows:

Chromosome number (N)	Number of specimens showing count	Total number of cells counted
24	12	27
25	6	8
26	23	121
27	16	51
28	16	51
29	3	4
30	4	10
38	1	3

This polymorphic species feeds exclusively on *Passiflora serratodigitata* in Trinidad, so its chromosomal variability is not associated with variability in host selection (*cf.* Emmel, Trew, and Shields 1973). The butterfly is found from Mexico into central South America. The discal color of the hindwing of this polymorphic species may be blue, green, or red; there is no apparent correlation between the color of the hindwing and the chromosome number. Extensive chromosomal variability similar to that found in Trinidad occurs throughout its range north to Mexico (Emmel, in prep.).

2. *Heliconius aliphera* (Godart) N=31

Counts were made in seven good nuclei in the testes of a male (TR-106) taken 1 mile west of Blanchisseuse, northwest Trinidad, on 4 September. All chromosomes were of the same size, and were extremely small and tightly clustered.

3. *Heliconius ricini* (Linnaeus) N=21, 22

Counts were made in 25 excellent nuclei in the testes of three individuals (TR-110, TR-111, TR-112) taken in hills above La Vache Bay, northwest Trinidad, on 4 September. The number of chromosomes per nucleus were either N=21 (5 cells) or N=22 (20 cells). All chromosomes were of equal size.

4. *Heliconius sara* (Fabricius) N=19, 21, 29

Counts were made in 12 nuclei in the testes of two male specimens (TR-121 and TR-122) taken at the Beebe Station at Simla, Trinidad, on 8 Septem-

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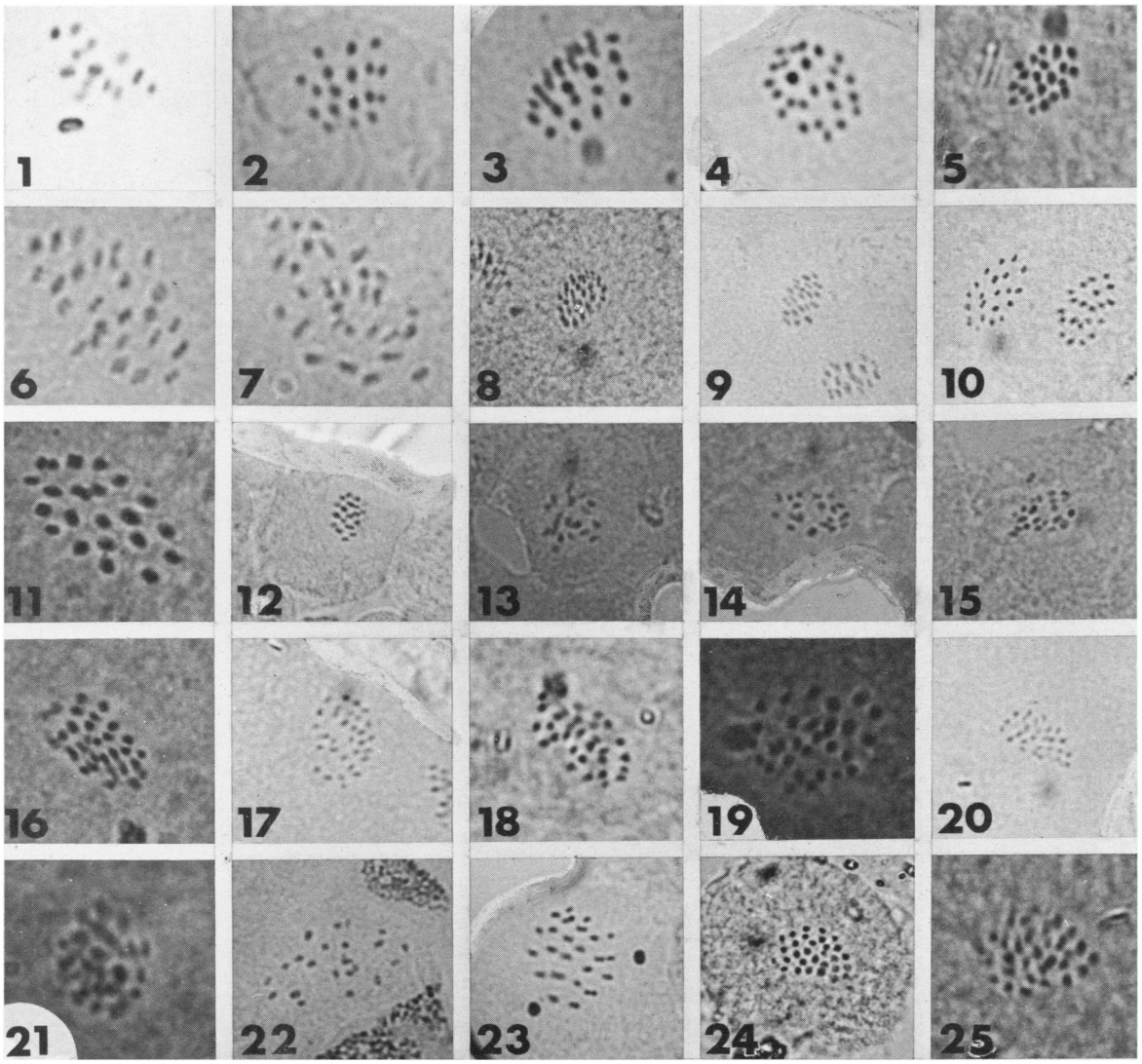
ber. In all cells, three chromosomes appeared larger than the rest. Wide numerical variance occurred in this species:

Chromosome number (N)	Specimen reference showing count	Total number of cells counted
19	TR-122	8
21	TR-122	2
29	TR-121	2

5. *Heliconius melpomene* (Linnaeus) N=19, 20, 21 Counts were made in eight nuclei in the testes of two male specimens (TR-124 and TR-125) collected at the Beebe Station at Simla, Trinidad, on 8 September. Three to five of the chromosomes were somewhat larger than the others. Considerable variability was observed within the species:



FIGURES 1–25. Metaphase (I or II) plates from testes of neotropical butterflies from Trinidad and Tobago. 1, *Euptychia hermes* (N=13, I) x 740; 2, *Euptychia hermes* (N=18, I) x 740; 3, *Euptychia hermes* (N=23, I) x 740; 4, *Euptychia hermes* (N=25, I) x 740; 5, *Mechanitis ishmia kayei* (N=21, I) x 1480; 6, *Heliconius doris* (N=26, I) x 1480; 7, *Heliconius doris* (N=30, I) x 1840; 8, *Heliconius aliphera* (N=31, I) x 740; 9, *Heliconius ricini* (N=20, I) x 740; 10, *Heliconius ricini* (N=21, I) x 740; 11, *Heliconius ricini* (N=22, I) x 1480; 12, *Heliconius sara* (N=19, I) x 740; 13, *Heliconius melpomene* (N=19, I) x 740; 14, *Heliconius melpomene* (N=20, I) x 740; 15, *Heliconius melpomene* (N=21, I) x 740; 16, *Agraulis vanillae* (N=31, I) x 1480; 17, *Anartia amathea* (N=31, I) x 740; 18, *Anartia jatrophe* (N=31, I) x 1480; 19, *Precis lavina zonatis* (N=29, I) x 1480; 20, *Dynamine arena* (N=30, I) x 740; 21, *Morpho peleides* (N=28, I) x 1840; 22, *Arawacus linus* (N=22, I) x 740; 23, *Arawacus linus* (N=24, I) x 740; 24, *Parides neophilus parianus* (N=30, II) x 740; 25, *Phoebus sennae* (N=31, I) x 1480.

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Chromosome number (N)	Specimen reference showing count	Total number of cells counted
19	TR-124	2
20	TR-124	3
21	TR-124, TR-125	3

6. *Heliconius isabella* (Crammer) N=31

Counts were made in 42 nuclei in the testes of eight different male specimens (TR-183, TR-184, TR-185, TR-186, TR-187, TR-189, TR-190, TR-191) taken at the Texaco Forest Reserve, Perrylands Road, near Cochrane, southwest Trinidad, on 9 September. All chromosomes appeared to be of equal size.

