Chromosome numbers in 71 Puerto Rican species of leaf beetles (Coleoptera: Chrysomelidae)[1,2]

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ABSTRACT

We summarize, and add to, the current knowledge of the chromosome numbers of 71 species of leaf beetles (Chrysomelidae) from Puerto Rico (41% of the total believed to be reported for the island), including 30 endemic species and subspecies. Meiograms for representative taxa are included.

Key words: Chromosomes, Chrysomelidae (Coleoptera), Puerto Rico, phylogeny

RESUMEN

Numero cromosomico de 71 especies puertorriqueñas de crisomélidos (Coleoptera: Chrysomelidae)

Se resume el, y se añade al, conocimiento de los números cromosómicos de 71 especies de crisomélidos de Puerto Rico (41% del total que se considera informado para la isla), incluyendo 30 especies endémicas. Se incluyen meiogramas de taxones representativos.

INTRODUCTION

As part of our ongoing effort towards the understanding of the biology, phylogeny, and systematics of the Chrysomelidae of the Greater

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Puerto Rico Region, we summarize, and add to, the current knowledge of the chromosome numbers of 71 species of leaf beetles (*Chrysomelidae) from Puerto Rico (41% of the total believed to be reported for the island)*, including 30 endemic species and subspecies (Santiago-Blay and Virkki, unpublished). The present list compiles the chromosome number and meiotic association mode for all Puerto Rican Chrysomelidae cytologically studied up to 1 January 1996. Previous to 1961, no published data existed on cytogentics of Puerto Rican chrysomelids.

The purpose of this list is to establish basic cytogenetic parameters for the Puerto Rican representatives of this large, phylogenetically, cytogenetically, and economically important beetle family. The chromosome number, together with frequency and distribution of chiasmata, gives an idea of the readiness of the species to experiment with the genetic variation concealed in its chromosomes. The recombination index = haploid chromosome number + average chiasma frequency per cell (Darlington, 1939; Rieger and Michaelis, 1958) gives the mean number of chromosome blocks actually segregating from one another at meiosis.

MATERIALS AND METHODS

Diploid (2n) numbers include the sex chromosomes; immediately after the number, the sex chromosomes are identified in brackets. Meiotic pairing is expressed in meioformulae and illustrated in selected meiograms (For definitions and nomenclature, see Virkki et al., 1992). Supernumerary chromosomes are marked with an "s". Although the meioformulae are superior to plain chromosome numbers, for they give information on the pairing relations and sex chromosome systems, they do not provide data on chiasmata. We have used the meiograms to illustrate representative cases. More data can be found in Virkki's papers herein cited. Most beetle chromosomes, even metacentrics, pair with only one chiasma, often distally located. The Puerto Rican *Longitarsus* sp. showing alleged procentric localization of chiasma(ta) is a rare phenomenon.

Notes, from 1 to 43 at the end of the list, represent our field (and sometimes laboratory) observations on food plants. For additional information, Martorell (1976) should be consulted. Notes 44 and following include synonymies, amendments, and other data. The arrangement of subfamilies (endings in -inae), tribes, other suprageneric taxa, and genera in Table 1 follow Seeno and Wilcox (1982).

TABLE 1.— *Taxon, karyoformula, meioformula, and pertinent literature of Puerto Rican chrysomelids.*

Taxon (locality noted when diagnostic)	Karyoformula	Meioformula (male, else noted)	Literature Cited
SUBFAMILY			
CRIOCERINAE			
Lemiini			
Lema dorsalis (Olivier 1891:201)[1]		$8 + Xy_p$	28
L. nigripes (Weise 1885: 145)[1]		$8 + Xy_p$	28
CRYPTOCEPHALINAE			
Pachybrachini			
Pachybrachis mendica Weise 1885: 153		$7 + Xy_r$	28
Cryptocephalini			
Cryptocephalus multiguttatus Suffrian 1885:147		13 + Xy	28
C. tristiculus Weise 1885:147[2]		13 + Xy	28
Diachus nothus (Weise 1885:152) (Cayey, Jájome)[3]	2n = 18♂	$8 + Xy_p$	28
D. nothus (Weise 1885:152) (Villalba, Toro Negro)[4]	2n = 32♂	$15 + Xy_c$	28
CHLAMISINAE			
Aulacochlamys carinaticollis (Lacordaire 1848:858)	2n = 32♂	16 + XY	28
Chlamisus straminea Suffrian 1866:293[4]	2n = 21♂	$9 + X_1X_2Y$	28
LAMPROSOMATINAE			
Oomorphus longifrons (Lacordaire 1848:629[5])		$13 + Xy_p$	28
EUMOLPINAE			
Eumolpini			
Alethaxius near *meliae* Blake 1945:326[4]		$5 + Xy_p$	28
Nodinini			
Metachroma amplicollis Blake 1947:312[6]	2n = 20(X,y)♂	$9+Xy_p$	28
M. fenestratum Blake 1947:312[7]	2n = 18(X,y)♂	$8 + Xy_p$	28
M. leiotrachelus Blake 1970:71[6]		$9 + Xy_p$	28

