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Chromosomes *in* Evolution *of* Eukaryotic Groups

Volume I

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CRC PRESS

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CRC Press, Inc.
Boca Raton, Florida

Library of Congress Cataloging in Publication Data

Main entry under title:

Chromosomes in evolution of eukaryotic groups.

Bibliography: p.
Includes index.
1. Chromosomes—Evolution. 2. Eukaryotic cells—Evolution. 3. Evolution. I. Sharma, Arun Kumar, 1923- II. Sharma, Archana Mookerjea.
QH371.C5 1983 574.87'322 82-9449
ISBN 0-8493-6496-5 (v. 1) AACR2
ISBN 0-8493-6497-3 (v. 2)

Direct all inquiries to CRC Press, Inc., 2000 Corporate Blvd., N.W., Boca Raton, Florida, 33431.

International Standard Book Number 0-8493-6496-5 (Volume I)
International Standard Book Number 0-8493-6497-3 (Volume II)

Library of Congress Card Number 82-9449
Printed in the United States

FOREWORD

Chromosomes of higher organisms exhibit myriads of forms of wide diversity, but their mechanism of origin is still a controversial issue. Their prokaryotic ancestry, so far considered as undisputed, has run into bad weather, due to the discovery of intervening sequences associated with the property of splicing. This theory, envisaging a gradual evolution of complexity in the chromosome from the genophore, is facing replacement by the concept of independent origin of eukaryotic chromosomes parallel to that of the prokaryota.

The chromosomes of higher organisms have undergone diverse modifications both during and after evolution. Several structural features are indeed of phylogenetic and evolutionary significance. At one end of the broad spectrum is the peculiar chromosome of the Dinophyceae with very little histone and absence of functional differentiation of segments. The other extreme is represented by the complex chromosome structure of primates, having reverse-banded segments associated with even special genetic attributes.

Structural features of chromosomes with high phylogenetic potential include, among others, the centromere — diffuse, polycentric, or localized; number and nature of nucleolar constrictions; sex chromosomes with special reference to their multiple mechanisms; early and late replication, heterochromatin, repeated DNA and banding pattern. The nature and position of repeats in introns and even exons, as brought out lately, may all reveal facts of fundamental significance to a evolutionist.

Aspects of chromosome behavior often stressed in the study of evolution are heteroploidy, fragmentation, and translocation. The association of such factors with the evolution of species is undeniable. However, all three mechanisms, excepting the relative infrequency of polyploids in animal systems, are widespread in eukaryota, though not restricted to any particular level of taxonomic hierarchy. In fact, in plant systems, such changes occur with equal prominence within and between species, as well as between genera and families. As such, their universal incidence at all levels of taxonomic hierarchy disqualifies them for consideration as specific parameters of phylogenetic significance. This understanding is of supreme importance in the application of chromosome science to the study of evolution.

The amount of data on the importance of chromosome structural analysis in the study of evolution is indeed enormous. The analysis of such a compendium of information is a task of tremendous magnitude. This exercise is also complicated as the paths of evolution are divergent. A definite pattern of chromosome evolution in the eukaryotic system is yet to be established, even in structural features of chromosomes of established phylogenetic significance. As a result it is difficult to draw a single undisputed phylogenetic tree for a plant or animal system as a whole, based solely on chromosomal characteristics.

It was initially desired to present the pathways of evolution of chromosomes in different groups of eukaryota according to their sequence in an established progression of complexity. Such a desire, however pious it may be, could not be fulfilled due to various reasons beyond our control for which we offer our apologies in advance. Limitations of space and time also did not permit a discussion of all the groups which may have to be taken up later in detail.

THE EDITORS

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Professor Sharma has been the General President of the Indian Science Congress Association (1980), Vice-President of the Indian National Science Academy, Chairman of the Indian National Committee of IUBS and Co-Chairman, Global Seminar on Role of Scientific Societies (AAAS/INSA/ISCA). He has been a member of the councils of all three Academies of India and President of several societies, including the Indian Botanical Society, Indian Society of Cell Biology, Genetic Association of India, Society of Cytologists and Geneticists, and others. His numerous Awards include the Shanti Swarup Bhatnagar Award of the Council of Scientific and Industrial Research, the J. C. Bose Award of the University Grants Commission, the Silver Jubilee Medal of the Indian National Science Academy, the Birbal Sahni Medal of the Indian Botanical Society, and the Jawaharlal Nehru Fellowship.

