

SEX CHROMATIN AND CHROMOSOME NUMBERS IN LEPIDOPTERA¹

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Three classes of sex chromatin (SC) distribution have been encountered in a sample of Canadian Lepidoptera. In 78 of the 103 species examined, females were SC positive and males were SC negative. In another 24 species, females and males were SC negative. Females and males of a single species, *Eucordylea resinosae*, had two equal-sized SC bodies in interphase nuclei. In no species were females found to be SC negative and males SC positive. Usually, presence of SC indicates an $XX\delta:XY\varphi$ sex-determining mechanism, and its absence, $XX\delta:XO\varphi$, but the exceptional occurrence of SC in females and males of a species suggests the need for caution in too universal an application of this interpretation. Chromosome numbers have also been determined for 53 of the 103 species. Male haploid numbers ranged from 11 to 61, but 30 was most frequently encountered.

Au cours d'un inventaire des Lépidoptères canadiens, on a trouvé trois classes de distribution de la chromatine sexuelle (CS). Chez 78 des 103 espèces examinées, les femelles avaient de la CS et les mâles n'en avaient pas. Chez 24 autres espèces, les femelles et les mâles n'en avaient pas. Les femelles et les mâles d'une seule espèce, *Eucordylea resinosae*, avaient deux corps de CS d'égales dimensions dans des noyaux interphasés. Aucune espèce ne présentait la situation suivante où la femelle n'avait pas de CS et le mâle en avait. D'ordinaire, la présence de CS indique un mécanisme de détermination du sexe de type $XX\delta:XY\varphi$, et son absence un mécanisme $XX\delta:XO\varphi$. Cependant, la présence exceptionnelle de CS chez les femelles et les mâles d'une espèce oblige à la prudence quant à l'application universelle de cette proposition. L'auteur détermina également les nombres chromosomiques de 53 des 103 espèces. Le nombre haploïde des chromosomes des mâles variait de 11 à 61, mais un nombre de 30 chromosomes était le plus souvent noté.

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Introduction

The manipulation of forest insect populations by the introduction of genetic or chromosomal lethals or by perturbation of the sex ratio requires prior knowledge of several aspects of genetic constitution: chromosome number, sex-determining mechanisms, and normal timing and course of meiosis. The detailed cytological analysis of lepidopteran chromosomes is complicated by their generally large number and small size. However, their exceptional combination of holokinetic chromosomes and female heterogamety dictates the necessity for such study, for the effects of these characteristics on the success of genetic interference with natural populations are but little understood.

Chromosome numbers of over 1000 species of Lepidoptera have been reported (Robinson, 1971), but most of these have concerned the so-called macrolepidoptera, particularly the butterflies. The microlepidoptera have been but little studied. Chromosome numbers are known for only about 70 species (Suomalainen, 1969a; Robinson, 1971), and most of these are European forms. Modal chromosome numbers for both groups lie in the 29 to 31 range. The standard Lepidopteran karyotype is monotonously uniform, with only slight gradation in size among the chromosomes. In some of the described species, one chromosome pair is markedly larger. Speculation has persisted that this pair in fact may represent the sex chromosomes (White, 1946), i.e., XX in males, XY in females, though the evidence to date on this point is mostly inferential

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(Suomalainen, 1969b). Apart from numerical differences and the possible presence of a larger pair, lepidopteran karyotypes provide little information on taxonomic relationships.

Smith (1945) first demonstrated sex chromatin (SC) in Lepidoptera when he found heteropycnotic bodies in the interphase nuclei of female *Choristoneura fumiferana*. Absence of similar bodies from males, and from female *Malacosoma disstria*, suggested to him the presence of alternative sex-determining mechanisms. Equating the SC with a heteropycnotic Y, he identified SC+ females as XY, and SC- females as XO. Traut and Mosbacher (1968) and Suomalainen (1969b) have since provided evidence supporting this interpretation. Indeed, some XYY females have two SC bodies, as might be expected by analogy with the mammalian situation (Suomalainen, 1969b). At any rate, presence of SC in females allows determination of sex ratios as early as the embryonated egg stage (Clarke *et al.*, 1975).

The importance of many species of Lepidoptera as forest insect pests has stimulated initiation of a survey of chromosome numbers and occurrence of sex chromatin in species occurring in Canada. Results to date have uncovered several experimentally favourable species, and provided further evidence on the relationship of sex chromatin to sex-determining mechanisms.

