Further cytological studies of Antipodean *Teleogryllus* species and their hybrids (Orthoptera: Gryllidae)

HAI-CHOO LIM
Department of Entomology and Lyman Entomological Museum of McGill University, Macdonald College, Ste Anne de Bellevue, Quebec

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Three additional populations of *T. oceanicus* and six intra- and inter-specific hybrids of *Teleogryllus* species have been studied. Some abnormal chromosome conditions, such as variation in number, occurrence of numerous univalents, chromosomal bridges, and polyploid cells, were found in the intraspecific hybrids of *T. commodus* and in interspecific hybrids.

The low fertility of intraspecific hybrids of *T. commodus* and the production of sterile progeny of interspecific crosses may be due to the unequal segregation and chromosomal incompatibility.

Introduction

Morphological studies (Leroy 1964; Chen *et al.* 1967), physiological investigations (Bigelow 1962; Bigelow and Cochaux 1962; Cochaux 1965; Hogan 1965, 1966), and cytological studies (Fontana and Hogan 1969; Lim *et al.* 1969) have confirmed that two different species of black field cricket occur in Australasia. The northern 'non-diapause' populations are referable to *Teleogryllus oceanicus* (Le Guillou, 1841), while the southern 'diapause' populations are *T. commodus* (Walker, 1869).

T. commodus from Western Australia differs morphologically (Chen *et al.* 1967) and cytologically (Lim *et al.* 1969) from other populations distributed in southeast Australia and in New Zealand. Typical *T. commodus* was described from Western Australia; all the latter populations studied, except one from South Island, New Zealand, are referable to *T. commodus*, subspecies *servillei* (Saussure, 1877) (Lim *et al.* 1969).

Materials and Methods

Specimens used in this study were all reared in the laboratories of the Lyman Entomological Museum and Department of Entomology, Macdonald College of McGill University. Three populations of *Teleogryllus*, all belonging to the 'non-diapause' *T. oceanicus* populations, in addition to those referred to by Lim *et al.* (1969), were included in the present investigations. These are designated as follows: *Qe* (from Darwin, Northern Territory, Australia); *Qo* (from the Ord River region, northern Kimberley District, Western Australia); and *Qf* (from Viti Levu, Fiji Islands). The first two were cultured from specimens received in 1968 through the kindness of Mr. K. Hodder, Darwin; specimens of the latter were reared from material collected in the field by Dr. D. K. McE. Kevan of Macdonald College in July, 1968. The sources of the other material studied, the techniques used, and the other symbols used here are explained in a previous paper (Lim *et al.* 1969).

The frequency of ring-form chromosomes and univalents were measured at diakinesis, and the frequency of unequal bivalents was determined at metaphase I. Some other changes take place during different stages, so that the data presented for these apply only to a particular stage, as indicated in the text.

Observations

I. T. oceanicus

Populations *Qe*, *Qo*, and *Qf* are all *T. oceanicus* and have karotypes that are similar to those of other populations of *T. oceanicus*, in that most of the chromosomes were acrocentric.

In the *Qe* population, only a single unequal bivalent was found. Of 184 cells from six individuals of the *Qf* population, 96 (52.2%) showed single heteromorphic pairs (Fig. 1) and 88 (47.8%) showed double heteromorphic pairs. Cells from the population *Qo* were singly heteromorphic only. The occurrence of ring-form chromosomes and univalents at diakinesis are summarized for these populations in Table I.

It is interesting to note that one or two fragment-like chromosomes, which could be seen very clearly during the diplotene and diakinesis stages, occurred in each of these three populations. They were small, dot-shaped, and very pale in appearance (Fig. 2). Fragment-like chromosomes were more common in the *Qe* than in the *Qf* and *Qo* populations. In some individuals of the *Qf* and *Qo* populations, fragment-like chromosomes were not found. In the *Qo* population,

TABLE I

Frequency of ring-form chromosomes and univalents at diakinesis (20 cells from each of 10 individuals)