He has been visiting lecturer to different centers of the world and led the Indian delegation several times to international conferences including the International Genetics Congress, the Hague (1963); the International Botanical Congress, Leningrad (1975); the International Cell Biology Congress, Berlin (1980); and the IUBS General Assembly, Bangalore (1975), and Ottawa (1982). He is the founding Editor of the international journal, *The Nucleus,* and member of the editorial board of several journals. He is co-author, with Archana Sharma of *Chromosome Techniques—Theory and Practice,* a standard reference and textbook.

Archana Sharma, Ph.D., D.Sc., F.N.A., F.A.Sc., F.N.A.Sc., is Professor of Genetics and Head of the Department of Botany, University of Calcutta (1980 to 1982). She obtained her M.Sc. (1951), Ph.D. (1955), and D.Sc. (1960) degrees from the University of Calcutta and specialized in cytogenetics and human genetics. She has made outstanding contributions to cytotaxonomy, the cause of polyteny in differentiated nuclei, and the development of new techniques for the study of chromosome structure. Her group is actively engaged in the study of chromosomal and genetic polymorphisms in normal and pathological human populations, differentiating patterns in the human fibroblast, and genetic polymorphisms in relation to environmental mutagensis and genetic diseases. Other significant research includes studies of the effect of metallic pollutants on genetic systems, both antagonistic and synergistic. She has more than 150 papers and several books to her credit.

Professor Sharma is a Fellow of all three Academies of India, member of the council of the Indian National Science Academy, member of the Science and Engineering Research Council of the Government of India, and General Secretary of the Indian Sci-

ence Congress Association, with which she has been involved for nearly two decades. As official delegate of the Government of India, she has participated in several international conferences, including the IUBS General Assembly Session at Helsinki, and the International Cell Biology Congress at Berlin, and has been the Visiting Scientist in the U.S.S.R. under the Government of India exchange program and a member of the delegation from the Academy to the People's Republic of China. She is the recipient of the Shanti Swarup Bhatnagar Award of the Council of Scientific and Industrial Research (1978) and the J. C. Bose Award of the University Grants Commission, and National Lecturer, University Grants Commission. She is the Editor of *The Nucleus,* and a member of the Editorial Board of a number of other journals.

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Volume I

Chapter 1

THE ROLE OF CHROMOSOME CHANGE IN THE EVOLUTION OF ORTHOPTEROID INSECTS

Bernard John

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I. INTRODUCTION

The chromosome changes that occur in the cell lineages of all eukaryotes as a mutational undercurrent are of three different kinds:

1. Structural mutations leading to either intra (inversion) or inter (translocation) chromosome rearrangements
2. Numerical mutations leading to either aneuploid or polyploid changes in members of the regular chromosome complement
3. Changes in the content of heterochromatin involving either the addition of supernumerary segments to normal members of the chromosome complement or else the addition of novel supernumerary chromosomes

The contribution which the chromosomes of orthopteroids have made to the evolution of the group can, therefore, only be gauged from an examination of the chromosome variation present within and between populations of extant species and kinds of differences demonstrated by such an examination.

These differences are of three kinds:

1. Intrapopulation polymorphisms in which distinct karyomorphs differing in respect of the structure, number, or heterochromatin content of their chromosomes coexist within individual populations of a given species.
2. Interpopulation polytypisms in which fixed karyomorphs are present within individual populations of a given species but where different populations differ in respect of the nature of these fixed differences. Most commonly, one or more forms of chromosome change present in a homozygous state in one population, or one series of populations, are absent from others in different geographical areas. In some such cases restricted polymorphic populations are sometimes present in hybrid zones of geographical overlap. The one unusual form of polytypism is that where a particular category of chromosome change reaches fixation as a permanent heterozygote in one sex but not the other. Here the fixed differences that obtain between different populations are concerned only with the form of permanent heterozygosity present in one of the sexes.
3. Interspecies differences in which closely related species differ in respect of chromosome structure, chromosome number, and/or heterochromatin content. Here, too, one or more chromosome changes present in a homozygous state in one taxon is absent in the other.