Materials and Methods

All material was collected and identified by staff of the Forest Insect and Disease Survey, Canadian Forestry Service, Sault Ste. Marie. The order of arrangement to family in Table I follows that suggested by Common (1970). For ease of reference, genera and species are listed alphabetically within families. Except for the intensively sampled Tortricidae, division into subfamilies has been avoided. Following Robinson (1971), it is felt that as desirable as such a division may ultimately prove to be, arrangement in this way might appear more meaningful than it actually is at the present time, particularly in the lesser sampled families.

Males were most active meiotically in the third to fifth instars. Study of meiotic stages in females was limited to diplotene-diakinesis found in the tips of pupal ovaries, as first metaphase was encountered only after tedious searching of squashed mature unfertilized eggs. Mitotic stages were obtained from third to fifth instar males and pupal females pretreated for 4 h with injected 0.02% aqueous colchicine. Gonads were dissected out in 1.12% sodium citrate, fixed in modified Kahle's fluid, squashed on albuminised slides, and stained with an aqueous solution of 0.07% basic fuchsin in 0.03% methyl green. Sex chromatin was scored in nuclei of silk glands dissected out and squashed in 2% acetocarmine. Chromosome number and sex chromatin determinations are based on a minimum of five individuals of each sex in each species. In most cases, sex chromatin scoring was accompanied by gonadal determination of sex.

Results

Sex Chromatin

Occurrence of sex chromatin has been examined in 103 species (74 genera in 18 families in 12 superfamilies) (Table I). All females in the Gracillariidae (1 species in 1 genus = 1:1), Coleophoridae (1:1), Cosmopterygidae (1:1), Pyralidae (5:2), Nymphalidae (2:2), Saturniidae (4:4), Sphingidae (1:1), and Lymantriidae (1:1) are SC+. In the Incurvariidae (1:1) and Lasiocampidae (3:1), females are all SC-. In the Tortricidae (31:21), Yponomeutidae (5:3), Oecophoridae (4:2), Gelechiidae (8:6), Geometridae (14:13), Notodontidae (7:4), Arctiidae (4:2), and Noctuidae (10:8), all females in a species are either SC+ or SC-. Both SC+ and SC- species occur in *Rhyacionia* (Tortricidae), *Argyresthia* (Yponomeutidae), *Exoteleia* (Gelechiidae), *Datana* (Notodontidae), and *Halisidota* (Arctiidae).

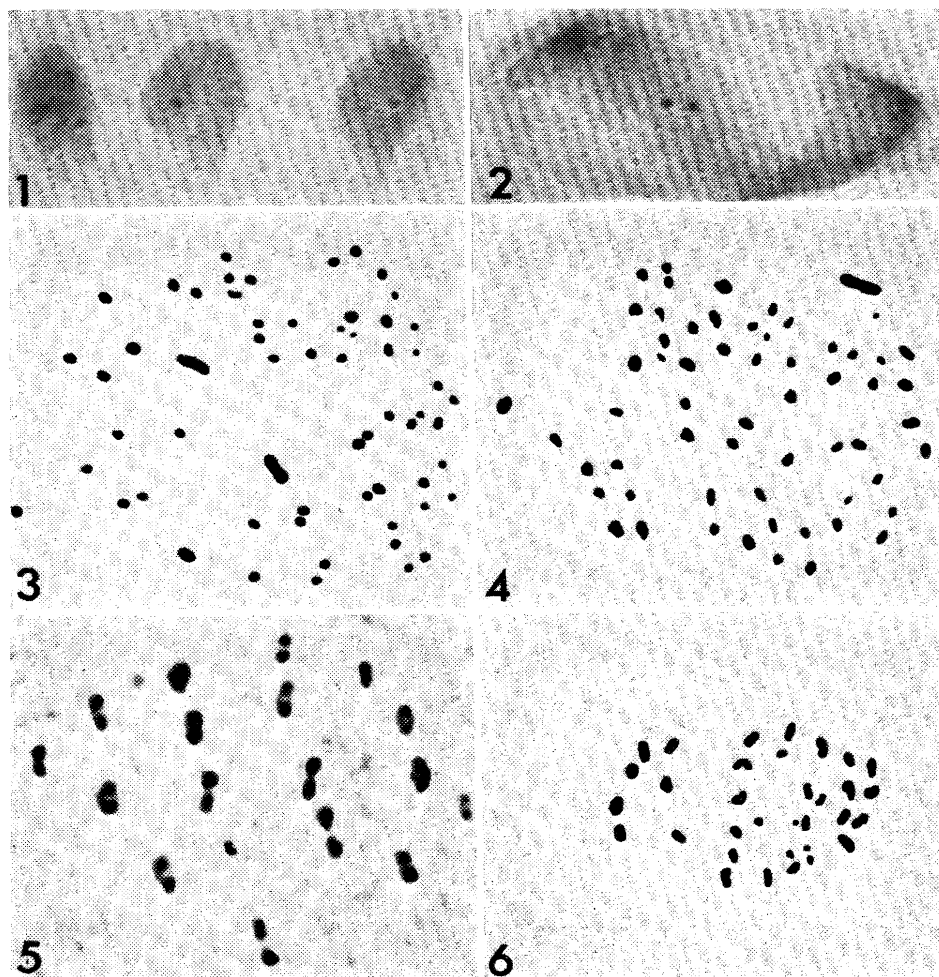
To date, only three classes of SC distribution have been found: species with SC+ females and SC- males; species with SC- females and males; and a single species, *Eucordylea resinosa* (Gelechiidae), with SC+ females and males. In all but the last