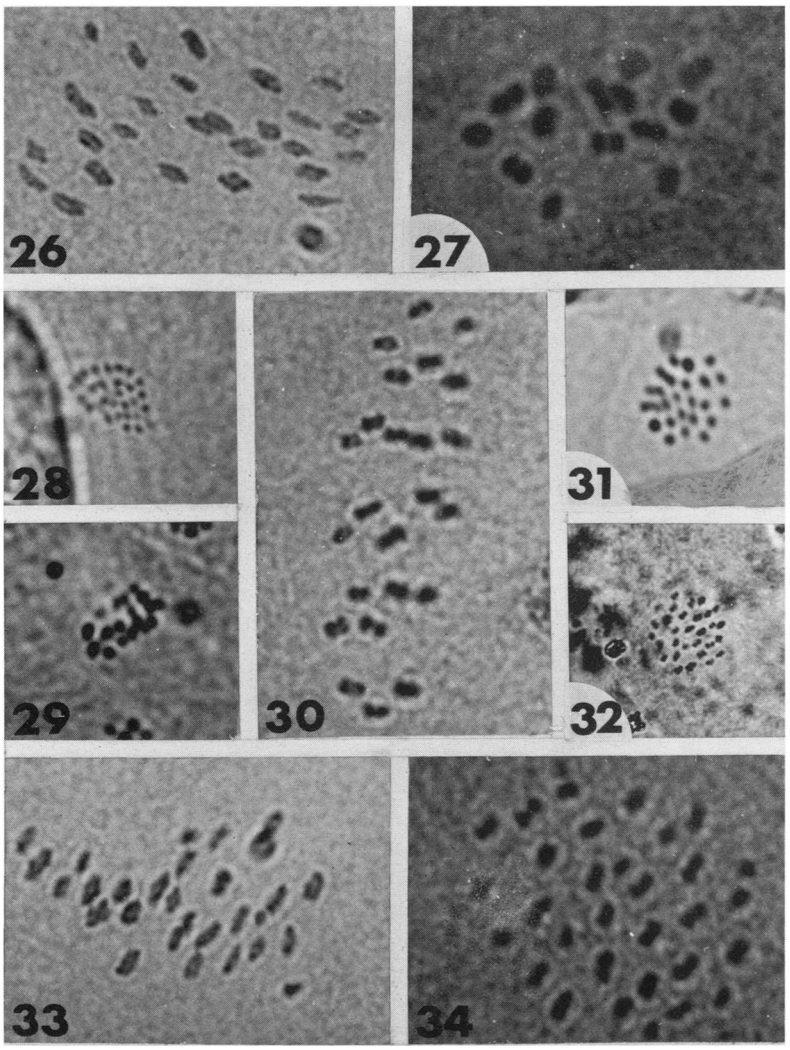
7. *Agraulis vanillae* (Linnaeus) N=31

Counts were made in five excellent nuclei in the testes of two individuals (TO-550 and TO-551) captured in the garden at Coral Reef Guest House on the Milford Road, Scarborough, Tobago, on 7 September. All chromosomes were of equal size. Many additional dividing cells were found in other meiotic stages.

D. NYMPHALIDAE:

1. *Anartia amathea* (Linnaeus) N=31

Counts were made in 27 excellent nuclei in the testes



FIGURES 26–34. Metaphase plates from testes of butterflies from Trinidad and Tobago. 26, *Heliconius doris* (N=27, I) x 1840; 27, *Tithorea harmonia megara* (N=14, I) x 1840; 28, *Eurema venusta* (N=30, I) x 1480; 29, *Mesosemia methion* (N=18, I) x 740; 30, Unidentified Skipper (N=24, I) x 740; 31, *Gesta gesta* (N=32, I) x 740; 32, *Wallengrenia* species (N=31, I) x 740; 33, *Heliconius doris* (N=28, I) x 1840; 34, *Heliconius isabella* (N=31, I) x 1840.

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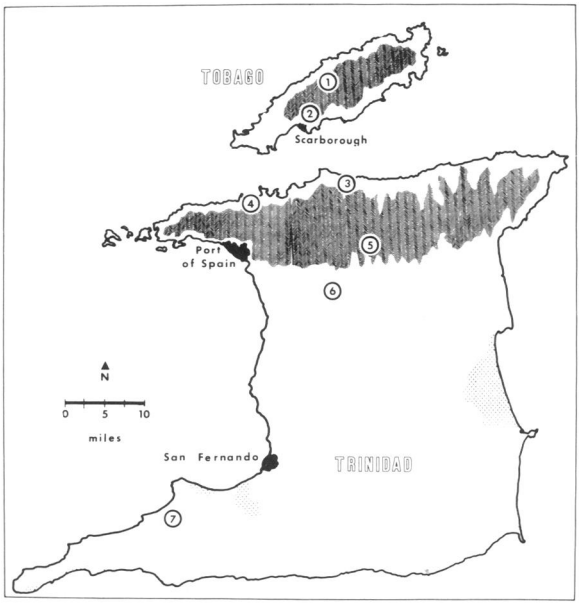

FIGURE 35. Principal collecting areas on Tobago and Trinidad: (1) 1 mile SW of Moriah, 500-ft. elevation; (2) Coral Reef Guest House area, Milford Rd., Scarborough; (3) 1 mile W of Blanchisseuse, NW Trinidad; (4) above La Vache Bay, NW Trinidad; (5) Simla, 4 mi. N of Arima, 1000-ft. elevation; (6) Pan American Guest House area, Piarco; (7) Texaco Forest Reserve, Perrylands Road No. 2, near Cochrane, SW Trinidad. The lightly shaded areas represent the Oropouche Swamp, southwest San Fernando, and the Nariva Swamp on the mideast coast. The heavily cultivated land between these swamp areas has very few butterfly species. The Forest Reserve oil concessions around (7) preserve reasonably good secondary rain forest, with a rich diversity of butterflies. The heavily shaded areas in northern Trinidad and central Tobago represent mountain ranges (to 3085-ft. and 1890-ft. elevations, respectively, on these islands).

of three individuals (TR-109, TR-148, and TR-149). Specimen TR-109 was taken in the hills above La Vache Bay, northwest Trinidad, on 4 September. Specimens TR-148 and TR-149 were captured in the garden at the Pan American Airways Guest House, Piarco, Trinidad, on 8 September. In all cells, three chromosomes were noticeably larger than the others.

2. *Anartia jatrophe* (Linnaeus) N=31
Counts were made in eight good nuclei in the testes of two individuals (TR-108 and TR-152). Specimen TR-108 was captured 1 mile west of Blanchisseuse, northwest Trinidad, on 4 September. Specimen TR-152 was taken in the garden of the Pan American Guest House, Piarco, Trinidad, on 8 September. In both specimens, all chromosomes appeared to be approximately the same size.

3. *Precis lavina zonatis* (Felder) N=29
Counts were made in 16 excellent nuclei in the testes of two individuals (TR-138 and TR-151). Specimen TR-138 was taken at the Beebe Station at Simla, Trinidad, on 8 September. Specimen TR-151 was captured at Piarco, Trinidad, on 8 September. All chromosomes were uniform in size.

4. *Mestra hypermestra cana* (Erich) N=31
Counts were made in two good nuclei in the testes of one male caught 1 mile southwest of Moriah, Tobago, on 7 September. All chromosomes were of approximately equal size.

5. *Dynamine arene* (Hubner) N=30
Counts were made in seven excellent nuclei in the testes of one male (TO-500) caught 1 mile southwest of Moriah, Tobago, on 6 September. All chromosomes were of equal size.

6. *Morpho peleides insularis* (Fruhstorfer) N=28
Counts were made in two nuclei in the testes of one male specimen (TR-196) collected at the Texaco Forest Reserve, Perrylands Road, near Cochrane, southwest Trinidad, on 9 September. One chromosome was larger than the remainder. The only representative of the morpho group on Trinidad, this large metallic blue species ranges from Mexico to southern Brazil.

E. PAPILIONIDAE:

1. *Parides neophilus parianus* (Rothschild and Jordan) N=30
A clear count was made in one excellent nucleus in the testes of one male (TR-129) captured at the William Beebe Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, on 8 September. All chromosomes were of equal size. A second specimen studied showed many maturing sperm masses, but no dividing cells.

F. PIERIDAE:

1. *Phoebis sennae* (Linnaeus) N=31
Counts were made in seven good nuclei in the testes of three individuals (TO-555, TO-557, and TO-558). All three specimens were captured in the garden of the Coral Reef Guest House on the Milford Road, Scarborough, Tobago, on 7 September. All chromosomes were of equal size.

2. *Eurema venusta* (Boisduval) N=30
A clear count was made in one nucleus in the testes of one male (TR-107) taken 1 mile west of Blanchisseuse in northwest Trinidad on 4 September. Six of the chromosomes appeared considerably smaller than the others.

3. *Eurema leuce* (Boisduval) N=31
A clear count was made in one nucleus in the testes

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of a male (TO-531) captured 1 mile southwest of Moriah, Tobago, on 7 September. All chromosomes appeared to be of equal size.

G. LYCAENIDAE:

1. *Arawacus linus* (Fabricius) N=22, 23, 24

Counts were made in eight nuclei in the testes of one male specimen (TR-202) collected in the Texaco Forest Preserve, Perrylands Road, near Cochrane, southwest Trinidad, on 9 September. Although all chromosomes were similar in size there was some variability in number from cell to cell: N=22 (3 cells), N=23 (1 cell), or N=24 (4 cells). All chromosomes were of equal size.

H. RIODINIDAE:

1. *Mesosemia methion* (Hewitson) H=18

Counts were made in five good nuclei in the testes of one individual (TR-118) captured at the Beebe Station at Simla, Trinidad, on 8 September. Six of the 18 chromosomes were slightly smaller than the others.

I. HESPERIIDAE:

1. *Gesta gesta* (Herrich-Schaffer) N=32

A clear count was made in one excellent nucleus in the testes of an individual (TO-508) captured 1 mile southwest of Moriah, Tobago, on 6 September. All chromosomes were of equal size and very large.

2. *Cymaenes* species N=31

Counts were made in four good nuclei in the testes of one individual (TO-521) captured 1 mile southwest of Moriah, Tobago, on 7 September. All chromosomes were of approximately the same size. Other dividing cells were found in the testes in later stages of meiosis.

3. *Chiomara* species N=31

Counts were made in three nuclei in the testes of one male specimen (TR-206) collected in the Texaco Forest Preserve, Perrylands Road, near Cochrane, southwest Trinidad, on 9 September. All chromosomes were of equal size.

DISCUSSION

The chromosome numbers and testes pigmentation of 27 species of neotropical Lepidoptera from populations on Trinidad and Tobago are given in table 1. Previously published counts of these species are listed where available. When compared with other previously published counts, the new data show that several neotropical genera display characteristic haploid numbers:

Parides:	(4 species)	N=30	(present paper; de Lesse 1967, 1970)
	(2 species)	N=31	(present paper; de Lesse 1967)
Phoebus:	(7 species)	N=31	(present paper; de Lesse 1967, 1970)
Eurema:	(18 species)	N=31	(present paper; de Lesse 1967)
	(1 species)	N=30	(present paper)
	(1 species)	N=29	(de Lesse 1967)
	(1 species)	N=28	(de Lesse 1967)
Dynamine:	(4 species)	N=29	(de Lesse 1967, 1970)
	(4 species)	N=30	(present paper; de Lesse 1967)
Mestra:	(2 species)	N=31	(present paper; de Lesse 1967)
	(1 species)	N=33	(de Lesse 1967)
Anartia:	(2 species)	N=31	(present paper; de Lesse 1967)
Agraulis:	(1 species)	N=31	(present paper; de Lesse 1967, 1970)

De Lesse (1967) concluded that the solely neotropical subgenus *Heliconius* of the Heliconiinae had a basic haploid number of N=21. There is considerable variation in chromosome number above and below this figure (present paper and Suomalainen *et al.* (1972)), but a base number of 21 chromosomes is still suggested by the data. Haploid numbers of 19 in certain *Heliconius sara* and *Heliconius melpomene* from Trinidad are the lowest counts reported for any true *Heliconius* to date.

Because of the small size and numerical variability of these butterfly chromosomes it appears that fragmentation of the holokinetic chromosomes may be the chief factor leading to numerical variation. De Lesse's observations also suggest fragmentation in *Heliconius,* as he reported counts of 21 for most species; 21, 24, 25, 26, 27 for *H. doris*; 31 for certain unspecialized, presumably primitive *Heliconius*; and 33 and 56 for *H. sapho.* This paper reports additional new counts of 19, 20, 28, 29, 30, and 38 for the genus *Heliconius.* The variability of chromosome number between individuals of the same species does not seem to be an artifact induced by preparation techniques. As more material becomes available of species with counts previously published from examination of single specimens, it appears that certain groups (heliconiines and ithomiines in particular) characteristically exhibit this variation, while many others (pierids, papilionids, and "typical" nymphalid genera) show only a monotonously constant number from species to species.

It should also be noted the discovery of extensive fragmentation occurring in other *Heliconius* besides *doris* lends support to the idea that fragmentation of lepidopteran chromosomes may be an important mechanism for rearranging genes controlling mi-

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TABLE 1. *Summary of available data on butterflies from Trinidad and Tobago.*

Species	Color of testes	Present count	Previous count	References
Euptychia penelope	Cherry red	36	—	—
Euptychia hermes	Yellow green	13, 18, 23, 25	—	—
Euptychia occirhoe	Pale green	18	—	—
Mechanitis ishmia kayei	Dusky rose	21	—	—
Tithorea harmonia megara	Rose	14	—	—
Heliconius doris	Light rose	24, 25, 26, 27 28, 29, 30, 38	24, 25, 26, 27 26, 27	de Lesse 1967 Suomalainen *et al.* 1972
Heliconius aliphera	Rose	31	31 30, 31	de Lesse 1967 Suomalainen *et al.* 1972
Heliconius ricini	Rose	21, 22	21	Suomalainen *et al.* 1972
Heliconius sara	Pale rose	19, 21, 29	21	Suomalainen *et al.* 1972
Heliconius melpomene	Rose	19, 20, 21	21	de Lesse 1967, Suomalainen *et al.* 1972
Heliconius isabella	Rose	31	30, 31	Suomalainen *et al.* 1972
Agraulis vanillae	Black	31	31	Suomalainen *et al.* 1972
Anartia amathea	Rose	31	30, 31, 32	de Lesse 1967
Anartia jatrophe	Carmen & dark rose	31	31	de Lesse 1967
Precis lavina zonatis	Dark carmen & dark rose	29	—	—
Mestra hypermestra cana	Pale green	31	—	—
Dynamine arene	Gold yellow	30	—	—
Morpho peleides insularis	Pale green	28	—	—
Parides neophilus parianus	Rose	30	—	—
Phoebis sennae	Dark rose	31	31	de Lesse 1967
Eurema venusta	Dusky rose	30	—	—
Eurema leuce	Chocolate	31	—	—
Arawacus linus	Pale green	22, 23, 24	—	—
Mesosemia methion	Pale rose	18	—	—
Gesta gesta	Yellow gold	32	—	—
Cymaenes sp.	Rose	31	—	—
Chiomara sp.	Yellow gold	31	—	—

metic phenotypes, thus allowing rapid evolution as a result of predator selection among new color morphs. This chromosomal evidence for extensive recombination could provide part of the explanation for the incredible phenotypic diversity observed in so many *Heliconius* species. Breeding experiments with diverse chromosomal forms of certain of these polymorphic species are underway in our laboratory to test this hypothesis.

Extensive specific variation in chromosome number occurs in the genus *Mechanitis*, where de Lesse (1967) reports counts of 15, 16, 17, 18, and 24 in different species. In the current study a count of 21 was observed in *Mechanitis ishmia kayei,* the first such count reported for the genus. From this fragmentary picture of chromosome number, it is possible that chromosomal increase allowing greater flexibility in genetic rearrangement could be playing an important role in this genus, too. Emmel, Trew, and Shields (1973) have reported extreme chromosomal variability (N=17 to 44) in California populations of a nearctic lycaenid butterfly, *Philotes sonorensis* Felder and Felder, and have suggested that gross rearrangement of the genetic material on the chromosomal level may be generally useful strategy for butterfly species faced by marginal environments or strong predation pressures.

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