Before embarking on an in-depth study of each of these three categories, it is necessary to define the range of organisms which the term orthopteroid encompasses (Table 1). The group includes five orders of insects, all of which are well known under the common names of roaches, mantids, termites, stick insects, crickets, and grasshoppers. In presenting the chromosome differences which occur within and between populations and species of these orders, I will concentrate on the relatively few well-worked examples rather than attempt to mention the very many more cases which have been noted but not analyzed in detail. An interested reader will find them well summarized in the recent reviews of White[1] and Hewitt.[2]

II. CHROMOSOME POLYMORPHISMS

In orthopteroid insects two categories of chromosome mutation, in particular, have been involved in the development of polymorphic populations:

Table 1
A CLASSIFICATION OF THE GENERA OF ORTHOPTEROID INSECTS REFERRED TO IN THIS ARTICLE

SUPERORDER ORTHOPTEROIDEA

Order 1 — Blattodea	
Family 1 — Blattidae	
Subfamily Blattinae	*Periplaneta*
Family 2 — Blattellidae	
Subfamily Blatellinae	*Blatella*
Family 3 — Blaberidae	
Subfamily 1 — Blaberinae	*Blaberus*
Subfamily 2 — Pycnoscelinae	*Pycnoscelus*
Order 2 — Mantodea	
Family 1 — Amorphoscelidae	*Amorphoscelus, Cliomantis, Glabromantis*
Family 2 — Eremiaphilidae	*Humbertiella*
Family 3 — Hymenopodidae	*Harpagomantis*
Family 4 — Mantidae	
Subfamily 1 — Amelinae	*Holaptilon*
Subfamily 2 — Caliridinae	*Leptomantis*
Subfamily 3 — Iridiopteryginae	*Bolbe, Halwania, Ima, Kongobatha*
Subfamily 4 — Mantinae	*Callimantis*
Subfamily 5 — Thespinae	*Promiopteryx, Pseudomiopteryx*
Subfamily 6 — Photininae	*Brunneria*
Order 3 — Isoptera	
Family 1 — Kalotermitidae	*Incisitermes, Kalotermes*
Family 2 — Rhinotermitidae	*Reticulitermes*
Family 3 — Termitidae	
Subfamily 1 — Apicotermitinae	*Acidnotermes, Microcerotermes*
Subfamily 2 — Termitinae	*Cubitermes, Crenetermes, Noditermes, Ophiotermes, Pericapritermes, Procubitermes, Thoracotermes, Tuberculitermes*
Subfamily 3 — Macrotermitinae	*Macrotermes, Odontotermes, Protermes, Pseudocanthotermes*
Subfamily 4 — Nasulitermitinae	*Nasutitermes*
Order 4 — Phasmatodea	
Family 1 — Phylliidae	
Subfamily Bacillinae	*Bacillus, Clitumnus, Clonopsis, Epibacillus, Leptynia*
Family 2 — Phasmidae	
Subfamily 1 — Lonchodinae	*Carausius*
Subfamily 2 — Necrosciinae	*Parasipyloidea*
Subfamily 3 — Phasminae	*Baculum, Ctenomorpha, Phobaeticus*
Subfamily 4 — Podocanthinae	*Didymuria, Extatosoma*
Order 5 — Orthoptera	
Suborder 1 — Ensifera	
Superfamily 1 — Gryllodea	
Family 1 — Gryllidae	
Subfamily 1 — Gryllinae	*Scapsipedus, Teleogryllus*
Subfamily 2 — Nemobiinae	*Allonemobius, Eunemobius, Neonemobius, Nemobius*
Subfamily 3 — Trigonidiinae	*Anaxipha*
Family 2 — Gryllotalpidae	*Gryllotalpa*
Superfamily 2 — Tettigoniodea	
Family 1 — Tettigoniidae	
Subfamily 1 — Meconematinae	*Xiphidiopsis*