species, SC, when present, is a single discrete body (Fig. 1). In *E. resinosae*, two bodies of approximately equal size occur in interphase cells of both males and females (Fig. 2). In no species have males been found to be SC+ and females SC-.

In all, 78 of the 103 species examined were SC+. The apparent deficit of SC- species may in part be attributable to the extensive sampling of the exclusively SC+ Tortricidae.

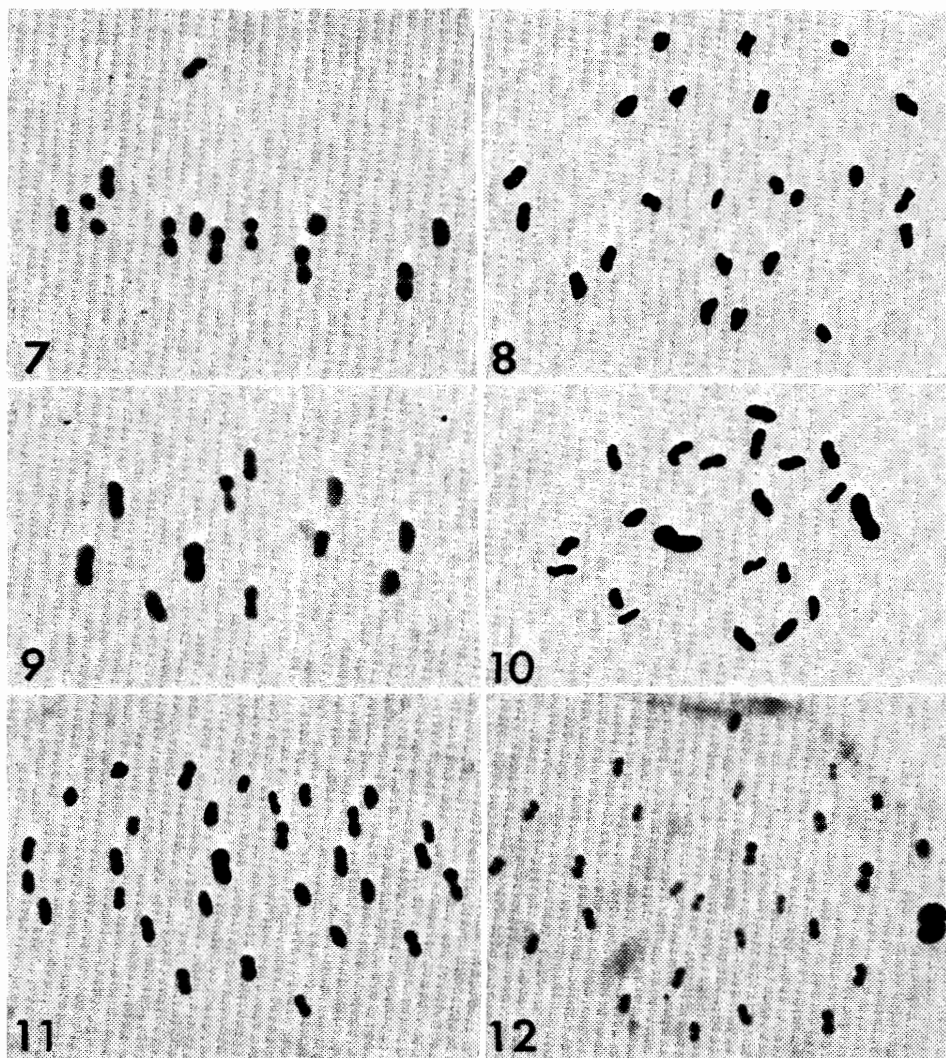
Chromosome Numbers

Chromosome numbers have been determined for 53 species (Table I). Male haploid numbers range from 11 in *Exoteleia pinifoliella* (Gelechiidae) to 61 in *Nepytia*