	Qe	*Qf*	*Qo*
Ring-form chromosomes			
without ring-form chromosome	3.7±0.12	5.9±0.18	1.3±0.07
with one ring-form chromosome	12.6±0.18	11.1±0.21	8.7±0.26
with two ring-form chromosomes	3.2±0.13	2.6±0.16	7.1±0.18
with three ring-form chromosomes	0.5±0.07	0.4±0.05	2.7±0.15
with four ring-form chromosomes	—	—	0.2±0.13
Univalents			
without univalent	0.3±0.04	2.4±0.10	6.0±0.19
with one univalent	7.3±0.17	9.3±0.16	10.6±0.18
with two univalents	10.3±0.10	7.7±0.16	3.2±0.18
with three univalents	2.1±0.12	0.6±0.06	0.2±0.04

the fragment-like chromosomes and nucleolus disappeared after the diplotene stage. However, such chromosomes proceeded to diakinesis in the other two populations. Polyploid cells occurred occasionally in the *Qf* (Fig. 3) and *Qo* populations. The occurrence of achromatic gaps in these three populations was not as common as was reported for other *T. oceanicus* populations by Lim *et al.* (1969).

II. Hybrids

The frequencies of the different chromosome structures which were observed in each individual hybrid are compared in Tables II*a* and II*b*.

A. Intraspecific Hybrids of T. commodus

(1) *Qaw*: South Australia (*Qa*) females × Western Australian (*Qw*) males.

Univalents were found to be very frequent in this hybrid, ranging from one to eight. Achromatic gaps (Fig. 4), chromosomal bridges, polyploid cells (Fig. 5), and unequal bivalents (Fig. 4) were also common. Because of the appearance of many univalents, the chromosome number varied: *n*♂ = 14–18.

(2) *Qzw*: North Island, New Zealand (*Qz*) females × Western Australia (*Qw*) males.

This hybrid showed less abnormality in chromosomal configuration than the previous one. At diakinesis some cells contained one or two additional small univalents (Fig. 6). This might have resulted from an exchange between the chromosomes because, during early diplotene, extra univalents were not observed; all of the cells contained 14 chromosomes. One or two unequal bivalents were found. Single chromosomal bridges occurred occasionally.

B. Intraspecific Hybrids of T. oceanicus

(1) *Qef*: Darwin (*Qe*) females × Fiji (*Qf*) males.

(2) *Qfo*: Fiji (*Qf*) females × Ord River (*Qo*) males.

Neither hybrid showed abnormality in chromosome structure or number. The karyotypes were very similar to those of other *T. oceanicus* populations reported by Lim *et al.* (1969).

C. Interspecific Hybrids

(1) *Qayrc*: Queensland (*Qayr*) females of *T. oceanicus* × Victoria (*Qc*) males of *T. commodus*.

(2) *Qzayr*: North Island, New Zealand (*Qz*) females of *T. commodus* × Queensland (*Qayr*) males of *T. oceanicus*.

Both interspecific hybrids produced sterile progeny, sterility presumably resulting from chromosomal incompatibility. The chromosome number varied, *n*♂ = 14–18 (Fig. 7*a*, *b*), depending on the occurrence of univalents. At metaphase I, most of the cells were normal with two to six univalents (Fig. 8). During anaphase I, unequal pairing of chromosomes caused the production of some abnormal configurations, such as unequal segregation and bridge formation (Fig. 9*a*, *b*). After the telophase, three to four or more univalents become disassociated with the dividing nucleus (Fig. 10*a*, *b*). Unequal size and shape of spermatids also occurred (Fig. 11). The anomalies in chromosome structures resulted in the formation of many nonfunctional sperm cells, most of which degenerated at different stages of development. The adult F_1 female hybrids did not lay eggs because their ovaries were nonfunctional. This was also a result of chromosomal incompatibility.