Table 1 (continued)
A CLASSIFICATION OF THE GENERA OF ORTHOPTEROID INSECTS REFERRED TO IN THIS ARTICLE

Subfamily 2 — Phaneropterinae	*Odontura, Poecilimon*
Subfamily 3 — Saginae	*Saga*
Subfamily 4 — Tettigoniinae	*Decticus, Metrioptera* (and see Table 53)
Suborder 2 — Caelifera	
Superfamily 1 — Acridoidea	
Family 1 — Acrididae	
Subfamily 1 — Acridinae	*Acrida, Austroicetes, Caledia, Chortoicetes, Cryptobothrus*
Subfamily 2 — Calliptaminae	*Calliptamus*
Subfamily 3 — Catantopinae	*Buforania, Cuparessa, Eurenephilus, Gonista, Leiotettix, Macrotona, Peakesia, Percassa, Pezotettix, Phaulacridium, Tolgadia*
Subfamily 4 — Cyrtacanthacridinae	*Patanga, Schistocerca*
Subfamily 5 — Eyprepocnemidinae	*Eyprepocnemis, Heteracris*
Subfamily 6 — Gomophocerinae	*Acyptera, Bootettix, Chloealtis, Chorthippus, Chrysochroan, Euthystira, Myrmeleotettix, Neopodismopsis, Omocestus, Stauroderus, Stenobothrus, Stethophyma*
Subfamily 7 — Melanoplinae	*Boonacris, Dichroplus, Melanoplus, Micropodisma, Miramella, Oedaleonotus, Podisma*
Subfamily 8 — Oedipodinae	*Acrotylus, Aerochoreutes, Camnulla, Chimerocephala, Circotettix, Conozoa, Derotemema, Encotophus, Gastrimargus, Locusta, Oedaleus, Oedipoda, Parapleurus, Trimerotropis*
Subfamily 9 — Romaleinae	*Spaniacris*
Family 2 — Eumastacidae	
Subfamily Morabinae	*Culmacris, Keyacris, Moraba,* P24, P25, P45, P52, P53, P85, P169, P196, *Vandiemenella, Warramaba*
Family 3 — Lentulidae	*Karruacris*
Family 4 — Pyrgomorphidae	*Atractomorpha*
Superfamily 2 — Tetrigoidea	
Family Tetrigidae	*Tetrigidea*

1. Spontaneous exchanges either within or between chromosomes leading to the production of structural rearrangements
2. Spontaneous amplification of particular chromosome regions resulting in the formation of supernumerary segments

These two events are also sometimes coupled so that amplification occurs at or following exchange events. In this way a small centric fragment, produced as a by-product of an exchange event, may enlarge into a supernumerary chromosome.

A. Inversion Systems

In chromosome systems with localized centromeres, which is true of all orthopteroids, inversions of chromosome material can be conveniently considered in two groups according to whether the centromere itself lies within (pericentric) or outside (paracentric) the inverted region. Paracentric inversions do not alter arm lengths or, therefore, arm ratios. Pericentric inversions, on the other hand, by producing a change in centromere position, may affect both arm length and arm ratio.

1. Paracentrics

There is only one case on record in orthopteroids of a polymorphism involving a

Table 2
STRUCTURE OF THE MARY'S PEAK POPULATION OF *BOONACRIS ALTICOLA*[3]

Year	No. of males: Heterozygous for In(2)MP-1	No. of males: Homozygous for bivalent #2	Total sample
1975	9 (60%)	6 (40%)	15
1976	25 (62%)	15 (38%)	40

Table 3
MEIOTIC BEHAVIOR OF HETEROZYGOUS IN(2)MP-1 BIVALENTS OF *BOONACRIS ALTICOLA*[3]

Meiotic stage	Year: 1975, $n = 9$	Year: 1976, $n = 10$	Totals
Pachytene			
Straight pairing	144 (60%)	201 (57%)	
Incomplete pairing	84 (35%)	129 (37%)	
Reverse loop pairing	11 (5%)	19 (62%)	
Totals	239	350	589
First anaphase			
Normal segregation	450 (95%)	470 (94%)	
Dicentric and acentric	15 (3%)	16 (3.2%)	
Dicentric only	7 (1.5%)	11 (2.2%)	
Acentric only	3 (0.6%)	3 (0.6%)	
Totals	475	500	975

paracentric inversion, that is, in the grasshopper *Boonacris alticola* (Acrididae, Melanoplinae), a species which has a chromosome complement of 21 rods and in which, as is most usual in orthopteroids, the autosomes are numbered from 1 to 10 in decreasing order of size.[3] A single population of this flightless form from Mary's Peak, Ore., U.S. proved to be polymorphic for a long paracentric inversion in autosome 2 designated as In(2)MP-1.

In both years over which the population was sampled there was an excess of individuals heterozygous for the inversion, which comprised some 60% of the entire population (Table 2). Since the basic and the inverted homozygote classes could not be distinguished, it was not possible to partition the homozygotes more precisely. The data relating to the meiotic behavior of the inversion heterozygotes were remarkably consistent over both years of sampling (Table 3). Of the 589 pachytene cells from heterozygous individuals, 59% showed straight pairing of the relatively inverted homologs. A further 36% showed asynapsis within the relatively inverted region, and only 5% formed a reverse loop of the kind expected from homologous pairing. In keeping with these figures, some 95% of the 975 anaphase-I cells examined showed normal segregation. Dicentrics and/or acentrics were present in the remaining 5%.

