STUDIES OF THE CHROMOSOMES OF NORTH AMERICAN RHOPALOCERA. 4. NYMPHALINÆ, CHARAXIDINÆ, LIBYTHEINÆ

by KODO MAEKI and CHARLES L. REMINGTON

This paper concludes the report of our first systematic survey of the groups of the Rhopalocera. The first supplement, giving new counts for species of various families, is in preparation. Our preceding papers (Maeki & Remington, 1960a, 1960b, 1961) gave notes on our techniques and sources of material and presented new data and discussions of the cytotaxonomy of the Hesperiidæ, Megathymidæ, Pieridæ, Papilionidæ, Lycænidæ (*sensu lato*), and part of the Nymphalidæ (*s. l.*).

For the Nymphalidæ we are following the subfamily classification of EHRLICH (1958), but we include the Libytheinæ as one more subfamily of the Nymphalidæ. In some compelling characters they seem to us closer to the Nymphalidæ than do the Danainæ, among others.

Most of the specimens for which the chromosomes are reported here were collected in 1959. Some additional species of Nymphalidæ are included in our first supplementary paper, and there are counts for several Acræinæ and Nymphalinæ and one Charaxidinæ in our forthcoming paper on African species.

As with the previous groups, we have noted in square brackets our designations of the individuals studied; this number will be found on the specimen and the slides of its testes, all preserved for permanent reference in the Peabody Museum of Yale University. In the lists that follow, "*n*" represents the haploid chromosome number, "I" refers to the primary spermatocyte division and "II" to the secondary spermatocyte division. No females were studied in these groups.

Fixed testes of several species not in the following descriptive list were sectioned and examined but did not show any meiotic divisions. The numbers of specimens of these species are as follows: 1 *Euphydryas* near *phaeton* (Drury) from Connecticut; 1 *Chlosyne nycteis* (Doubleday & Hewitson); 1 *Vanessa atalanta* (Linné) from Connecticut; 5 *Nymphalis milberti* (Godart) from Colorado; 1 *Polygonia vau-album* (Schiff.) from Connecticut; and 1 *Limenitis arthemis* (Drury) from Vermont.

A. NYMPHALIDÆ – NYMPHALINÆ:

1. *Dryas julia* (Fabricius). *N* = 31. Counts were made in 25 nuclei (I) and 20 nuclei (II) in testes of 8 males [M54-1, M54-2, M54-3, M54-4, M54-6, M54-7, M54-8, M54-9] taken at El Salto, S. L. P., Mexico, 4 August 1959. Three chromosomes are distinctly smaller than the others, which are fairly uniform in size.

2. *Dione juno* (Cramer). *N* = 31. Counts were made in 7 nuclei (I) and 5 nuclei (II) in testes of 1 male [M55] taken at El Salto, 4 August 1959. Four chromosomes appear to be small and 27 large.

3. *Euptoieta hegesia* (Cramer). *N* = 31. Counts were made in 20 nuclei (II) in testes of 1 male [M15] taken at Ciudad Victoria, Tamps., Mexico, August 1959. The caryotype shows 1 large, 27 medium, and 3 distinctly smaller chromosomes. No primary divisions were found.

4. *Speyeria cybele charlottii* (Barnes). *N* = 29. Counts were made in 30 nuclei (I) and 30 nuclei (II) in testes of 7 males [245, 246, 247, 259, 263, 261, 958] taken about 6 miles east of Somerset, Gunnison Co., Colorado, August 1959 and 17 July 1960. Divisions were plentiful and sufficient counts were easily obtained; very many more could have been added, but it was clear that the number was invariable in these 7 males. The same number was consistently found in 3 males [1015, 1017, 1019] taken at Rabbit Ears Pass, 22 July 1960. Several individuals from near Somerset with diverse numbers in a single pair of testes were also studied and will be reported separately in a paper on hybridization. As with some of the following species of *Speyeria*, it is likely that the *cybele* concept of L. P. GREY represents a superspecies of several genetically partly incompatible populations which must eventually be regarded as separate species. Possibly some of these young species will even prove to have different chromosome numbers, but we have not yet sampled sufficiently to have data bearing on this point.

5. *Speyeria aphrodite ethne* (Hemming). *N* = 29. Counts were made in 30 nuclei (I) and 20 nuclei (II) in testes of 3 males [254, 256, 266] taken 6 miles east of Somerset, 15 August 1959. There appear to be four size classes in the normal caryotype: 2 largest, 6 large, 20 medium, 1 small. As with S. *cybele charlotti* and S. *atlantis nikias*, the sample from the Somerset locality also included males with various numbers of non-synapsing chromosomes in the first meiotic division and therefore presumably of hybrid origin.

6. *Speyeria coronis halcyone* (Edwards). *N* = 30. Counts were made in 20 nuclei (I) and 20 nuclei (II) of 3 males [701, 702, 703] taken in Clear Creek Canyon, el. 6300′, 26 June 1960, *leg.* C. L. REMINGTON & J. DONALD EFF. There are 4 large, 16 medium, and 10 small elements. Three

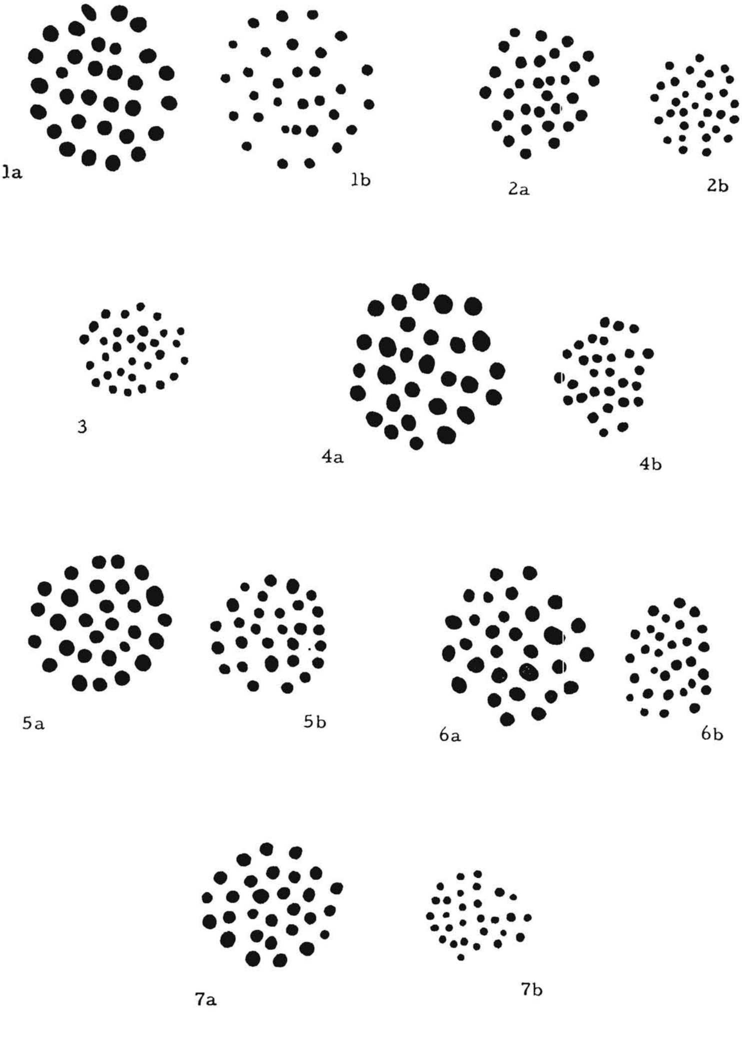


Fig. 1a — *Dryas julia* (I); fig. 1b — same; fig. 2a — *Agraulis juno* (I); fig. 2b — same; fig. 3 — *Euptoieta hegesia* (II); fig. 4a — *Speyeria cybele charlottii* (I); fig. 4b — same (II); fig. 5a — S. *aphrodite ethne* (I); fig. 5b — same (II); fig. 6a — S. *coronis halcyone* (I); fig. 6b — same (II); fig. 7a — S. *zerene sinope* (I); fig. 7b — same (II). [On plates 1-5 are camera lucida drawings of caryotypes, not necessarily showing precise size relationships of individual chromosomes; magnifications all 3900 diameters; I = primary and II = secondary spermatocyte divisions.]

other males [707, 724, 726] taken at the same time showed no suitable divisions. One other male [704]taken with these gave an anomalous count which will have to be discussed later.

7. *Speyeria zerene sinope* dos Passos & Grey. $N = 29$. Counts were made in 10 nuclei (I) and 10 nuclei (II) in testes of 2 males [1060, 1061] taken on the western slope of Rabbit Ears Pass, Routt Co., Colorado, 23 July 1960, *leg.* C. L. & P. S. REMINGTON. A third male taken at the same time showed no suitable divisions, but many more excellent nuclei could have been counted in these 2 males. There are 7 large, 21 uniformly medium, and 1 small chromosomes.

8. *Speyeria callippe meadii* (Edwards). $N = 30$. Counts were made in 15 nuclei (I) and 15 nuclei (II) in testes of 1 male [166] taken at Gothic, Gunnison Co., Colorado, 30 July 1959. The number was later verified in a second male [756] taken 6 miles east of Somerset, 29 June 1960. Two chromosomes are distinctly larger and 2 smaller than the other 26, rather uniform elements. No meiotic divisions were found in two males [104, 757] taken at the same localities in 1959 and 1960.

9. *Speyeria egleis secreta* dos Passos & Grey. $N = ?$ Counts were made in testes of one male [1030] taken on the western slope of Rabbit Ears Pass, 22 July 1960, *leg.* C. L., P. S., & E. E. REMINGTON. A rapid tally shows an unclear condition which requires longer study before interpretation can be appropriate. We have fixed testes of 15 other *secreta* males and must section some of these before the caryotype of this paradoxical *Speyeria* can be reported with certainty.

10. *Speyeria atlantis nikias* (Ehrmann). $N = 29$. Counts were made in 80 nuclei (I) and 65 nuclei (II) in testes of 11 males [25, 48, 49, 50, 59, 79, 80, 107, 164, 167, 305] taken at Gothic, 17 to 30 July and 22 August 1959. A twelfth male [979] taken at Gothic, 18 July 1960, showed several primary divisions, all with $n = 29$; this male is of the uncommon "Appalachian type" with very dark disc on the underside of the hind wing. Other males [1045, 1075] taken 2 mi. E. of Clark and on the west slope of Rabbit Ears Pass, Routt Co., Colorado, 22 and 23 July 1960, by C. L. & J. E. REMINGTON also showed $n = 29$ in the several primary spermatocytes examined. Two chromosomes are very large, 6 moderately large, and the other 21 are uniform and a little smaller. As with S. *charlottii* and S. *ethne* (above), a few males showed some asynaptic first metaphase chromosomes; they are probably wild hybrids between separate species of the superspecies *atlantis*.

11. *Speyeria hydaspe sakuntala* (Skinner). $N = 29$. Counts were made in 10 nuclei (I) and 10 nuclei (II) in testes of 1 male [1051] taken on the west slope of Rabbit Ears Pass, 23 July 1960, *leg.* C. L.

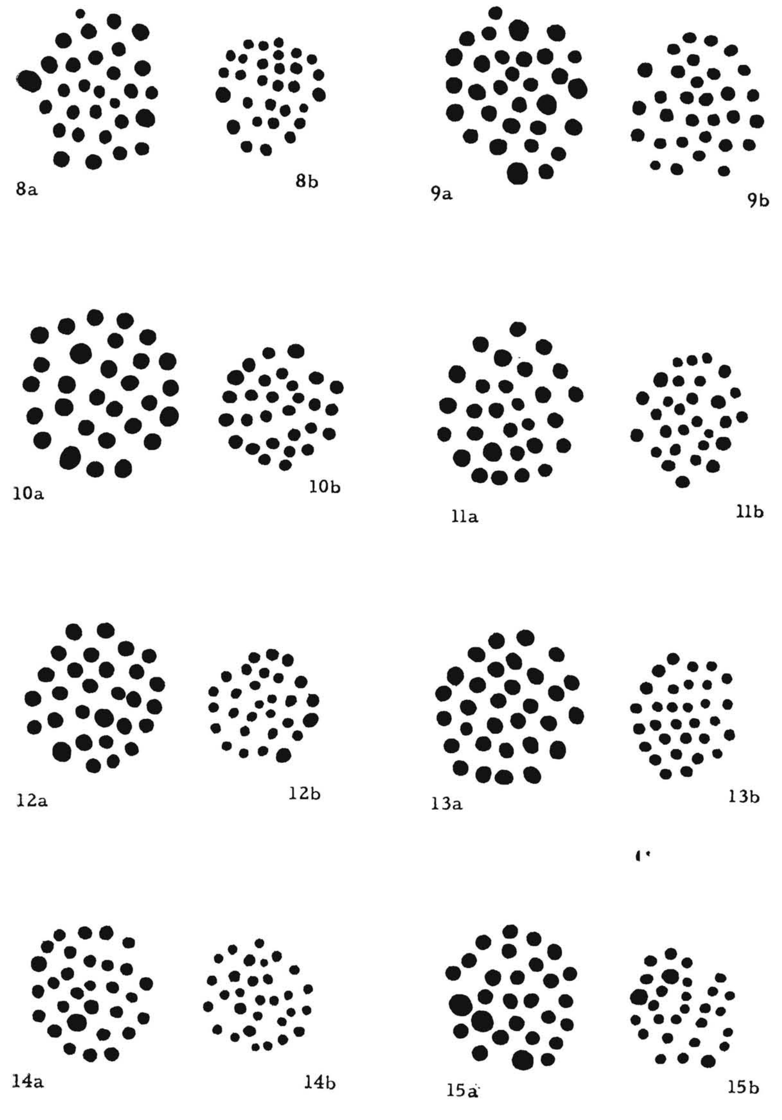


Fig. 8a — *Speyeria callippe meadii* (I); fig. 8b — same (II); fig. 9a — S. *atlantis,* variant; fig. 9b — same (II); fig. 10a — S. *atlantis nikias* (I); fig. 10b — same (II); fig. 11a — S. *hydaspe sakuntala* (I); fig. 11b — same (II); fig. 12a — S. *normonia eurynome* (I); fig. 12b — same (II); fig. 13a — *Boloria titania* (I); fig. 13b — same (II); fig. 14a — *B. selene* (I);fig. 14b — same (II); fig. 15a — *B. eunomia* (I); fig. 15b — same (II).

REMINGTON. Suitable divisions were numerous in this male. There are 2 very large, 5 moderately large, 18 medium, and 4 small elements. Other males taken at the same time showed many abnormal meiotic metaphases and will have to be re-studied when more time is available.

12. *Speyeria mormonia eurynome* (Edwards). $N = 29$. Counts were made in 50 nuclei (I) and 40 nuclei (II) in testes of 4 males [5, 11, 12, 31] taken at Gothic, 17 July 1959, and 1 male [203] taken at Copper Lake, el. 10,800'. Gunnison Co., Colorado, 7 August 1959. The count was verified in numerous nuclei from 3 males [763, 784, 785] taken at Gothic, 30 June and 2 July 1960. The caryotype shows 2 chromosomes distinctly larger and 2 or 3 distinctly smaller than the other 24 or 25.

13. *Boloria titania helena* (Edwards). $N = 31$. Counts were made in 20 nuclei (I) and 20 nuclei (II) in testes of 5 males [21, 53-1, 53-2, 184, 186] taken near Copper Lake, 17 and 19 July and 1 August 1959. In general, the chromosomes are extremely uniform in size, but 1 small element is visible in primary spermatocyte metaphases.

14. *Boloria selene tollandensis* (Barnes & Benjamin). $N = 30$. Counts were made in 10 nuclei (I) and 10 nuclei (II) in testes of 1 male [860] taken at Gothic, 9 July 1960, *leg.* W. A. Christian. The count was verified in a second male [859] taken at the same time. There are 1 large, 27 medium, and 2 small elements. No meiotic divisions were found in 2 other males taken at Gothic, 10 and 25 July 1960.

15. *Boloria eunomia cælestis* (Hemming). $N = 28$. Counts were made in 15 nuclei (I) and 10 nuclei (II) in testes of 1 male [54] taken at Copper Lake, 19 July 1959. There are 3 large, 22 medium, and 3 small elements.

16. *Euphydryas anicia eurytion* (Mead). $N = 31$. Counts were made in 10 nuclei (I) and 10 nuclei (II) in testes of 1 male [828] taken at Copper Lake, 4 July 1960. There are 1 very large, 10 fairly large, and 20 smaller chromosomes. This is the high altitude form. A complicated cytological condition in a lower sample is being discussed elsewhere.

17. *Chlosyne harrisii* (Scudder). $N = 31$. Counts were made in 5 nuclei (I) in testes of 1 male [542] taken at Karner, Albany Co., New York, 7 June 1960, *leg.* R. W. PEASE, JR. There are 6 large elements, the others being uniform and smaller. No secondary divisions were found.

18. *Chlosyne palla* (Boisduval). $N = 31$. Counts were made in 20 nuclei (I) in testes of 1 male [27] taken at Gothic, 17 July 1959. This count was verified in numerous primary spermatocyte divisions in a male [790] taken at Gothic, 2 July 1960. Seven other males [85, 86, 87, 778, 779, 788, 789] taken at Gothic, July 1959 and 1960, and 1 male [1113] taken at Rabbit Ears Pass, 23 July 1960, showed no meiotic divisions,

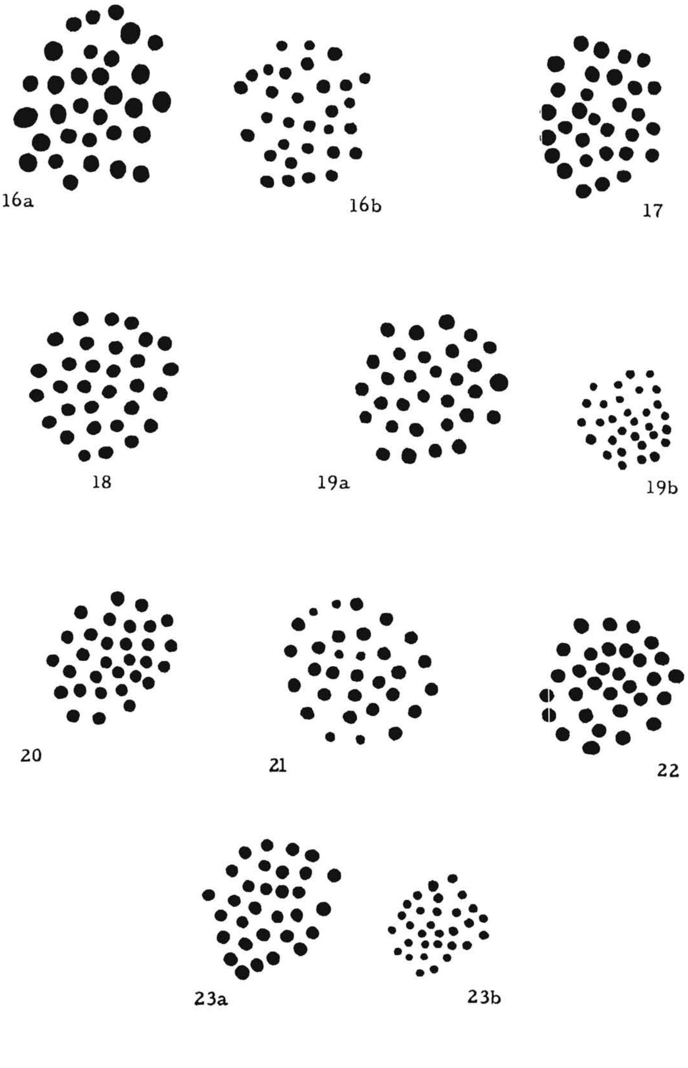


Fig. 16a — *Euphydryas anicia eurytion* (I); fig. 16b — same (II); fig. 17 — *Chlosyne harrisii* (I); fig. 18 — *C. palla* (I); fig. 19a — *C. damœtas* (I); fig. 19b — same (II); fig. 20 — *Phyciodes tharos* (I); fig. 21 — *P. phaon* (I); fig. 22 — *Polygonia zephyrus* (I); fig. 23a — *Vanessa virginiensis* (I); fig. 23b — same (II).

and no secondary spermatocytes were found in male 27. The chromosomes are uniform in size.

19. *Chlosyne damœtas* (Skinner). $N = 31$. Counts were made in numerous nuclei (I) and (II) in testes of 2 males [26-2, 51] taken near Copper Lake 17 and 19 July 1959. A third male [26-1] taken with 26-2, showed no suitable nuclei. While there is no difference in number between this high altitude sibling and *C. palla,* there appears to be a significant difference in size distribution; *C. damœtas* has 2 large, 23 medium, and 6 small chromosomes.

20. *Phyciodes tharos* (Drury). $N = 31$. Counts were made in 20 nuclei (I) of 1 male [317-4] taken at West Rock, New Haven, Connecticut, 3 September 1959. No secondary spermatocyte divisions were found. Four other males taken with this one showed no suitable meiotic divisions.

21. *Phyciodes phaon* (Edwards). $N = 31$. Counts were made in 13 nuclei (I) in 3 males [F107, F111, F112] taken at the Corkschew Swamp, near Immokalee, Collier Co., Florida, 19 April 1960, *leg.* K. MAEKI. Three chromosomes are about one-third the size of the others. No secondary divisions were found. No meiotic divisions were found in 8 other males taken at the same time nor in 4 males taken at the Archbold Biological Station, 22 April 1960.

22. *Polygonia zephyrus* (Edwards). $N = 31$. Counts were made in 15 nuclei (I) in testes of 2 males [111-1, 111-2] taken at Gothic, 23 July 1959. No secondary divisions were found. All the chromosomes are similar in size. Both of these males had passed the preceding winter as adults and were extremely battered and worn. A third male [288] taken at Gothic 17 August 1959 had no meiotic divisions; it was fresh and had undoubtedly emerged within a few days.

23. *Vanessa virginiensis* (Drury). $N = 31$. Counts were made in 15 nuclei (I) and 5 nuclei (II) in testes of 1 fresh male [336] taken at West Rock, 7 September 1959. There are 2 large. 25 medium, and 4 small chromosomes.

24. *Junonia cœnia* (Hübner). $N = 31$. Counts were made in 9 nuclei (I) and 10 nuclei (II) in testes of 1 male [M22-1] taken at Ciudad Victoria, 1 August 1959. A second male taken at the same time showed no meiotic divisions. There are 4 distinctly smaller chromosomes; the others appear to be uniform in size.

25. *Junonia evarete zonalis* (C. & R. Felder). $N = 31$. Counts were made in 25 nuclei (I) in testes of 1 male [M33-1] taken at Ciudad Victoria, 2 August 1959. At this locality these two *Junonia* were flying together in approximately equal numbers, both were fresh, and no phenotypic intermediates were found: — clear justification for their

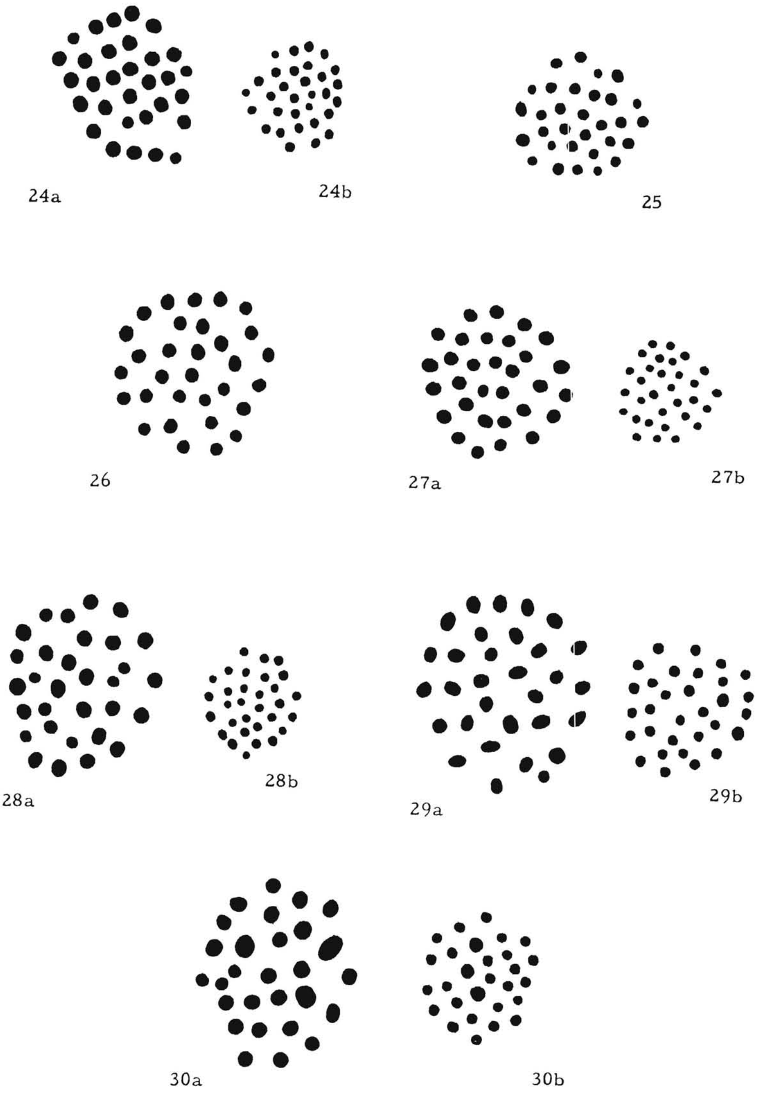


Fig. 24a – *Junonia cœnia* (I); fig. 24b – same (II); fig. 25 – *J. evarete* (I); fig. 26 – *Anartia fatima* (I); fig. 27a – *A. jatrophæ* (I); fig. 27b – same (II); fig. 28a – *Metamorpha steneles* (I); fig. 28b – same (II); fig. 29a – *Hamadryas glauconome* (I); fig. 29b – same (II); fig. 30a – *Biblis hyperia* (I); fig. 30b – same (II).

being ranked as separate species. The caryotype showed no numerical difference, hardly surprising in a group as invariable as the Nymphalini, even from genus to genus. However, the size relations are different, *J. evarete* having 6 small chromosomes, and all the other 25 synapsed chromosomal units are somewhat smaller than those of *J. cœnia.*

26. *Anartia fatima* (Fabricius). $N = 31$. Counts were made in 15 nuclei (I) in testes of 2 males [M19-1, M19-3] taken at Ciudad Victoria, 1 August 1959. No secondary divisions were found. A third male taken at the same time showed no suitable nuclei for counts. Six chromosomes are somewhat smaller than the others, which are uniform in size.

27. *Anartia jatrophæ* (Johannson). $N = 31$. Counts were made in 20 nuclei (I) and 15 nuclei (II) in testes of 2 males [M2-1, M2-3] taken at Ciudad Victoria, 1 August 1959. A third male taken at the same time had no suitable divisions, the caryotype shows 27 large and 4 smaller chromosomes. The same number characterizes race *guantanamo* Munroe in Florida, where we found numerous primary and secondary divisions with $n = 31$ in 2 males [F91, F122] taken at the Corkscrew Swamp, 19 April 1960, *leg.* K. MAEKI.

28. *Metamorpha stelenes* (Linné). $N = 31$. Counts were made in 20 nuclei (I) and 15 nuclei (II) in testes of 2 males [M27-1, M27-2] taken at Ciudad Victoria, 2 August 1959. There are 26 chromosomes with large but diverse size and 5 small elements.

29. *Hamadryas glauconome* (Bates). $N = 31$. Counts were made in 16 nuclei (I) and 7 nuclei (II) in testes of 2 males [M57-1, M57-2] taken at El Salto, S. L. P., Mexico, 4 August 1959. There are 25 rather uniformly large and 6 smaller chromosomes.

30. *Biblis hyperia* (Cramer). $N = 28$. Counts were made in 18 nuclei (I) and 13 nuclei (II) in testes of 5 males [M1-1, M1-3, M1-4, M1-5, M1-6] taken at Ciudad Victoria, 1 August 1959. A sixth male taken at the same time showed no meiotic divisions. There are 3 large, 21 medium, and 4 small chromosomes. The caryotype, like the facies of the imago, suggests that the relationship of this genus to its supposed near relatives such as *Hamadryas* should be re-investigated.

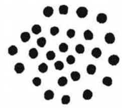
31. *Limenitis weidemeyerii* (Edwards). $N = 30$. Counts were made in 30 nuclei (I) and 30 nuclei (II) in testes of 6 males [2, 125, 127, 158, 176, 177] taken near Gothic, on 16, 27, 28, and 31 July 1959. Dividing cells were numerous even in males which had presumably been flying for many days. There is little diversity of chromosomal size in this species.

32. *Limenitis astyanax* (Fabricius). $N = 30$. Counts were made in 15 nuclei (I) and 20 nuclei (II) in testes of 2 males [385, 386] taken at West Rock, 23 August 1959. There are 2 elements smaller than the other

31a

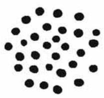
31b

32a



32b

33a



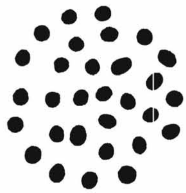
33b

34a

34b

35a

35b



36a

36b

37a

37b

Fig. 31a – *Limenitis weidemeyerii* (I); fig. 31b – same (II); fig. 32a – *L. astyanax* (I); fig. 32b – same (II); fig. 33a – *L. archippus* (I); fig. 33b – same (II); fig. 34a – *Asterocampa celtis* (I); fig. 34b – same (II); fig. 35a – *A. leilia* (I); fig. 35b – same (II); fig. 36a – *Anæa aidea* (I); fig. 36b – same (II); fig. 37a – *Libytheana bachmanii* (I); fig. 37b – same (II).

28, which are fairly uniform in size. A "proserpina"-type, presumed to be a hybrid with *arthemis*, taken at the same time shows no synaptic failure in the 15 primary spermatocyte divisions found.

33. *Limenitis archippus* (Cramer). $N = 30$. Counts were made in 45 nuclei (I) and 35 Nuclei (II) in testes of 4 males [320-1, 320-2, 320-3, 320-4] taken at Woodbridge, New Haven Co., Connecticut, 3 September 1959, and 1 male [409] ex-pupa 6 October 1959, mother from Woodbridge. There are 12 large, 15 medium, and 3 small elements.

34. *Asterocampa celtis* (Boisduval & Leconte). $N = 31$. Counts were made in 30 nuclei (I) and 20 nuclei (II) in testes of 5 males [344, 348, 391-1, 391-2, 391-3] taken on West Rock, 23 August to 11 September 1959. There are 28 large and 3 smaller chromosomes. The condition of the wings indicates that 4 of these males were young; the other was very battered and undoubtedly old, but nevertheless normal meiosis was still taking place in its testes.

35. *Asterocampa leilia* (Edwards). $N = 31$. Counts were made in 15 nuclei (I) and 10 nuclei (II) in testes of 1 male [M17] taken at Ciudad Victoria, 1 August 1959. Apparently 10 of the chromosomes are distinctly larger and 5 smaller than the rest. Dr. W. J. REINTHAL kindly verified the determination.

B. NYMPHALIDÆ – CHARAXIDINÆ:

1. *Anæa aidea* (Guérin). $N = 30$. Counts were made in 20 nuclei (I) and 10 nuclei (II) in testes of 3 males [M39-1, M39-2, M39-3] taken at Ciudad Victoria, 2 August 1959. The chromosomes are all very large and are rather uniform.

C. NYMPHALIDÆ – LIBYTHEINÆ:

1. *Libytheana bachmanii* (Kirtland). $N = 31$. Counts were made in 20 nuclei (I) and 10 nuclei (II) in testes of 7 males [M14-1, M14-2, M14-3, M14-5, M14-6, M14-7, M14-8] taken at Ciudad Victoria, 1 August 1959. The chromosomal size is diverse, with 4 elements being distinctly smaller than the others. MICHENER (1943) suggested that *Libytheana* from northern Mexico is *L. carinenta mexicana* Michener "or may show intergradation between [*L. bachmanii*] *larvata* and *mexicana*". He differentiated *L. carinenta* from *L. bachmanii* on the basis of the shape of the median distal process of the 8th abdominal tergum of the male. In this character our specimens are almost a perfect match with *L. bachmanii* from South Carolina and with MICHENER's drawing of *bachmanii* (his fig. 4).

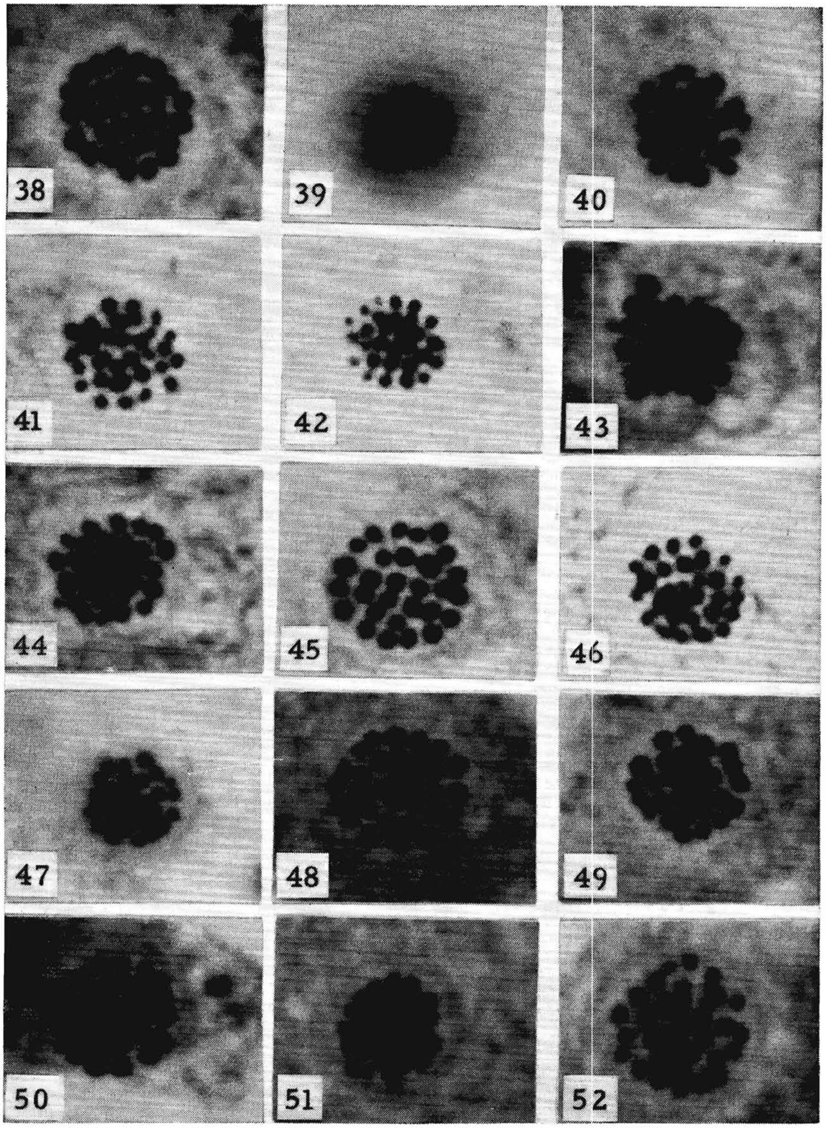


Fig. 38 – *Dryas julia* (I); fig. 39 – *Euptoieta hegesia* (II); fig. 40 – *Speyeria cybele charlottii* (I); fig. 41 – *S. coronis halcyone* (I); fig. 42 – *S. zerene sinope* (I); fig. 43 – *S. callippe meadii* (I); fig. 44 – *S. atlantis*, variant; fig. 45 – *S. atlantis nikias* (I); fig. 46 – *S. hydaspe sakuntala* (I); fig. 47 – *S. mormonia eurynome* (II); fig. 48 – *Boloria titania* (I); fig. 49 – *B. eunomia* (I); fig. 50 – *Chlosyne palla* (I); fig. 51 – *Junonia evarete* (I); fig. 52 – *Anartia fatima* (I).

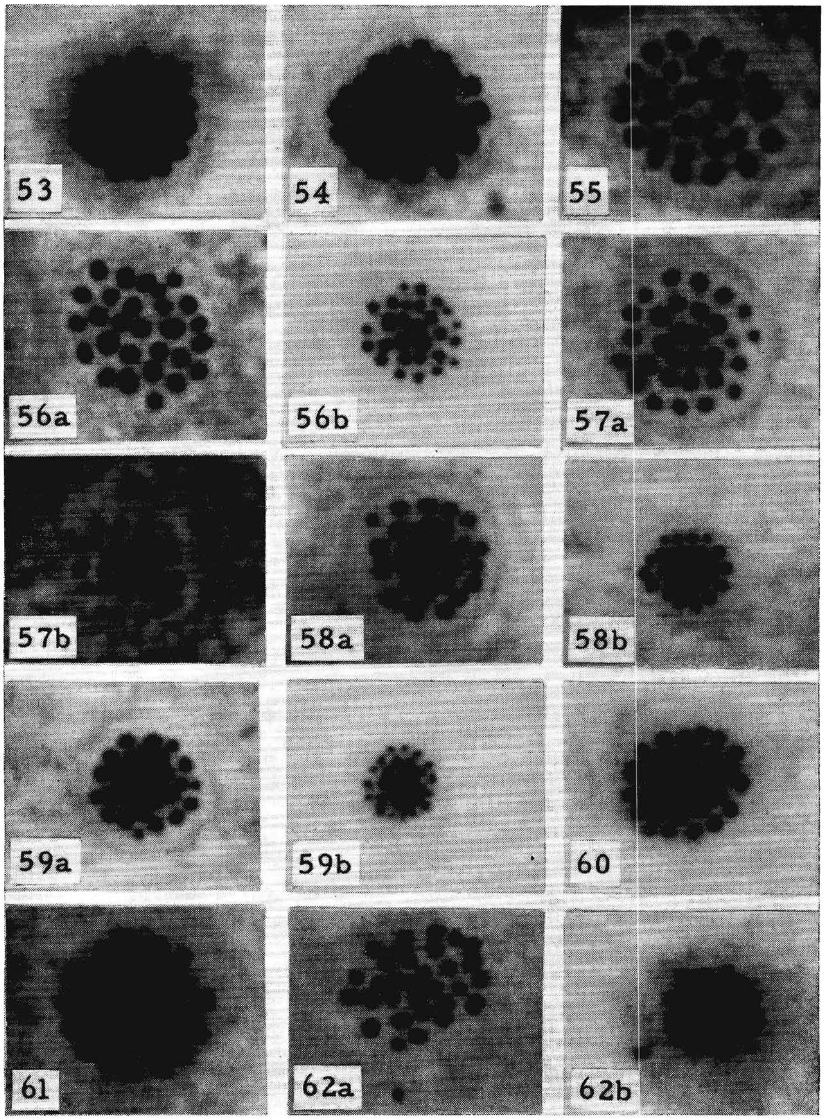


Fig. 53 – *Anartia jatrophæ* (I); fig. 54 – *Metamorpha steneles* (I); fig. 55 – *Hamadryas glauconome* (I); fig. 56a – *Biblis hyperia* (I): fig. 56b – same (II); fig. 57a – *Limenitis weidemeyerii* (I); fig. 57b – same (II); fig. 58a – *L. astyanax* (I); fig. 58b – same (II); fig. 59a – *L. archippus* (I); fig. 59b – same (II); fig. 60 – *Asterocampa leilia* (I); fig. 61 – *Anæa aidea* (I); fig. 62a – *Libytheana bachmanii* (I); fig. 62b – same (II).

Table 6. CHROMOSOME NUMBERS OF THE NYMPHALIDÆ: NYMPHALINÆ, CHARAXIDINÆ, LIBYTHEINÆ.

Species	Number (*n*)	Division	Reference
D. Nymphalinæ:			
DRYAS JULIA (Fabr.)	31	♂ (I, II)	Present paper
AGRAULIS JUNO (Cramer)	31	♂ (I, II)	Present paper
EUPTOIETA HEGESIA (Cram.)	31	♂ (II)	Present paper
Boloria pales (Schiff.)	30	♂ (I, II)	de Lesse, 1953
Boloria aquilonaris (Stichel) (= *arsilache* auctt.)	30	♂ (I, II); 29-30 ♀ (I)	Federley, 1938 de Lesse, 1953
Boloria napæa (Hoffmsg.)	31	♂ (I, II)	de Lesse, 1953
Boloria græca (Staud.)	31	♂ (I, II)	de Lesse, 1960
Boloria eunomia ossianus (Herbst)	28	♀ (I)	Federley, 1938
BOLORIA EUNOMIA CÆLESTIS (Hem.)	28	♂ (I, II)	Present paper
Boloria selene selene (Schiff.)	30	♂ (I, II), ♀ (I)	Federley, 1938
BOLORIA SELENE TOLLANDENSIS (Barnes & Benj.)	30	♂ (I, II)	Present paper
Boloria freija (Thunb.)	31	♂ (I), ♀ (I)	Federley, 1938
Boloria frigga (Thunb.)	31	♀ (I)	Federley, 1938
Boloria thore scandinavica (Rygge)	30	♀ (I)	Federley, 1938
Boloria thore jezoensis (Mats.)	31	♂ (I, II)	Maeki, in press
Boloria euphrosyne (Linné)	31	♂ (I, II), ♀ (I)	Federley, 1938 Lorkovič, 1941
Boloria titania titania (Esper)	31	♂ (I, II)	de Lesse, 1953
BOLORIA TITANIA HELENA (Edw.)	31	♂ (I, II)	Present paper
Argyronome laodice (Pallas)	31	♂ (I)	Maeki, 1953a, b Maeki & Makino, 1953
Argyronome ruslana (Motsch.)	26	♂ (I)	Maeki & Makino, 1953 Maeki, 1953b
Issoria lathonia (Linné)	30	♂ (I, II), ♀ (I)	Federley, 1938
Brenthis ino ino (Rott.)	12-13	♂ (I, II); 13-14 ♀ (I)	Federley, 1938
Brenthis ino tigroides (Fruhs.)	14	♂ (I)	Maeki, 1953a, b Maeki & Makino, 1953
Brenthis daphne rabdia (Butler)	14	♂ (I, II)	Maeki, in press
Brenthis daphne daphne (Schiff.)	13	♂ (I, II)	de Lesse, 1960
Fabriciana niobe (Linné)	29	♂ (I, II); 28-29 ♀ (I)	Federley, 1938 de Lesse, 1960
Fabriciana adippe (Schiff.)	29	♂ (I, II); 28 ♀ (I)	Federley, 1938 Lorkovič, 1941 Maeki, in press
Fabriciana nerippe (Felder)	29	♂ (I, II)	Maeki, in press

[1]Tables 1 (Papilionidæ), 2 (Hesperioidea), 3 (Pieridæ), 4 (Lycænidæ), and 5 (3 subfamilies of Nymphalidæ) are in Parts 1, 2, and 3 of this series of papers (*Journ. lepid. soc.* 13: 199; 14: 51-53, 136-141; 1960-61).

Table 6 – continued.

Mesoacidalia charlotta (Haw.) (= *aglaja*) (3 sspp.)	29	♂ (I, II), ♀ (I)	Federley, 1938 Maeki, 1953a, b Maeki & Makino, 1953 de Lesse, 1960
SPEYERIA CYBELE (Fabr.)	29	♂ (I, II)	Present paper
SPEYERIA APHRODITE (Fabr.)	29	♂ (I, II)	Present paper
SPEYERIA CORONIS (Behr)	30	♂ (I, II)	Present paper
SPEYERIA ZERENE (Bdv.)	29	♂ (I, II)	Present paper
SPEYERIA CALLIPPE (Bdv.)	30	♂ (I, II)	Present paper
SPEYERIA ATLANTIS (Edw.)	29	♂ (I, II)	Present paper
SPEYERIA HYDASPE (Bdv.)	29	♂ (I, II)	Present paper
SPEYERIA MORMONIA (Bdv.)	29	♂ (I, II)	Present paper
Argynnis paphia (Linné)	29	♂ (I, II); 28 ♀ (I)	Federley, 1938 Maeki, 1953a, b Maeki & Makino, 1953 de Lesse, 1960
Argynnis anadyomene (Felder)	37	♂ (I)	Maeki & Makino, 1953 Maeki, 1953b, 1961
Damora pandora (Schiff.)	29	♂ (I)	de Lesse, 1960
Damora sagana (Dbldy.)	31	♂ (I)	Maeki, in press
Argyreus hyperbius (Linné)	31	♂ (I, II)	Maeki, 1953b
Euphydryas iduna (Dalman)	31	♀ (I)	Federley, 1938
Euphydryas maturna (Linné)	31	♂ (I, II), ♀ (I)	Beliajeff, 1930
Euphydryas aurinia (Rott.)	30	♂ (I, II)	Federley, 1938 Lorkovič, 1941
EUPHYDRYAS ANICIA EURYTION (Mead)	31	♂ (I, II)	Present paper
Melitæa cinxia (Linné)	31	♀ (I)	Federley, 1938
Melitæa phœbe "auctt."	31	♂ (I)	de Lesse, 1960
Melitæa diamina (Lang.)	31	♂ (I)	de Lesse, 1960
Melitæa trivia (Schiff.)	31	♂ (I, II)	de Lesse, 1960
Melitæa transcaucasica Turati	29	♂ (I, II)	de Lesse, 1960
Melitæa didyma (Esper)	28	♂ (I, II)	de Lesse, 1960
Melitæa persea (Kollar)	ca. 27-28	♂ (II)	de Lesse, 1960
Melitæa montium Belt.	27	♂ (I, II)	de Lesse, 1960
Mellicta athalia (Rott.)	31	♂ (I, II), ♀ (I)	Federley, 1938 de Lesse, 1960
Mellicta varia (Meyer-Dür)	31	♂ (1)	de Lesse, 1960
CHLOSYNE HARRISII (Scud.)	31	♂ (1)	Present paper
CHLOSYNE PALLA (Edw.)	31	♂ (1)	Present paper
CHLOSYNE DAMŒTAS (Skin.)	31	♂ (I, II)	Present paper

Table 6 — continued.

PHYCIODES THAROS (Dury)	31	♂ (I)	Present paper
PHYCIODES PHAON (Edw.)	31	♂ (I)	Present paper
Cyrestis thyodamas Bdv.	31	♂ (I)	Maeki, 1953b
Araschnia levana (Linné) (2 sspp.)	31	♂ (I, II)	Lorkovič, 1941 Maeki, 1953a, b Maeki & Makino, 1953
Araschnia burejana Bremer	31	♂ (II)	Maeki, 1953a b Maeki & Makino, 1953
Polygonia c-album (Linné) (sev. sspp.)	31	♂ (I, II), ♀ (I)	Kernewitz, 1914, 1915 Beliajeff, 1930 Federley, 1938 Maeki, 1953a, b Maeki & Makino, 1953
Polygonia c-aureum (Linné)	31	♂ (I)	Maeki & Makino, 1953 Maeki, 1953b
Polygonia vau-album (Schiff.)	31	♂ (I)	Maeki, in press
Polygonia egea (Cramer)	31	♂ (I)	de Lesse, 1960
POLYGONIA ZEPHYRUS (Edw.)	31	♂ (I)	Present paper
Vanessa atalanta (Linné)	31	♂ (I, II)	Federley, 1938
Vanessa indica (Herbst)	31	♂ (I, II)	Maeki, 1953a, b Maeki & Makino, 1953
Vanessa cardui (Linné)	31	♂ (I, II)	Lorkovič, 1941
VANESSA VIRGINIENSIS (Dru.)	31	♂ (I, II)	Present paper
Nymphalis antiopa (Linné)	31	♂ (I, II) ♀ (I)	[Stevens, 1906 — error?] Federley, 1938 de Lesse, 1960
Nymphalis xanthomelas (Esper) (2 sspp.)	31	♂ (I)	Lorkovič, 1941 Maeki, 1953a, b Maeki & Makino, 1953
Nymphalis polychloros (Linné) (2 sspp.)	31	♂ (I, II)	Lorkovič, 1941 Maeki, 1953a, b Maeki & Makino, 1953
Nymphalis canace (Linné)	31	♂ (I)	Maeki & Makino, 1953 Maeki, 1953b
Nymphalis io (Linné)	31	♂ (I, II)	Maeki, 1953a b Maeki & Makino, 1953
Nymphalis urticæ (Linné) (2 sspp.)	31	♂ (I, II)	Beliajeff, 1930 Federley, 1938 Maeki, 1953a, b Maeki & Makino, 1953
Precis almana (Linné)	31	♂ (I, II)	Maeki, 1953b
JUNONIA CŒNIA (Hbn.)	31	♂ (I, II)	Present paper
JUNONIA EVARETE (Felder)	31	♂ (I)	Present paper

Table 6 – continued.

ANARTIA FATIMA (Fabr.)	31	♂ (I)	Present paper
ANARTIA JATROPHÆ (Joh.)	31	♂ (I, II)	Present paper
METAMORPHA STELENES (L.)	31	♂ (I, II)	Present paper
HAMADRYAS GLAUCONOME (Bates)	31	♂ (I, II)	Present paper
BIBLIS HYPERIA (Cramer)	28	♂ (I, II)	Present paper
Limenitis populi (Linné) (2 sspp.)	30	♂ (I, II), ♀ (I)	Federley, 1938 Maeki, in press
Limenitis camilla (Linné) (2 sspp.)	30	♂ (I, II)	Beliajeff, 1930 Maeki, 1953a, b Maeki & Makino, 1953
Limenitis glorifica (Fruhs.)	30	♂ (I)	Maeki & Makino, 1953 Maeki, 1953b
Limenitis rivularis (Scop.)	30	♂ (I)	Maeki, in press
Limenitis anonyma (Lew.)	30	♂ (I)	de Lesse, 1960
LIMENITIS WEIDEMEYERII Edw.	30	♂ (I, II)	Present paper
LIMENITIS ASTYANAX (Fabr.)	30	♂ (I, II)	Present paper
LIMENITIS ARCHIPPUS (Cram.)	30	♂ (I, II)	Present paper
Neptis philyra (Mén.)	30	♂ (I)	Maeki, in press
Neptis pryeri (Butler)	30	♂ (I)	Maeki, in press
Neptis aceris (Esper)	30	♂ (I, II)	Maeki, 1953a, b Maeki & Makino, 1953
ASTEROCAMPA CELTIS (Bdv. & Lec.)	31	♂ (I, II)	Present paper
ASTEROCAMPA LEILIA (Edw.)	31	♂ (I, II)	Present paper
Apatura ilia (Linné)	31	♂ (I)	Maeki, 1953a, b Maeki & Makino, 1953
Thaleropis jonia (Eversm.)	31	♂ (I)	de Lesse, 1960
Hestina japonica (Felder)	30	♂ (I)	Maeki, 1953a, b Maeki & Makino, 1953
Sasakia charonda (Hew.)	29	♂ (I, II)	Maeki, 1953a, b Maeki & Makino, 1953
E. Charaxidinæ:			
ANÆA AIDEA (Guérin)	30	♂ (I, II)	Present paper
F. Libytheinæ:			
Libythea celtis (Linné) (2 sspp.)	31	♂ (I, II)	Lorkovič, 1941 Maeki, 1953a, b Maeki & Makino, 1953
LIBYTHEANA BACHMANII (Kirt.)	31	♂ (I, II)	Present paper

Discussion

Table 6 shows the chromosome numbers of the 98 Nymphalinæ, 1 Charaxidinæ, and 2 Libytheinæ for which counts have now been recorded. Of the 36 species described in the present paper, 33 are species and 3 are subspecies new to cytology. All 3 previously reported species are *Boloria*, and the Nearctic races have the same numbers as their Palearctic conspecifics. The classification of the Nymphalinæ is still in an uncertain state, particularly at the generic level and to some extent in the interrelationships of the tribes. For the Argynnini we were influenced in our grouping by recent work of dos Passos and Grey (1945) and Warren (1955), for the Melitæini by Higgins (1955) and Bauer (1961), for *Precis* and *Junonia* by Munroe (1951) and de Lesse (1952), and for all nymphaline groups by Shirozu (1960). As noted above, we regard the libytheines as comfortable members of the broadened family Nymphalidæ. That the charaxidines and acræines deserve the full status of subfamilies seems less likely.

The groups with one distinctive chromosome number are the Nymphalini (all 23 species in 2 genera have $n = 31$), the Limenitini (all 11 species in 2 genera have $n = 30$), the Heliconiini (3 genera, 1 species each, have $n = 31$), and the Libytheinæ (both accepted genera, 1 species each, have $n = 31$). Obviously too few are known in the last two groups for confident generalizing.

A large enough proportion of the bolorians and argynnans is now known cytologically to allow some evaluation of their current systematics in the light of this character. There is a little diversity in number, and few large deviations from the basic 30-31 for the bolorians and 29 for the argynnans. The major chromosomal deviants are also somewhat anomalous in their genitalic morphology. *Boloria eunomia* has been set apart as a monospecific genus or subgenus, *Proclossiana;* so far it is also the only bolorian with $n = 28$. *Brenthis ino* and *daphne* are radically different from other argynnines in chromosome number (13-14); they had been recognized as somewhat isolated genitalically, but perhaps this genus deserves even more distinctive treatment taxonomically. *Argyronome ruslana* and *Argynnis anadyomene* are extremely atypical of argynnines in haploid number, although each has a presumed congener which is cytologically like most of the related genera. Size relations of the chromosomes of these two species may give clues to the evolution of their caryotypes (*e. g., Papilio cresphontes* and *P. thoas*, see Maeki & Remington, 1960a). The caryotypes support Grey's (1958) view that *anadyomene* ($n = 37$) stands well away from *paphia* ($n = 29$). Can it be that the genus *Argyronome* of Warren is also too heterogeneous, with *laodice* ($n = 31$) and *ruslana* ($n = 26$) having such different caryotypes?

Counts are known for a member of each of a majority of the superspecies of the Nearctic genus *Speyeria*. The cytological evidence, being published elsewhere, points to the likelihood that these "species" contain numerous biologically separate semispecies in the sense of LORKOVIC (1955, 1958).

As with various *Papilio, Pieris, Aricia, Agrodiætus,* and *Erebia* (see our first three papers), different chromosome numbers have been reported for geographic populations within supposed "species" of Nymphalinæ. Any of the following pairs may be found to be best treated as two species rather than two subspecies:

Boloria thore	(Finland)	–	$n = 30$ (♀)
	(Japan)	–	$n = 31$ (♂)
Brenthis ino	(Finland)	–	$n = 12\text{-}13$ (♂)
	(Japan)	–	$n = 14$ (♂)
Brenthis daphne	(Italy)	–	$n = 13$ (♂)
	(Japan)	–	$n = 14$ (♂).

The early Finnish counts need to be verified, since FEDERLEY was faced with special problems in oogenesis, but the recent counts for Italian and Japanese *B. daphne* should be considered certain. Each of the other pairs of geographically remote populations show no difference in number: *Boloria eunomia, B. selene, B. titania, Fabriciana adippe, Mesoacidalia charlotta, Argynnis paphia, Araschnia levana, Polygonia c-album, Vanessa cardui, Nymphalis xanthomelas, N. polychloros, N. urticæ, Limenitis populi, L. camilla, Libythea celtis.*

The timing of male meiosis in relation to the seasonal physiology of Lepidoptera is of particular interest to us. Studies on this subject in moths as well as butterflies are being presented elsewhere, but comments are appropriate here on the meiotic timing in the many Nymphalini which hibernate as adults. We have reported chromosome counts for 2 males of *Polygonia zephyrus* whose condition and date indicated with certainty that they had overwintered as adults and were about eleven months old. In most hibernating Nymphalini meiosis apparently takes place before winter. Testes of numerous males of *Nymphalis xanthomelas, N. antiopa, N. io, N. urticæ, N. canace,* and *Polygonia vau-album* fixed in Japan in spring and early summer were full of mature sperm and had no meiosis in progress. It is notable that the only exception in the Japanese hibernators studied was *Polygonia c-album;* like our Colorado *P. zephyrus,* it has post-hibernation meiosis. In 1959 we fixed testes of 5 *N. milberti* collected at Gothic from 19 July to 22 August. Some of these had recently eclosed, and at least one had apparently overwintered as an imago, but none showed any meiosis. We also found no meiosis in testes of a *P. vau-album album* (Bdv. & Lec.) from Connecticut fixed 27 September 1960 nor in testes of a *Vanessa atalanta* from Connecticut fixed 20 September 1960. These were both pre-hibernators. With *Polygonia* it is clear that meiosis occurs extensively, perhaps solely, following hibernation in males which do hibernate. In contrast, meiosis occurs in *Nymphalis* either prior to hibernation or extremely early in spring but not later.

In these four papers we have summarized the chromosome numbers for 359 species of Rhopalocera. Total additional species or probable species listed by DE LESSE (1960) are the following: 13 Hesperiidæ, 9 Pieridæ, 51 Lycænidæ. Thus, the numbers of about 460 species of the butterflies have now been recorded. This is more than triple the number listed at the time of the latest (1956) edition of the Makino *Atlas*. It is likely that soon a majority of the recognized Palearctic and Nearctic species will have been studied. Probably no other large group of animals except *Drosophila* approaches that degree of cytotaxonomic knowledge for this vast region.

SUMMARY

1. The chromosome numbers and some size relations are reported for 34 species of Nymphalinæ, 1 of Charaxidinæ, and 1 of Libytheinæ from Mexico, Colorado, Connecticut, and Florida. Of these, 33 are species new to cytology. All counts are from spermatocyte divisions.

2. The haploid number is consistently 31 in the Nymphalini and Heliconiini, 30 in the Limenitini, and is 31 in the only two Libytheinæ known. The number tends to be 30-31 in the bolorian Arynnini and 29 in the argynnan Argynnini, with a few deviants.

3. The timing of meiosis in Nymphalini which hibernate in the imaginal stage is discussed. *Nymphalis* spp. apparently complete meiosis before or immediately after hibernation, whereas *Polygonia c-album* and *P. zephyrus* have most or all meiosis taking place during the long post-hibernation period.

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HOW TO KNOW THE BUTTERFLIES. By Paul R. and Anne H. Ehrlich. 1961. 262 pp., 525 figs. Publisher: Wm. C. Brown Co., 135 South Locust St., Dubuque, Iowa, U. S. A.; price $2.75 (paper cover, spiral-bound) and $3.25 (cloth-bound).

This, like the fine *Guide* by A. B. KLOTS, is much more than a field manual; it is a good introduction to "knowing" the North American butterflies. The main text is in the form of an identification key, accompanied by excellent drawings by Mrs. EHRLICH of most of the species and by summary statements of the geographic distribution, flight periods, and larval foodplants for each. It is intended only for determination down to species. The Skippers are arbitrarily separated from the "Butterflies" (= Papilionoidea only) and omitted from the volume. A major merit of the book is the 30-page introduction to the practice of lepidopterology. The ingredients of this palatable first course are: techniques of collecting and preparing specimens; making genitalic and other dissections and recognizing the principal structures; and comments on problems of variation, classification, and amateur research.

Butterfly taxonomy has moved so rapidly in recent years and has become so sophisticated in some groups that no one person is qualified to deal authoritatively with all groups, even for North America. Dr. EHRLICH has solved this problem by inducing several of the most active specialists to prepare the sections on their groups. These are: D. L. BAUER, H. K. CLENCH, C. F. DOS PASSOS, J. C. DOWNEY, L. P. GREY, A. B. KLOTS, W. S. MCALPINE, and K. H. WILSON. As always with an array of