TABLE II*a*

The frequency of ring-form chromosomes and univalents at diakinesis in the hybrids (20 cells from each of 10 individuals)

	No. ring-form chromosomes				No. of univalents								
Hybrids	0	1	2	3	0	1	2	3	4	5	6	7	8
Qaw	11.3 ±0.26	8.1 ±0.22	0.6 ±0.22	—	0.1 ±0.03	3.8 ±0.21	5.7 ±0.21	4.6 ±0.12	2.8 ±0.13	1.8 ±0.17	0.5 ±0.10	0.3 ±0.06	0.3 ±0.06
Qayrc	13.8 ±0.10	5.6 ±0.26	0.6 ±0.08	—	3.9 ±0.34	5.3 ±0.14	5.3 ±0.23	3.0 ±0.25	1.4 ±0.15	0.9 ±0.13	0.2 ±0.19	—	—
Qzayr	8.7 ±0.24	8.2 ±0.14	2.7 ±0.22	0.4 ±0.16	—	1.5 ±0.17	3.7 ±0.29	5.9 ±0.23	4.2 ±0.24	3.5 ±0.13	0.8 ±0.10	0.3 ±0.04	0.1 ±0.03
Qzw	7.2 ±0.37	8.3 ±0.22	3.9 ±0.22	0.6 ±0.07	9.9 ±0.26	8.6 ±0.19	1.5 ±0.11	—	—	—	—	—	—
Qfo	3.2 ±0.18	10.1 ±0.16	5.9 ±0.12	0.8 ±0.07	2.8 ±0.17	14.7 ±0.14	2.5 ±0.10	—	—	—	—	—	—
Qef	7.8 ±0.19	10.2 ±0.12	2.0 ±0.11	—	3.0 ±0.14	11.1 ±0.12	4.6 ±0.11	1.2 ±0.07	—	—	—	—	—

TABLE II*b*

Variation in chromosome number and the mean frequency of unequal bivalents distributed in the hybrids (20 cells from each of 10 individuals)

	Variation in chromosome number					Number of unequal bivalents					
Hybrids	14	15	16	17	18	1	2	3	4	5	6
Qaw	6.9 ±0.15	7.9 ±0.27	4.3 ±0.24	0.6 ±0.11	0.3 ±0.06	—	1.8 ±0.11	15.1 ±0.29	3.1 ±0.21	—	—
Qayrc	5.0 ±0.19	7.0 ±0.17	4.9 ±0.13	2.2 ±0.09	0.9 ±0.10	—	—	3.3 ±0.22	10.2 ±0.19	5.3 ±0.27	1.2 ±0.16
Qzayr	6.4 ±0.16	7.9 ±0.19	4.2 ±0.17	1.5 ±0.09	—	—	2.5 ±0.17	14.8 ±0.15	2.7 ±0.19	—	—
Qzw	11.0 ±0.24	8.8 ±0.22	0.2 ±0.13	—	—		With one unequal bivalent only				
Qfo	—	—	—	—	—	14.2 ±0.07	5.8 ±0.07	—	—	—	—
Qef	—	—	—	—	—	11.2 ±0.22	8.2 ±0.34	0.6 ±0.09			

Discussion

The two intraspecific *T. oceanicus* hybrids in the present study showed no important anomaly in chromosome number or structure, undoubtedly indicating that these three populations are conspecific. Although the populations from Fiji and northern Australia are geographically widely separated, little, if any, progress toward speciation has occurred. The occurrence of polyploid cells was similar to that previously reported for *Teleogryllus* species, i.e., fusion between neighboring cells or failure of chromosomes to segregate (Lim *et al.* 1969).

Although the hybrid obtained by crossing South Australian with North Island, New Zealand, populations of *T. commodus servillei* was previously found to show chromosome structures similar to those of the parent populations (Lim *et al.* 1969), and although these populations are very similar morphologically (Chen *et al.* 1967), minor differences must exist between them. This was demonstrated by the crosses between these populations and a population of typical *T. commodus* from Western Australia, for the hybrid (*Qaw*) between South Australian and Western Australian populations showed greater dissimilarity in chromosome structures such as the occurrence of univalents, the variation in chromosome number, etc. (Tables II*a*, II*b*) than did (*Qzw*) obtained by crossing North Island, New Zealand, and Western Australian populations. The dissimilarities in chromosome structures found in these two hybrids again strongly indicates that the Western Australian population differs genetically from the other populations of *T. commodus* so far studied. This is further emphasized by the fact that the F_1 progeny of both of these hybrids showed low fertility, which might have been caused by the abnormal segregation and chromosome disassociation in F_1 offspring. Nevertheless, some viable germ cells were produced, so that the western and eastern populations are not reproductively isolated in the laboratory and may be considered to be conspecific even though subspecifically distinct.

Sterile progeny are produced from crosses of *T. commodus* and *T. oceanicus* because of chromosome disassociation and incompatibility. White (1954) points out that some very closely related species might have a very strong isolating mechanism, while less closely related species might have a weaker one. The two *Teleogryllus* species here studied belong to the first category. They are morphologically very similar, have the same chromosome number, some similarities in chromosome behavior and structure, and they are probably derived from a common ancestor. However, crosses between these two species produce only sterile hybrids, and, even in intraspecific crosses between populations, some hybrids are less fertile than either parental population.

The occurrence of many unequal bivalents (ranging from two to six) in the interspecific *Teleogryllus* hybrids is mainly due to the unequal pairing of chromosomes, rather than to duplication or deletion in one of the chromosome pairs. This is given as the reason for the formation of chromosomal polymorphism in *Pteronemobius taprobanensis* (Walker) by Manna and Bhattacharjee (1964). The chromosome set received from each parent is uneven in size and shape in *Teleogryllus* and fails to pair, so that asynapsis occurs in the F_1 progeny.

The variation in chromosome number in the intraspecific hybrids of *T. commodus* and in the interspecific hybrids between that species and *T. oceanicus* depends on the occurrence of numerous univalents (ranging from one to eight). This may be a result of disassociation between chromosomes or be caused by abnormalities of the spindle apparatus, or, as indicated by Fontana and Hogan (1969), may be due to some genic