The straight pairing observed in this case must, of course, be nonhomologous and cannot lead to crossing over. The interrupted pairing (partial asynapsis) in the inverted region has the same effect. Hence, the contraction of the linkage group, the most

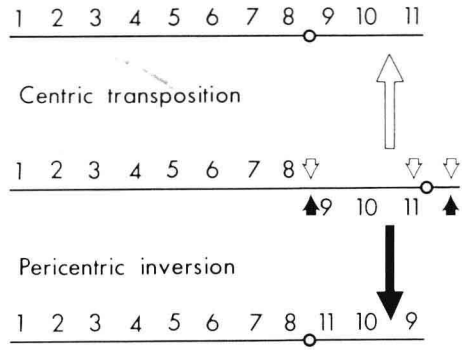

FIGURE 1. Two modes of pericentric rearrangement. In heterozygotes for a centric transposition, straight pairing at pachytene will, by definition, be homologous in character.

$$\frac{9.10.11}{9.10.11}$$

In a pericentric inversion heterozygote straight pairing will be nonhomologous.

$$\frac{9.10.11}{11.10.9}$$

obvious effect of inversion hybridity, is achieved in this case without any serious accompanying sterility of the kind expected following regular crossing over within reverse pairing loops.

Essentially the same result was obtained[4] in a study of a single mutant individual of the grasshopper *Camnulla pellucida* collected at Olema, Marin County, Calif., U.S. which was heterozygous for a paracentric inversion occupying approximately 10% of the length of one of the two longest autosomes. Here reverse loops were present in not more than 4% of the 297 pachytene cells analyzed with a further 8% of the cells showing partial asynapsis and the remainder, 88%, with straight pairing. An analysis of 603 cells in anaphase I and II, scored for the presence of dicentric bridges and acentric fragments, indicated that crossing over within the inversion could not have occurred in more than 8% of the meiocytes.

2. Pericentrics

By contrast with the apparent rarity of paracentric inversion polymorphisms, pericentric polymorphisms are much more common in orthopteroids. It has been suggested by several authors[2,5] that these polymorphisms are better described simply as centric shifts, since in all of them there is no reverse looping of the kind conventionally assumed to be diagnostic for inversions. Consequently, they might also be explained as a result of a three-break centric transposition,[6] which would, of course, be expected to produce straight pairing at pachytene (Figure 1).

The behavior of paracentric inversion heterozygotes in orthopteroids, outlined in Section II.A.1, shows that the absence of reverse loop pairing does not militate against an inversion explanation in the case of pericentric rearrangements. The important difference between the two hypotheses rests on the precise nature of pairing. In a centric transposition system the straight pairing is homologous in nature. As such, it does not prohibit crossing over and such crossing over would, of course, give rise to a dicentric and an acentric chromatid at first anaphase, as would also arise following crossing over within a reverse loop in the case of a heterozygous pericentric inversion. In a pericentric inversion system the straight pairing is nonhomologous and so prohibits crossing over. The fact that in the pericentric rearrangements of orthopteroids there is