Figs. 1 and 2. Sex chromatin in silk gland nuclei ($\times ca. 650$). Fig. 1. *Choristoneura fumiferana* ♀, with typical single SC body. Fig. 2. *Eucordylea resinosae* ♂, with two equal-sized SC bodies. Figs. 3 to 6. Chromosome numbers in male and female Lepidoptera ($\times ca. 2000$). Figs. 3, 4 and 6 were drawn with the aid of a camera lucida. Fig. 3. *Choristoneura fumiferana* ♀, $2n=60$, with two larger chromosomes. Fig. 4. *C. biennis* ♀, $2n=60$, with one larger chromosome, presumably the X. The Y cannot be identified with certainty. Fig. 5. *Halisidota maculata* ♂, $n=17$, with only a slight gradation in size of bivalents. Fig. 6. *H. maculata* ♀, $2n=33$.

canosaria (Geometridae). However, the most commonly encountered numbers are, in order, 30 and 31. The intensively sampled families differ somewhat in modal numbers. In the Tortricidae, for example, the Tortricinae are invariably $n=30$, while the Olethreutinae are predominantly $n=28$. No clear modal number emerges for the Gelechiidae, with four species in the 29-31 range and three, all in the same genus, with 11 or 12. Numbers in the Geometridae range from 29 to 61. Clearly, chromosome numbers in some families are more stable than in others.



Figs. 7 to 10. Chromosome numbers in male and female Lepidoptera ($\times ca. 2000$). Figs. 8 and 10 are camera lucida drawings. Fig. 7. *Exoteleia dodecella* δ , $n=12$. Fig. 8. *E. dodecella* δ , $2n=23$. Fig. 9. *E. pinifoliella* δ , $n=11$. Note the larger bivalent. Fig. 10. *E. pinifoliella* δ , $2n=21$. The larger chromosome is present in duplicate, and is therefore an autosome. Figs. 11 and 12. Variation in size of the larger bivalent (centre) to the rest of the complement. Fig. 11. *Acleris variana* δ , $n=30$, illustrating the typical size relationship of the larger bivalent (centre) to the rest of the complement. Fig. 12. *Petrova albicapitana* δ , $n=27$, with one exceptionally large bivalent.

TABLE I
Sex chromatin and chromosome numbers of Lepidoptera species

Family	Host, locality†	SC†		Chromosome number			
		♂	♀	n	2n	n	2n
INCURVARIOIDEA							
INCURVARIIDAE							
<i>Paraclemensia acerifoliella</i> Fitch	A31	---	---				
TORTRICOIDAEA							
Tortricinae							
<i>Acleris variata</i> Fern.	a47, e47	—	+	30*			
<i>Archips cerasivoranus</i> Fitch	P47, 59	—	+	30*			
<i>servidanus</i> Clem.	R27	—	+	30*			
<i>Cenopsis pettitana</i> Rob.	A11, W11	—	+	30*			
<i>Choristoneura biennis</i> Free.	b63	—	+	30*			60**
<i>conflictana</i> Wlk.	L47	—	+	30*			
<i>fumiferana</i> Free.	e47	—	+	30*			60*
<i>occidentalis</i> Free.	i64	—	+	30*			
<i>pinus pinus</i> Free.	f52, 55	—	+	30*			
<i>Croesia semipurpurana</i> Kft.	R47	—	+	30*			
<i>Sparganothis directana</i> Wlk.	P47	---	+	30*			
Olethreutinae							
<i>Anchylopera burgesiana</i> Zell.	R25	—	+				
<i>Badebecia urticana</i> Hbn.	F21	—	—				
<i>Ecdyolopha insititiana</i> Zell.	T27	—	+				
<i>Epinotia corylana</i> McD.	C41	---	+				
<i>cruciana</i> Linn.	U59	---	+				
<i>mononana</i> Kft.	C61	---	+				
<i>solandriana</i> Linn.	F34, 47	---	+	28*			
<i>Episimus argutus</i> Clem.	S3	---	+				
<i>Eucozma gloriola</i> Heinr.	f7	---	+				
<i>Griselda radicans</i> Wlshm.	e58	---	+	29*			
<i>Gypsonoma hainbachiana</i> Kft.	L2	---	+	25*	50*		
<i>Petrova albicapitana</i> Busek	f47, 61	---	+	27*			
<i>Pseudexentera oregonana</i> Wlshm	N22	---	+				
<i>Rhyacionia adana</i> Heinr.	h23	---	—				
<i>buoliana</i> Schiff.	h27	---	+	28*			

TABLE I (contd.)
Sex chromatin and chromosome numbers of Lepidoptera species

Family	Host, locality‡	SC†		Chromosome number			
		♂	♀	n	2n	n	2n
<i>Sciaphila duplex</i> Wlshm.	N52	—	+	28			
<i>Spilonota laticiana</i> Heinr.	d60	—	+				
<i>Taniva abolineana</i> Kft.	e34	—	+				
<i>Zeiraphera canadensis</i> Mut. and Free.	e47	—	+	28*	56*		
<i>fortunana</i> Kft.	e34, 44	—	+	28*			
TINEOIDEA							
GRACILLARIIDAE							
<i>Gracillaria invariabilis</i> Braun	08	—	+				
YPONOMEUTOIDEA							
YPONOMEUTIDAE							
<i>Argyresthia oreasella</i> Clem.	D35	—	+	30			
<i>pygmaeella</i> Hbn.	U10, 33	—	—	43			
<i>thuiella</i> Pack.	j47	—	—	31			
<i>Atreva aurea</i> Fitch	B26	—	—	31			
<i>Zelleria haimbachi</i> Busck	f47	—	+	31			
GELECHIOIDEA							
COLEOPHORIDAE							
<i>Coleophora laricella</i> Hbn.	d30	—	+				
OECOPHORIDAE							
<i>Depressaria groteella</i> Rob.	G27, 34	—	+	29*			
<i>heraciana</i> De Geer	E32	—	+				
<i>Psilocorsis faginella</i> Cham.	H43	—	—				
<i>quercicella</i> Clem.	Q50	—	—		54*		
COSMOPTERYGIDAE							
<i>Chrysoteleta ostryaella</i> Cham.	K31	—	+				
GELECHIIDAE							
<i>Anacamptis innocuella</i> Zell.	M25, 27, 34	—	+	29*			
<i>Euclidylea resinosae</i> Free.	g47	+	+	30*			
<i>Euclidylea</i> sp.	g13	—	+	29*			
<i>Exoteleta dodecella</i> Linn.	h5, 13, 27, 28	—	—	12	24		23
<i>nepheos</i> Free.	g38	—	+	12	24		24
<i>pinifoliella</i> Cham.	f29, 34	—	—	11*	22*		21*
<i>Filatima demissae</i> Kcft.	D4	—	+				
<i>Pulicavaria piceaella</i> Kft.	e13	—	+	30*			

TABLE I (contd.)
Sex chromatin and chromosome numbers of Lepidoptera species

Family	Host, locality‡	SC†		Chromosome number			
		♂	♀	n	2n	n	2n
PYRALOIDEA							
PYRALIDAE							
<i>Phlyctaenia coronata</i> Hufn.	V16	—	+				
<i>Tetralopha aplastella</i> Hlst.	L56, N56	—	+				
<i>asparatella</i> Clem.	A18, 56; N15	—	+	27*	54*		
<i>expansens</i> Wlk.	Q34, R40	—	+		50*		
<i>robustella</i> Zell.	g30	—	+				
PAPILIONOIDEA							
NYMPHALIDAE							
<i>Nymphalis antiopa</i> Linn.	L42, N2, 47	—	+	30*			60*
<i>Polygonia interrogationis</i> Fabr.	X6	—	+	30			
GEOMETROIDEA							
GEOMETRIDAE							
<i>Campaea perlata</i> Gn.	N47	—	—				
<i>Caripeta angustiorata</i> Wlk.	f47	—	+	29	58		
<i>divisata</i> Wlk.	f47	—	+	29	58		
<i>Ectropis crepuscularia</i> Schiff.	N19	—	+				
<i>Erannis tiliaria</i> Harr.	L47	—	+				
<i>Hydria prunivorata</i> Ferg.	O60	—	—				
<i>Lambdina f. fiscellaria</i> Fn.	k52	—	—	38*			
<i>Nepytia canosaria</i> Wlk.	e37, 62	—	+	61*			
<i>Operophera bruceata</i> Hlst.	A47	—	+				
<i>Palaearctia vernata</i> Peck	A47	—	+				
<i>Phigalia titea</i> Cram.	X47	—	+				
<i>Plagadis alcoalaria</i> Fn.	F8	—	—	31			
<i>Protoboarmia porcelaria indicataria</i> Wlk.	f47	—	+	31		31	
<i>Thera juniperata</i> Linn.	c47	—	+				
BOMBYCOIDEA							
LASIOCAMPIDAE							
<i>Malacosoma americanum</i> Fabf.	O23	—	—	31			
<i>californicum pluviale</i> Dyar	O24	—	—	31			
<i>disstria</i> Hbnr.	N49	—	—	31			
SATURNIIDAE							
<i>Actias luna</i> Linn.	A47	—	+				
<i>Anisota senatoria</i> J. E. Smith	Q20, R17	—	—				

TABLE I (contd.)
Sex chromatin and chromosome numbers of Lepidoptera species

Family	Host, locality†	SC†		Chromosome number			
		♂	♀	n	♂	n	♀
<i>Automeris io</i> Fabr.	I46	—	+				
<i>Dryocampa rubicunda</i> Fabr.	A43	—	+	31		31	
SPHINGOIDEA							
SPHINGIDAE							
<i>Lapara bombycoides</i> Wlk.	f16	—	+				
NOTODONTOIDEA							
NOTODONTIDAE							
<i>Datana integerrima</i> G. and R.	J51	—	+				
<i>ministra</i> Dru.	F12, J51, X39	—	—				
<i>perspicua</i> G. and R.	S19	—	+				
<i>Heterocampa guttivitta</i> Wlk.	A8	—	+	29			
<i>Nadata gibbosa</i> J. E. Smith	A9	—	—				
<i>Schizura concinna</i> J. E. Smith	F53, U17	—	+	31			
<i>unicornis</i> J. E. Smith	U47	—	+				
NOCTUOIDEA							
LYMANTRIDAE							
<i>Orgyia leucostigma</i> J. E. Smith	X52	—	+				
ARCTIIDAE							
<i>Halisdota caryae</i> Harr.	J51	—	+				
<i>maculata</i> Harr.	C54, L8	—	—				
<i>tessellaris</i> J. E. Smith	J1	—	+	17		34	33
<i>Hyphantria cunea</i> Dru.	X45, 57	—	+				
NOCTUIDAE							
<i>Acronicta dactylina</i> Grt.	L48	—	+				
<i>lepusculina</i> Gn.	L47	—	+				
<i>Enargia decolor</i> Wlk.	L47	—	+				
<i>Feralia jocosus</i> Gn.	e47, k47	—	—	30		60	
<i>Ipinorpha pleonectusa</i> Grt.	N47	—	—				
<i>Nycteola cinerea</i> N. and D.	L16, 27, 41	—	+				
<i>frigida</i> Wlk.	U14, 27	—	+	28			
<i>Orthosia hibisci</i> Gn.	L47	—	—	25			
<i>Pyrrhia exprimens</i> Wlk.	L47	—	+	28			
<i>Xylomyges dolosa</i> Grt.	N56	—	—	31			

† SC = sex chromatin

*with one larger pair of chromosomes

**with a single larger chromosome

‡Unless otherwise noted, all collections came from Ontario.

Host plant. A, *Acer saccharum*. B, *Ailanthus* sp. C, *Alnus rubra*. D, *Amelanchier* sp. E, *Asclepias syriaca*. F, *Betula papyrifera*. G, *Corylus* sp. H, *Fagus grandifolia*. I, *Juglans chereia*. J, *J. nigra*. K, *Ostrya virginiana*. L, *Populus balsamifera*. M, *P. grandidentata*. N, *P. tremuloides*. O, *Prunus pennsylvanica*. P, *P. virginiana*. Q, *Quercus macrocarpa*. R, *Q. rubra*. S, *Rhus typhina*. T, *Robinia pseudo-acacia*. U, *Salix* sp. V, *Sambucus canadensis*. W, *Tilia canadensis*. X, *Ulmus americana*. a, *Abies balsamea*. b, *A. lasiocarpa*. c, *Juniperus communis*. d, *Larix decidua*. e, *Picea glauca*. f, *Pinus banksiana*. g, *P. resinosa*. h, *P. sylvestris*. i, *Pseudotsuga menziesii*. j, *Thuja occidentalis*. k, *Tsuga canadensis*. Localities. 1, Amherstburg. 2, Atherley. 3, Balsam. 4, Bonnechere. 5, Bowmanville. 6, Caledonia. 7, Capreol. 8, Chapleau. 9, Denbeigh. 10, Dryden. 11, Durham. 12, Foley. 13, Galt. 14, Geraldton. 15, Goderich. 16, Gogama. 17, Grand Bend. 18, Hilton Beach. 19, Huntsville. 20, Ingersoll. 21, Jellicoe. 22, Kapuskasing. 23, Kemptville. 24, Larder Lake. 25, Latchford. 26, Leamington. 27, Lindsay. 28, Listowell. 29, Little Current. 30, Matheson. 31, Merrickville. 32, Nakina. 33, New Liskeard. 34, North Bay. 35, Pagwa River. 36, Pass Lake. 37, Pembroke. 38, Port Burwell. 39, Port Dover. 40, Rainy Lake. 41, Red Lake. 42, Renfrew. 43, Richards Landing. 44, Rosseau Rd. 45, St. Catharines. 46, St. Thomas. 47, Sault Ste. Marie. 48, Searchmont. 49, Sioux Lookout. 50, Sioux Narrows. 51, Strathroy. 52, Sudbury. 53, Sundridge. 54, Swastika. 55, Thessalon. 56, Timmins. 57, Trenton. 58, Tweed. 59, Wawa. 60, Welland. 61, White River. 62, Wiarton. 63, Canal Flats, B. C. 64, Innaha, Ore.

The oogonial chromosome counts obtained in five SC+ species and three SC- species agree with the interpretation that SC identifies the presence of a Y chromosome. In SC+ *Choristoneura fumiferana* (Fig. 3) and *C. biennis* (Tortricidae) (Fig. 4), *Dryocampa rubicunda* (Citheroniidae), and *Nymphalis antiopa* (Nymphalidae), chromosome numbers in females are identical to those in males. In SC- *Halisidota maculata* (Arctiidae), males are $n=17$ (Fig. 5), $2n=34$, while females are $2n=33$ (Fig. 6). Females of two of the three *Exoteleia* species (Gelechiidae) are SC-. *E. dodecella* males are $n=12$ (Fig. 7), $2n=24$, while the SC- females are $2n=23$ (Fig. 8). Males of *E. pinifoliella* are $n=11$ (Fig. 9), $2n=22$; the SC- females are $2n=21$ (Fig. 10). Unfortunately, *E. nepheos*, a SC+ species, has proven difficult to obtain, and preliminary determination of females as $2n=24$ awaits confirmation from better preparations.

Of the 53 species, 24 have karyotypes with only a slight gradation in size of bivalents. In the other 29, one chromosome pair is clearly larger than the rest; in most of these species, the difference is moderate (e.g., *Acleris variana*, Fig. 11), but differentiation reaches an extreme in *Petrova albicapitana* (Fig. 12), as one bivalent is larger by far than the rest.

Evidence from females on the nature of this larger pair is to date equivocal. In the SC-, $2n=21$ females of *Exoteleia pinifoliella* (Fig. 10), the large chromosome is present in duplicate, indicating that in this species it is not the sex pair. *Halisidota maculata* lacks a larger pair in both sexes. Of the SC+ species, a larger chromosome pair is present in duplicate in males and females of *Nymphalis antiopa* and *Choristoneura fumiferana*, (Fig. 3) and in duplicate in males but only once in females in *Choristoneura biennis* (Fig. 4). If the larger chromosome in *C. biennis* proves to be an X, as it certainly appears to be, then the Y chromosome in it and the closely related *C. fumiferana* are of different sizes.

Discussion

In the only other extensive study of SC, Traut and Mosbacher (1968) reported its occurrence in 73 of 82 species. The 78 of 103 SC+ Lepidoptera in the present study is a significantly lower proportion, but the families studied were, for the most part, different from those of Traut and Mosbacher. As frequency of SC can vary greatly among families, the disparity may not be significant. Combined data for both studies indicate that SC occurs in 151 of 185 species, and it is clear that the majority of Lepidoptera are SC+.

Smith (1945) suggested that SC+ females are XY, and SC-, XO. Of the four species studied chromosomally by Traut and Mosbacher (1968), SC+ females in three had chromosome numbers identical to those in males, while the SC- females in the fourth had one less chromosome. Suomalainen (1969b) found that in three species with cytologically demonstrable XYY females, somatic cells contained two SC bodies approximately proportional in size to the Ys. In the present study, all SC+ females examined cytologically are XY, and the three SC-, apparently XO. All of these results suggest that SC indicates the presence of an XY sex-determining mechanism. However, there are a number of exceptions. *Bactra furfurana* females, though of XYY constitution, have only a single SC body (Suomalainen, 1969b): the second Y is apparently isopycnotic. Traut and Mosbacher (1968) reported three species with SC+ females and males. On the basis of size and number of the SC, two of these cases they attributed to heteropycnosis of an autosome and the Y. Cytological confirmation of their interpretation was lacking.

In *Eucordylea resinosa*, males and females have two SC bodies of approximately equal size. There is no indication from the $n=30$ males of the possible origin of these

bodies, and in the absence of chromosome counts from females, the nature of this discrepancy must remain speculative. However, it is possible that in addition to normal heteropycnosis in *Y*-containing females, alternative forms may exist: e.g., differential degrees of pycnosity of the *Y*, as in Suomalainen's (1969b) *XY**Y* females, pycnosity of supernumerary chromosomes or all or part of some autosomes, or variants of sex-determining mechanisms, analogous to those described in mammalian systems. Any firm conclusion on these points must await intensive investigation of the variant species involved.

The 1000 or so described lepidopteran chromosome numbers exhibit a clear mode of 29 to 31 (Robinson, 1971), though lower or higher numbers may form ancillary peaks. Thirty-one is often considered to be ancestral, for not only is it the most frequent, but it occurs in most of the families examined to date. Changes in chromosome number are thus attributed to fragmentation or fusion (White, 1973), processes made cytologically acceptable by the holokinetic nature of Lepidoptera chromosomes. Bauer (1943) and White (1946) have suggested that the larger pair of chromosomes frequently encountered in species with high, presumably derived, chromosome numbers may represent the sex chromosomes. In essence, members of the sex pair are exempt from the capacity for numerical increase endowed by holokinetic organisation, for their fragmentation would incur an intolerable selective burden. Of the high chromosome-numbered species encountered in the present study, a larger pair is found in the geometrids *Nepytia canosaria* ($n=61$) and *Lambdina f. fiscellaria* ($n=38$), but not in the yponomeutid *Argyresthia thuiella* ($n=43$). In neither of these families is a larger pair present in the typical, and presumably ancestral, 29 to 31 karyotype, a fact consistent with the large sex chromosome hypothesis. However, of the lower numbered taxa studied, it is clear from Table I that the Tortricidae, Oecophoridae, Gelechiidae, and Pyralidae are characterised by a similar larger pair. Its frequent concurrence with lower chromosome numbers, as in the tortricid subfamily Olethreutinae, suggests that in many species the larger pair may merely represent an autosomal fusion product.

In the tortricid *Choristoneura biennis*, the larger chromosome is present only once in females, indicating that in this species at least it is part of the sex-determining mechanism. In the gelechiid *Exoteleia pinifoliella*, the larger chromosome is an autosome, being present in duplicate in males and females of this *XX♂*, *XO♀* species. In this case, it presumably is an autosomal fusion product, reflective of the extensive reduction in number by fusion characteristic of this genus. Clearly, any generalisation on the sex chromosome nature of the larger pair must await further analysis of oogonial chromosomes in a more extensive series of species. Successful identification of the sex pair rests on a difference in size between *X* and *Y*, a condition that does not apply in the other three *XX♂*:*XY♀* species examined.

From the cytological data on Lepidoptera accumulated to date, it is clear that a firm understanding of taxonomic interrelationships and chromosome evolution will have to be based on more than a simple cataloguing of male haploid chromosome numbers (Robinson, 1971). The occurrence of SC in the majority of females is of great utility in identifying sex, but investigation of the exceptional classes will undoubtedly help to identify the exact mechanisms involved. An unresolved problem is the nature of the large chromosome pair, and its systematic relationship, if any, to the sex determining mechanism. Hopefully, improved cytological techniques will soon expand our knowledge in this area.

References

- Bauer, H. 1943. Chromosomenforschung. Fortschr. Zool. 7: 256-287.
 Clarke, C., Sheppard, P. M. and Scali, V. 1975. All-female broods in the butterfly *Hypolimnas bolina* (L.). Proc. R. Soc. Lond. Ser. B, 189: 29-37.

- Common, I. F. B. 1970. *Lepidoptera*. In *Insects of Australia*. Edited by D. F. Waterhouse. Melbourne Univ. Press, Victoria. pp. 765-866.
- Robinson, R. 1971. *Lepidoptera genetics*. Pergamon Press, Toronto.
- Smith, S. G. 1945. The diagnosis of sex by means of heteropycnosis. *Sci. Agric.* **25**: 566-571.
- Suomalainen, E. 1969a. Chromosome evolution in the *Lepidoptera*. In *Chromosomes today*. Edited by C. D. Darlington and K. R. Lewis. Oliver and Boyd, Edinburgh, **2**: 132-138.
- Suomalainen, E. 1969b. On the sex chromosome trivalent in some *Lepidoptera* females. *Chromosoma*, **28**: 293-308.
- Traut, W. and Mosbacher, G. C. 1968. Geschlechtschromatin bei *Lepidopteren*. *Chromosoma*, **25**: 343-356.
- White, M. J. D. 1946. The evidence against polyploidy in sexually reproducing animals. *Am. Nat.* **80**: 610-619.
- White, M. J. D. 1973. *Animal cytology and evolution*. 3rd ed. William Clowes, London.

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