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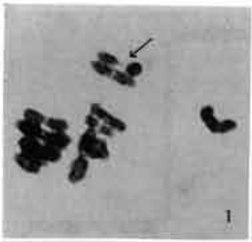
FIG. 1. Metaphase I of Fiji Island population (*Qf*) of *T. oceanicus*, showing a single heterozygote (arrow). FIG. 2. Diakinesis of Darwin population (*Qe*) of *T. oceanicus*, one pale dot-shaped fragment-like chromosome (arrow). FIG. 3. Polyploid cells of Fiji population of *T. oceanicus*. FIG. 4. Metaphase I of intraspecific hybrid (*Qaw*) of *T. commodus*, showing unequal bivalents and achromatic gaps. FIG. 5. Polyploid cells of intraspecific hybrid (*Qaw*) of *T. commodus*. FIG. 6. Diakinesis of intraspecific hybrid (*Qzw*) of *T. commodus*, showing two small univalents (arrows). FIG. 7. Diakinesis of interspecific hybrids (*a*) *Qayrc*, (*b*) *Qzayr*. Variation of chromosome number depends on the occurrence of univalents. FIG. 8. Metaphase I of interspecific hybrid (*Qayrc*), four univalents shown. FIG. 9. Anaphase I of interspecific hybrids (*a*) *Qayrc*, (*b*) *Qzayr*, showing unequal segregation and chromosome bridges. FIG. 10. Telophase of interspecific hybrids (*a*) *Qayrc*, (*b*) *Qzayr*, showing some univalents unassociated with the dividing nucleus. FIG. 11. Interspecific hybrid (*Qzayr*) showing uneven size of spermatids.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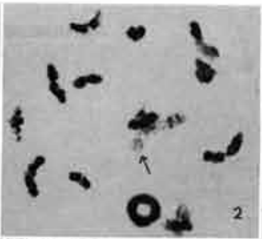
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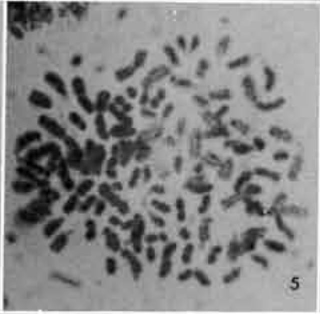
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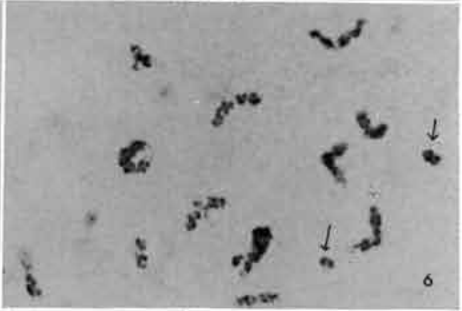
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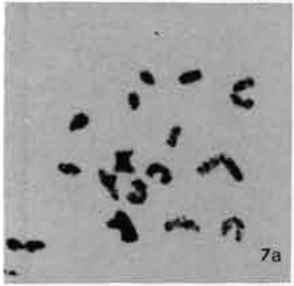
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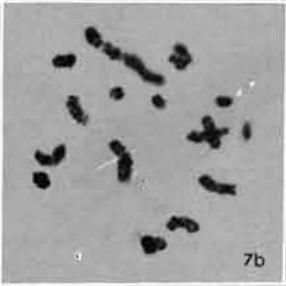
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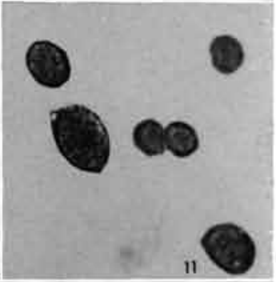
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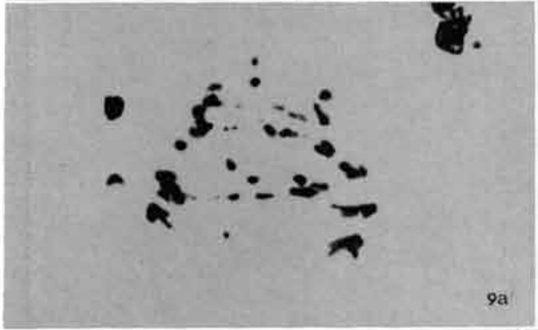
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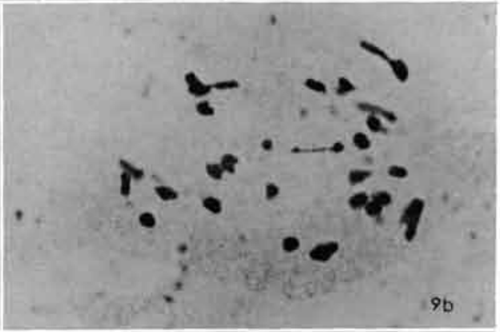
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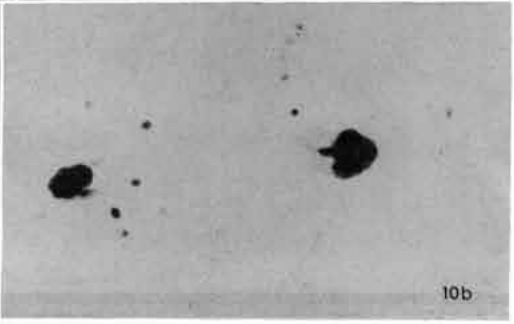
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and mechanical causes which act and interact on the chromosome cycle. The formation of numerous univalents in the interspecific hybrids and in some of the intraspecific hybrids of either of these species of *Teleogryllus* seems to be one of the characteristics of these two species. This special condition may also be a causal factor of sterility of the F_1 generation.

In conclusion, in spite of the skepticism of Fontana and Hogan (1969), it is clear that *Teleogryllus commodus* and *T. oceanicus* both occur in Australia, and that they are indeed very closely related but distinct biological species having a very strong reproductively isolating mechanism. The Western Australian population of *T. commodus* differs genetically from more easterly populations of the same species. This western population must be considered to be the typical subspecies, *T. commodus commodus* (Walker), while southeastern Australian populations and that from North Island, New Zealand, belong to the subspecies *T. c. servillei* (Saussure) (Lim *et al.* 1969).

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