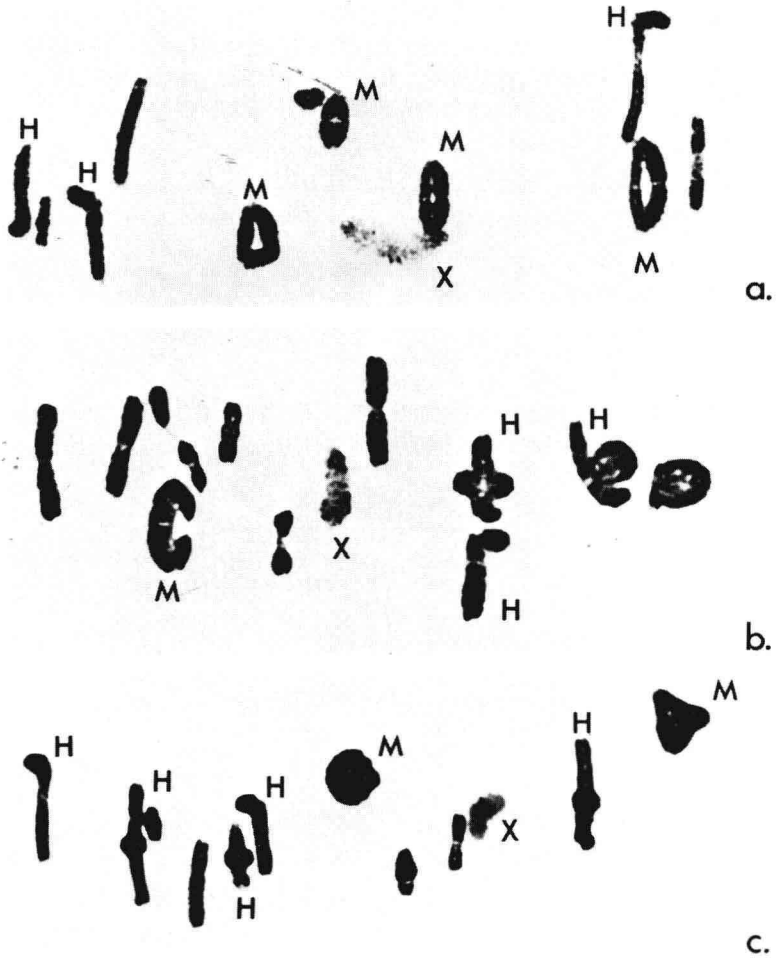

FIGURE 2. Heterozygosity for pericentric inversion in trimerotropine grasshoppers. (a) *Trimerotropis thalassica*, (b) and (c) *T. pseudofasciata*, both with $2n = 23\sigma$, XO. M denotes a metacentric bivalent, homozygous for inversion, while H identifies a bivalent heterozygous for an inversion.

neither reverse looping at pachytene nor dicentrics and acentrics at anaphase I is only explicable if the straight pairing is indeed nonhomologous. Added to this, in at least one case, that of the grasshopper *Trimerotropis helferi*, reverse loops were seen in two out of several hundred pachytene cells.[7]

Pericentric inversion polymorphisms are known in many grasshoppers. In America, for example, such polymorphisms occur in at least 20 species of the predominantly western genera *Trimerotropis, Circotettix,* and *Aerochoreutes* (Acrididae, Oedipodinae), while in Australia several species of morabine grasshoppers are similarly polymorphic.[8] There are, however, only six studies which deal in some detail with the distribution of the polymorphisms within individual species and we shall confine our attention to these. All of them suffer from some disadvantage or other. Thus, most of them are relatively short-term studies, so we have little accurate information concerning their stability. Undoubtedly the most complete studies to date are in the trimerotropines. Here the number of chromosomes involved in the inversion system varies considerably. Only 1 pair is polymorphic in *T. helferi, C. coconino,* and *C. crotalum*, whereas in *T. sparsa* populations are polymorphic for pericentric inversions in at least 7 of the 11 pairs of autosomes, and in *T. thalassica* up to 10 of the 11 autosome pairs may be polymorphic (Figure 2).

Table 4
FREQUENCIES OF THE 13 DIFFERENT M-INVERSION MORPHS PRESENT IN TWO ARGENTINIAN POPULATIONS OF *TRIMEROTROPIS PALLIDIPENNIS* [9]

	M4		M5		M6			M7			M8		
Population	Acro	Telo	Telo	Meta	Telo	Submeta	Meta	Telo	Submeta	Meta	Telo	Submeta	Meta
Choele-Choel	0.11	0.89	0.97	0.03	0.44	0.00	0.66	0.03	0.63	0.14	0.14	0.13	0.73
Sierra de la Ventana	0.62	0.38	0.95	0.05	0.52	0.17	0.31	0.45	0.36	0.33	0.33	0.12	0.55

Table 5
CYTOLOGICAL CHARACTERISTICS OF THREE ARGENTINIAN POPULATIONS OF *TRIMEROTROPIS PALLIDIPENNIS* [9]

		M4—M8 autosomes			
Population	Climatic characteristics	Inversions per male	Heterozygous bivalents per male	Mean cell Xa frequency	Mean no. interstitial Xta per cell
Laguna Blanca	Coldest climate, precordillera	Nil	Nil	20.42 ± 1.18	7.34 ± 1.29
Choele-Choel	Typical desert area	5.16 (4—6)	1.16 (0—4)	17.33 ± 1.08	1.23 ± 0.60
Sierra de la Ventana	Mildest climate, most rainfall, at eastern border of species range	4.10 (2—6)	2.43 (0—4)	15.60 ± 0.89	1.49 ± 0.71

Most trimerotropine species are confined to North America. Two species have, however, invaded South America. One of these, *T. pallidipennis*, extends from southern Canada over the whole of western U.S. and Mexico but is absent from Central America. It is, however, found southward all along the Andes in Peru, Ecuador, Bolivia, Chile, and Argentina. From here, it has extended to lower altitudes by invading adjacent arid or semiarid regions. Consequently, in South America it exhibits an amazing plasticity in its adaptation to ecological and altitudinal situations.