TABLE 1.—*(Continued) Taxon, karyoformula, meioformula, and pertinent literature of Puerto Rican chrysomelids.*

Taxon (locality noted when diagnostic)	Karyoformula	Meioformula (male, else noted)	Literature Cited
Adoxini			
Chalcosicya crotonis (Fabricius 1792:327)	2n = 16♂	$7 + Xy_p$	28
Myochrous portoricensis Blake 1947:25[8]		$9 + Xy_p$	28
CHRYSOMELINAE			
Leucocera laevicollis Weise 1885:156[9]		$11 + Xy_p$	1, 28
GALERUCINAE			
Galerucini			
Yingaresca varicornis (Weise 1885:157)[10]	2n = 42♂	20 + neoXY[44]	28
Erynephala near *maritima* LeConte 1865:218[11]	2n = 30♂	14 + neoXY	28
Neolochmaea obliterata (Olivier 1808:635)[12]		$12 + Xy_p$[45]	28
Luperini: Diabroticites			
Diabrotica graminea Baly 1886:443[13]		9 + X	15, 28
Acalymma annulatum (Suffrian 1867:307)	2n = 19(X) + 5s♂	9 + X[46]	28
A. innubum (Fabricius 1795:117)[13]		9 + 0 - 2s + X	28
A. bivittatum (Fabricius 1801:455)[13]	2n = 23(X)♂	11 + X	28
Luperini: Cerotomites			
Cerotoma ruficornis Olivier 1791:200[14]	2n = 33(X)♂	16 + X[47]	28
ALTICINAE			
Oedionychini:Disonychina			
Disonycha spilotrachela Blake 1928:96[15-17]	$2n = 30(2X_1, 2X_2)$♀ $2n = 29(X_1, X_2, y)$♂	$13 + X_1y + X_2$	22, 29
D. comma White 1990[18]	$2n = 40(2X_1, 2X_2)$♀ $2n = 39(X_1, X_2, y)$♂	$18 + X_1y + X_2$	29
D. leptolineata Blatchley		$19 + X_1y + X_2$	29
D. eximia Harold 1876:6[19]	$2n = 44(2X_1, 2X_2, 2X_3)$♀ $2n = 42(X_1, X_2, X_3, y)$♂	$19 + X_1y + X_2 + X_3$	22, 29

TABLE 1.—*(Continued) Taxon, karyoformula, meioformula, and pertinent literature of Puerto Rican chrysomelids.*

Taxon (locality noted when diagnostic)	Karyoformula	Meioformula (male, else noted)	Literature Cited
Pseudodisonycha portoricensis Blake 1954:248		16 + 0 - 10s + Xy	27
Oedionychini:Oedionychina			
Omophoita albicollis Fabricius 1797:76[22,23]		10 + X + y	14
O. cyanipennis Fabricius 1796:97[8,20,21]	2n = 22(X,y)♂	10 + X + y	19, 23
Alagoasa bicolor (Linné 1757:593)[20,24]	2n = 22(X,y)♂	10 + XX ♀	14
		10 + X + y ♂	17, 20
Other Alticinae			
Phyllotreta guatemalensis Jacoby 1885:369[25,61]		$15 + Xy_p$	17, 29
Aphthona lamprocyanea Blake 1964:11[26]		11 + X + y[48]	17, 21, 26
Glyptina sp.		$13 + Xy_p$	15
Homoschema obesum Blake 1950:22[27]		$4 + X_1X_2Y$	14
H. nigriventre Blake 1950:18[27]		3 + XY	21, 24, 25
H. fraternum Blake 1950:16[49]		3 + XY	this paper
H. latitarsum Blake 1950:16		2 + neoXY	27
Apraea portoricensis Blake 1947:94[28]		5 + XY[50]	15
Longitarsus oakleyi Blake 1964:16[8]		13 + Xy[51]	27
Longitarsus near *varicornis* Blake 1964:14[29]		14 + Xy	27
Longitarsus sp.[30]		12 + neoXY[48]	27
Phyllotrupes near *acutangula* Chevrolat 1834:68		17 + 0 - 18s + Xy	27
Cyrsylus volkameriae (Fabricius 1792:28)[20,52]	$2n = 30(2X_1, 2X_2)$♀	$13 + X_1X_2y_1y_2$[52]	16, 21
	$2n = 30(X_1, X_2, y_1, y_2)$♂		
Systena basalis Jacquelin-DuVal 1856:129[8]		15 + neoXY	17, 21
Syphraea cubana (Bryant 1924:302)[31,54]	2n = 24(X,y)♂	11 + X + y	17, 21, 26
S. cylindrica (Weise 1885:160)[32,54]	2n = 24(X,y)♂	11 + X + y	26
S. near *maldonadoi* (Blake 1965:109)[43,54]	2n = 24(X,y)♂	11 + X + y	26

TABLE 1.—*(Continued) Taxon, karyoformula, meioformula, and pertinent literature of Puerto Rican chrysomelids.*

Taxon (locality noted when diagnostic)	Karyoformula	Meioformula (male, else noted)	Literature Cited
Macrohaltica jamaicensis (Fabricius 1792:16)[21,55]		$11 + X + y$	17, 21, 26
Lysathia ludoviciana (Fall 1910:157)[21,56]	$2n = 24(X,y)$♂	$11 + X + y$	17, 18, 26
L. occidentalis Suffrian 1868:197[21,34,55]		$11 + X + y$	17, 21, 26
Nesaecrepida rufomarginata Blake 1964:22		$11 + X + y$	26, this paper
Strabala puertoricensis Blake 1953:132[12]		$15 + X_1X_2Y$[53]	21
Epitrix cucumeris (Harris 1851:100)[35]		$12 + Xy_p$	17, 21
E. fasciata Blatchley 1918:56[35]		$12 + Xy_p$	17
Chaetocnema brunnescens Horn 1889:259		$11 + Xy_p$	this paper
Heikertingerella krugi Weise 1885: 163[36]		4 + neoXY	27
Aedmon eugeniae Blake 1943:423[37]		$18 + Xy_p$	27
A. morrisoni Blake 1943:433[37]		$18 + Xy_p$	27
A. oakleyi Blake 1943:422		$18 + Xy_p$	27
HISPINAE			
Sceloenoplini			
Sceloenopla mantecada Sanderson 1967:135[3]	$2n = 18(X,y)$♂	$8 + Xy_p$	30
Chalepini			
Chalepus sanguinicollis Linné 1771:530		$8 + Xy_p$	30
CASSIDINAE			
Stolaini			
Hilarocassis exclamationis (Linné 1767:577)[39,57]		$16 + Xy_p$	30
Chelymorpha multipunctata Olivier 1890:384[40]		$10 + Xy_p$	30
Physonotini			
Physonota jamaicensis (Linné 1758:364)[41,58]		$8 + Xy_p$	30

TABLE 1.—*(Continued) Taxon, karyoformula, meioformula, and pertinent literature of Puerto Rican chrysomelids.*

Taxon (locality noted when diagnostic)	Karyoformula	Meioformula (male, else noted)	Literature Cited
Cassidini			
Agroiconota propinqua (Boheman 1855:289)[40,59]	$2n = 38(X,y)♂$	$18 + Xy_p$	30
Deloyala guttata (Olivier 1790:383)[42]	$2n = 20(X,y)♂$	$9 + Xy_p$	30
Charidotella quadrisignata (Boheman 1855:150)[43,59]		$11 + Xy_p$	30
C. sexpunctata (Fabricius 1781:109)[40,59,60]		$10 + Xy_p$	30

Status Code:

= New for science.

= Known from Puerto Rico only, possibly endemic.

= New to Puerto Rico.

= Notable agricultural pest.

Food plants:

1. *Melicoccus bijugatus* (Sapindaceae). 2 *Dalbergia ecastaphyllum* (Papilionaceae). 3. *Rapanea coriacea* (Myrsinaceae). 4. *Croton rigidus* (Euphorbiaceae). 5. *Comocladia dodonea* (Anacardiaceae). 6. *Bucida buceras* (Combretaceae). 7. *Eugenia stahlii* (Myrtaceae). 8. *Phyla nodiflora* (Verbenaceae). 9. *Malpighia punicifolia* (Malpighiaceae). 10. *Cordia sulcata f. lima* (Boraginaceae). 11. *Cordia stenophylla* (Boraginaceae). 12. *Diodia sarmentosa* (Rubiaceae). 13. *Cucurbita moschata* (Cucurbitaceae). 14. *Desmodium incanum* (Papilionaceae). 15. *Ipomoea imperati (Convolvulaceae)*. 16. *Turnera ulmifolia* (Turneraceae). 17. *Passiflora foetida* (Passifloraceae). 18. *Croton lobatus* (Euphorbiaceae). 19. *Amaranthus* sp. (Amaranthaceae). 20. *Clerodendron aculeatum* (Verbenaceae). 21. *Jussiaea sp* (Onagraceae). 22. *Stachytarpheta jamaicensis* (Verbenaceae). 23. *Heliotropium indicum* (Boraginaceae). 24. *Aegiphila martinicensis* (Verbenaceae). 25. *Cleome spinosa* (Capparaceae). 26. *Tragia volubilis* (Verbenaceae). 27. *Stigmaphyllon tomentosum* (Malpighiaceae). 28. *Tabebuia heterophylla* (Bignoniaceae) and *Bursera simaruba* (Burseraceae). 29. *Heliotropium angiospermum* (Boraginaceae). 30. *Piptocoma antillana* (Asteraceae). 31. *Acalypha puertoricense* and *Acalypha* cultivar (Euphorbiaceae). 32. *Croton astroites* (Euphorbiaceae). 33. *Croton rigidus* (Euphorbiaceae). 34. *Cuphea carthaginensis* (Lythraceae). 35. *Nicotiana tabacum* (Solanaceae). 36. *Inga laurata* (Mimosaceae). 37. *Mecranium amygdalinum* (Melastomataceae). 38. *Ocotea coriacea* (Lauraceae). 39. *Jacquemontia cumenensis* (Convolvulaceae). 40. *Ipomoea* sp. (Convolvulaceae). 41. *Cordia sp* (Boraginaceae). 42. *Ipomoea batata* (Convolvulaceae). 43. *Jacquemontia pentandra* (Convolvulaceae).

TABLE 1.—*(Continued) Taxon, karyoformula, meioformula, and pertinent literature of Puerto Rican chrysomelids.*

Synonymies, amendments, etc.

44. Amended from Petitpierre et al., 1988 (it was 12 + Xy_p). 45. Same, it was included as *Yingaresca*, with 2n = 40; 19 + neoXY. 46. Smith and Virkki (1978) gave 2n = 19♂; 9 + X + 2s for a Canadian sample. 47. Smith (1972) found 16 + X for Canadian material. Different color morphs in Puerto Rico have the same meioformula. Identification not to subspecies. 48. 11 + X + Y in Petitpierre et al., 1988. 49. Identified by Jan Bechyné. 50. With a supernumerary in some cells. See Virkki, 1964. 51. Amended from Smith and Virkki (1978) and Petitpierre et al., 1988 (it was 13 + X and 13 + XY, respectively). 52. *Cyrsylus cyanipennis* (Weise 1885) in other references. 53. Also individuals with 14 + X_1X_2Y. *Strabala ambulans puertoricensis* in Petitpierre et al., 1988. 54. Formerly *Hermaeophaga*. 55. Formerly *Altica*. 56. Formerly *Luperodes antillarum* Blake (Galerucinae). See Virkki, 1979a. 57. Formerly included in *Mesomphalia* and in *Stolas*. 58. Also included in *Eurypepla*. 59. Formerly included in *Metriona*. 60. Known to have numerous synonyms, Borowiec, 1989. 61. As *P. fallaciae* Csiki 1939:64 in some publications.

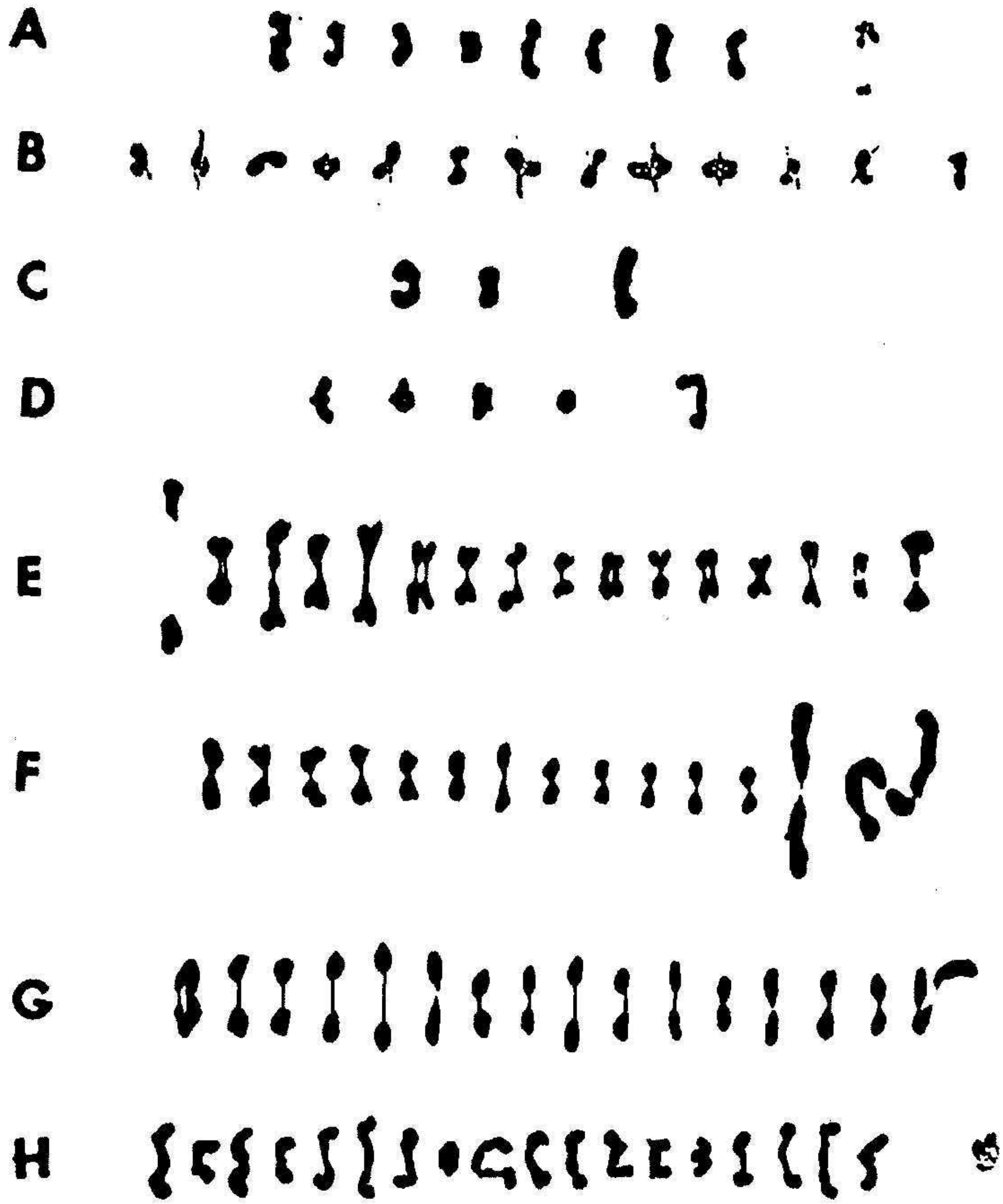

FIGURE 1A TO H. Meiograms of Criocerinae (A) and Alticinae (B to H) showing great variation in chromosome numbers and sex chromosome systems. 1374x.
A.) *Lema nigripes,* 8 + Xy_p. B.) *Longitarsus* sp., 12 + neoXY. C.) *Homoschema latitarsum,* 2 + neoXY. D.) *Heikertingerella krugi,* 4 + neoXY. E.) *Systena basalis,* 15 + neoXY. F.) *Cyrsylus volkameriae,* 13 + $X_1X_2y_1y_2$. The largest autosome pair has a condensation pattern similar to the sex chromosomes. G.) *Strabala puertoricensis,* 18 + X_1X_2y. H.) *Aedmon eugeniae,* 18 + Xy_p.

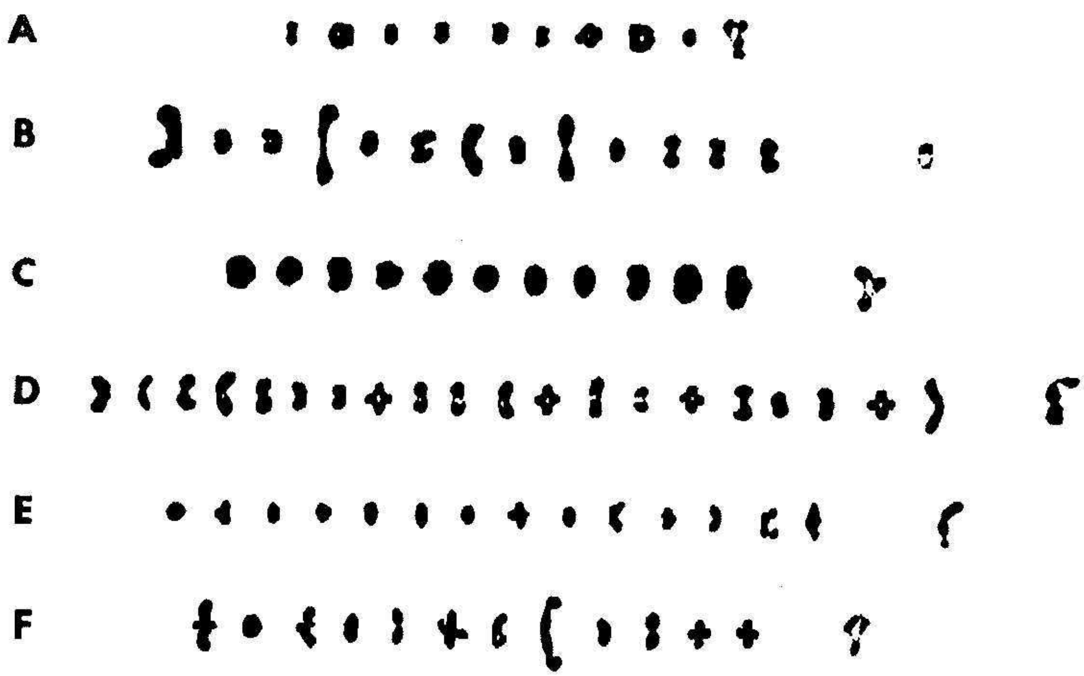

FIGURE 2 A TO F. Meiograms of Chlamisinae (A), Lamprosomatinae (B), Chrysomelinae (C), and Galerucinae (D to F). 1500x.
A.) *Chlamisus straminea*, 9 + X_1X_2Y. B.) *Oomorphus longifrons*, 13 + Xy_p. C.) *Leucocera laevicollis*, 11 + Xy_p. D.) *Yingaresca varicornis*, 20 + neoXY. E.) *Erynephala* nr. *maritima*, 14 + neoXY. F.) *Neolochmaea obliterata*, 12 + Xy_p.

RESULTS AND DISCUSSION

The 71 species and 47 genera included in this list comprise about 41% and 65%, respectively, of the taxa believed to inhabit Puerto Rico (Santiago-Blay and Virkki, unpublished). Thirty of the species listed (about 43%) are endemic, and most of the others are Antillean endemics. Four species appear to be new to science. Those four and three other records are new to Puerto Rico. Eleven species are notorious agricultural pests.

When closely related taxa have similar chromosome number, cytogeneticists have traditionally suggested their possible relatedness *via* chromosomal rearrangements (King, 1993; White, 1978). Those changes in chromosome structure affect meiosis and their effects would be evident in crosses between parentals that differ in the presence of such rearrangements (Sites and Moritz, 1987). The prediction is that the hybrids formed would have a decreased fitness (but see Coyne et al., 1991, 1993 for rare examples and critical discussions on this prediction).

If chromosomal rearrangements are uncommon, how could a major change in chromosomal structure become fixed in a population? The

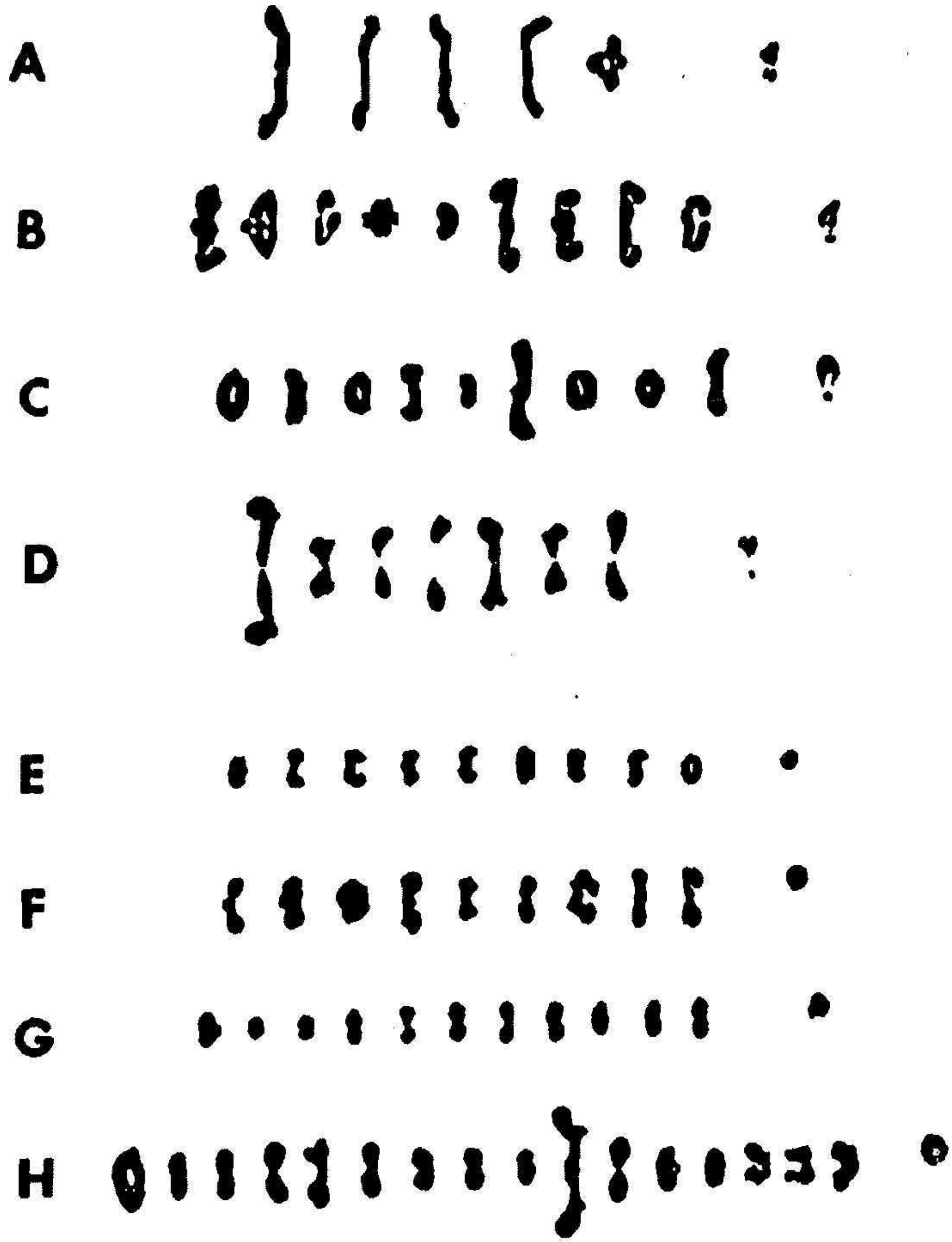

FIGURE 3 A TO H. Meiograms in Eumolpinae (A to D) and diabroticite Galerucinae (E to H). 1410x.
A.) *Alethaxius* nr. *meliae*, 5 + Xy_p. B.) *Metachroma leiotrachelum*, 9 + Xy_p. C.) *Myochrous portoricensis*, 9 + Xy_p. D.) *Chalcosicya crotonis*, 7 + Xy. E.) *Diabrotica graminea*, 9 + X. F.) *Acalymma innubum*, 9 + X. G.) *Acalymma bivittatum*, 11 + X. H.) *Cerotoma ruficornis*, 16 + X.

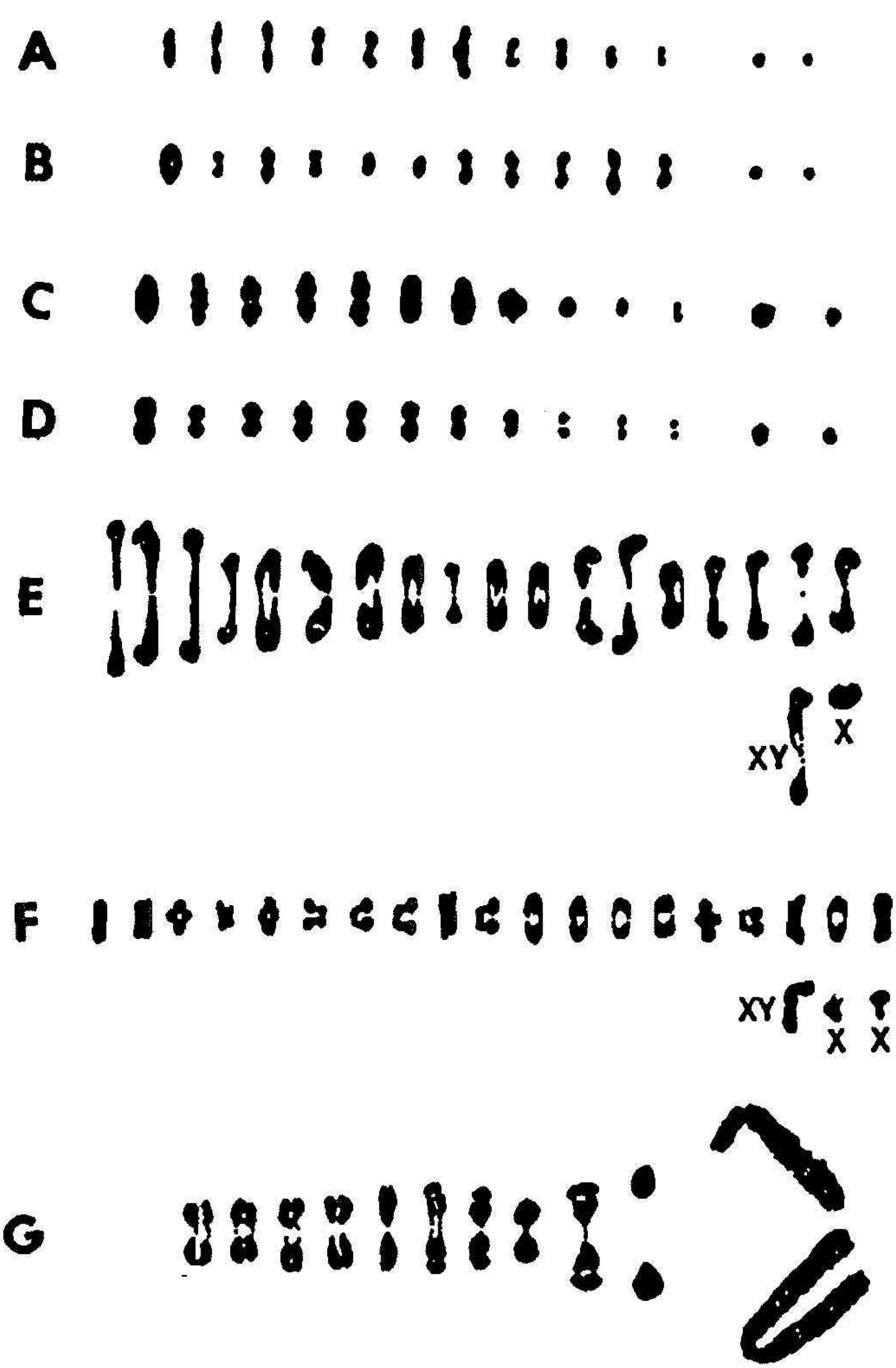

FIGURE 4 A TO G. Meiograms of Alticinae with sex chromosome system having inherent univalents. 1846x.
A.) *Nesaecrepida rufomarginata*, 11 + X + y. B.) *Lysathia occidentalis*, 11 + X + y. C.) *Syphraea cubana*, 11 + X + y. D.) S. *cylindrica*, 11 + X + y. E.) *Disonycha comma*, 18 + $X_1y + X_2$. F.) *D. eximia*, 19 + $X_1y + X_2 + X_3$. G.) *Omophoita albicollis*, 10 + X + y.

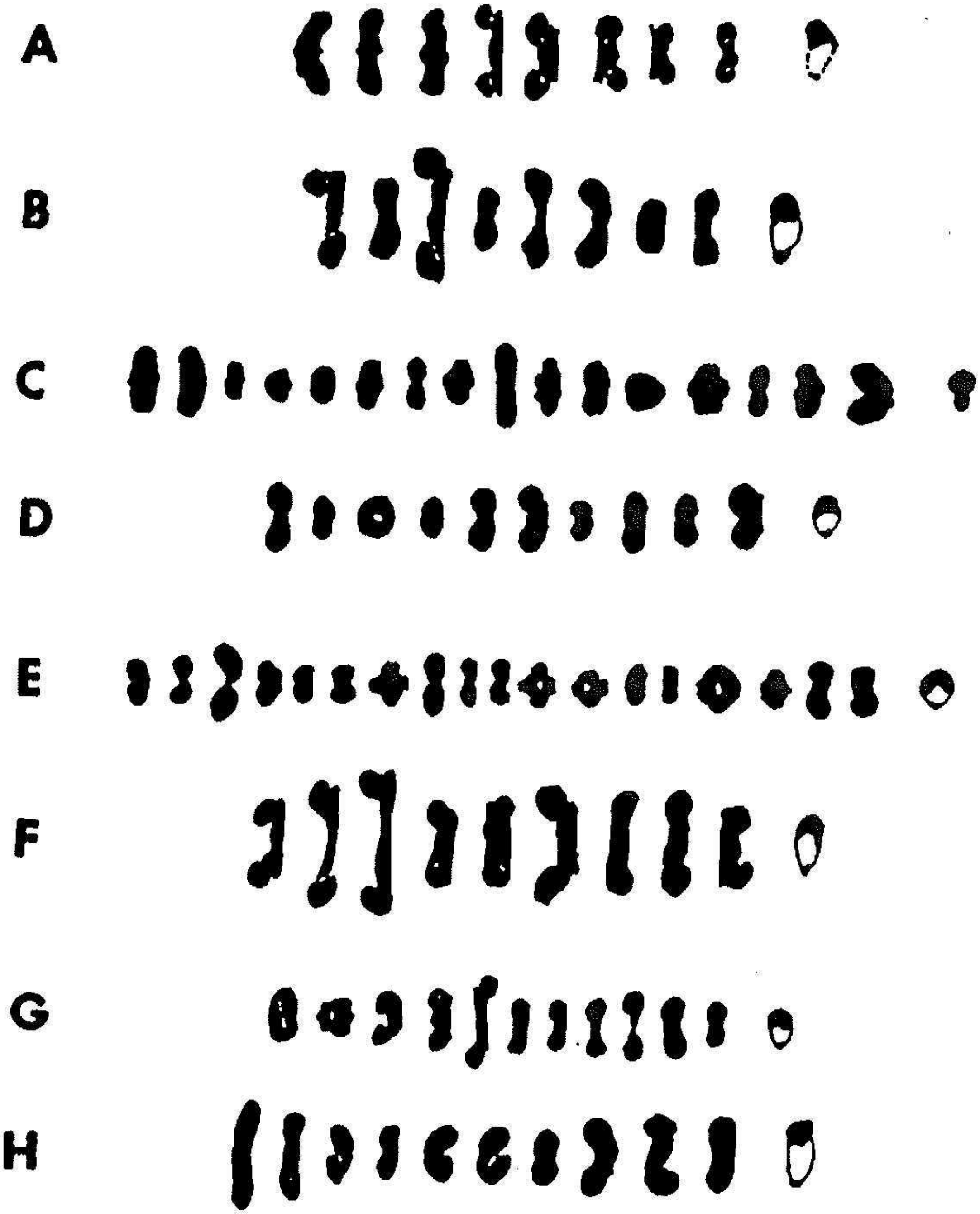

FIGURE 5 A TO H. Meiograms of Hispinae (A and B) and Cassidinae (C to H). 1833x. A.) *Sceloenopla mantecada*, 8 + Xy_p. B.) *Chalepus sanguinicollis*, 8 + Xy_p. C.) *Hilarocassis exclamationis*, 16 + Xy_c. D.) *Chelymorpha multipunctata*, 10 + Xy_p. E.) *Agroiconota propinqua*, 18 + Xy_p. F.) *Deloyala guttata*, 9 + Xy. G.) *Charidotella quadrisignata*, 11 + Xy_p. H.) *C. sexpunctata*, 10 + Xy_p.

random effects in the genetic structure of small populations (genetic drift), directional selection of the non-hybrids, and non-Mendelian mechanisms, such as meiotic drive, have all been postulated (Walsch, 1982). These mechanisms are based on Sewall Wright's metaphor of a fitness landscape in which, in this case, hybrids for chromosomal rearrangements would be less fit than either parental homozygous form, leading to the formation of relatively reproductively isolated populations during episodes of drastic population reduction (Coyne, 1984).

More experimental and theoretical work is needed to better document the role of chromosomal rearrangements in evolution. In the meantime, the best one can do is to continue garnering chromosomal data and suggesting possible hypothetical relationships amongst taxa.

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