If the 11 autosomes of the haploid set are numbered in decreasing size order, the three largest chromosomes (L1 to 3) are homozygous metacentrics throughout the entire species range. Similarly, the three smallest pairs (S9 to 11) are invariably homozygous rods. In certain of the southern populations, however, the five medium-sized autosomes (M4 to 8) are polymorphic for a series of pericentric inversions[9] (Table 4), a condition which is never found in North America. Of the three populations sampled in Argentina (Table 5), that from Laguna Blanca, near the Andes, shows the same structural characteristics as the North American populations. In the two polymorphic populations there are significantly more homozygous M inversions per male in Choele-Choel and significantly more heterozygous M inversions per male in Sierra de la Ventana. Added to this, the total number of M inversions per male is significantly greater in Choele-Choel.

The two polymorphic populations have a reduced mean cell chiasma frequency compared to that of Laguna Blanca. The mean frequency at Choele-Choel is, however, significantly higher than that at Sierra de la Ventana. The reduction is, thus, most pronounced in the population with the highest number of heterozygous inversions. The number of interstitial chiasmata is not significantly different in the two poly-

Table 6
CHIASMA DISTRIBUTION DATA FOR 18 INDIVIDUALS OF *TRIMEROTROPIS PSEUDOFASCIATA* FROM SANTA CRUZ ISLAND AND FOR 10 INDIVIDUALS FROM SAN NICOLAS ISLAND[5]

Population	Karyomorph	Distal Xta (%)
Santa Cruz Island, sheep area	L_2 Metacentric	81
	L_1L_3	
	Basic homozygote	23
	Inversion heterozygote	34
	Inversion homozygote	81
	M_8—S_{11} Telocentric	82
	M_{4-7}	
	Basic homozygote	53
	Inversion heterozygote	99
	Inversion homozygote	82
San Nicolas Island, basic island karyotype	L_2 Metacentric	76
	L_1L_3 Telocentric	29
	M_{4-8} Telocentric	56
	S_{9-11} Telocentric	83

Note: In the basic island karyotype referred to, all chromosomes other than the L2 and the X (both fixed metacentrics) are telocentric. The L1, 3, M5, 6, and 7 are polymorphic on the islands.

morphic populations, though in both there is a marked and highly significant reduction compared to the population at Laguna Blanca. Thus, apart from the virtual abolition of crossing over within the inverted regions themselves, there is a marked movement of the chiasmata distally in the M bivalents in both polymorphic populations.

A somewhat similar situation involving patterned chromosome variation with respect to pericentric inversion has been described in *T. pseudofasciata* in North America[5] on comparison of mainland populations from Jacalitos and Bakersfield (California) and from Sand Mountain and Hawthorne (Nevada) with those of five of the Californian Channel Islands, namely Santa Rosa, Santa Cruz, San Nicolas, Santa Catalina, and San Clemente. The mainland populations were fixed for inversions in the L_1, L_2, L_3, and M_5 chromosomes but polymorphic for the M_6, M_7, M_8, and S_9. Only minor differences existed between the different mainland populations with reference both to the kind and the frequency of inversions present. The average percentage of the autosomal complement that was structurally heterozygous was, however, low compared to island populations with an equivalent number of inverted elements.

In the island populations the L_2 was the only autosome fixed as an inversion homozygote, although the L_1, L_3, and M_{5-7} chromosomes were all polymorphic. On any one island the densest populations had more different chromosomes polymorphic and a higher average number of inversions per individual. Similarly, between islands, there was a direct relationship between average population density and the number of different chromosomes carrying inversions. Thus, in *T. pseudofasciata* inversion heterozygosity does not fall off at geographic margins. Only areas that are ecologically marginal, as gauged by population density, show reduced chromosomal polymorphism.

Chiasma comparisons, carried out by Weissman, indicated that: