

OCCASIONAL PAPERS OF THE MUSEUM OF
ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

CARYOLOGY OF FOUR CHILEAN SPECIES OF
GRYLLACRIDOIDS OF THE GENUS *HETEROMALLUS*
(ORTHOPTERA: GRYLLACRIDOIDEA:
RHAPHIDOPHORIDAE)BY ALEJO MESA¹

THE apterous, slender-legged, cricket-like insects of the genus *Heteromallus* Brunner are confined to central and southern Chile and Patagonia. They are nocturnally active, hiding by day in the debris of the forest floor and in talus crevices; some live in caves. The genus is a member of the circum-Antarctic subfamily Macropathinae of the family Rhaphidophoridae—a family of worldwide distribution, all the species of which are apterous and many of them troglophilous. Rhaphidophorids share many presumably primitive characteristics with members of the families Stenopelmatidae, Gryllacrididae, and Schizodactylidae, and with them form a natural assemblage which has been variously placed in recent classifications. I follow Richards (1954) and Hubbell (*in litt.*) in grouping these four families in the superfamily Gryllacridoidea, assigned to a position near the base of the phyletic lines leading to the Tettigoniidae and Gryllidae. Since no consensus has yet been reached on the exact relationship of the gryllacridoid families to each other and to the tettigoniids and gryllids, caryological evidence bearing on these questions may prove helpful in answering them.

Of about one thousand species of gryllacridoids known, only twenty (including the four here treated) have been studied caryologically. These twenty include representatives of all four families. Even this small amount of information is enough to suggest the occurrence of considerable diversity in chromosome numbers between the families and within each family. The chromosomal sex-determination mechanisms, on the other hand, are all basically of the ♂XO-♀XX type found in the majority of the Orthoptera, and the two described exceptions,

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Schizodactylus monstrosus (Drury) and *Dolichopoda linderii* (Dufour), have surely acquired the Y-chromosome in relatively recent times.

ACKNOWLEDGMENTS.—I was invited by Dr. Theodore H. Hubbell, of the University of Michigan Museum of Zoology, to accompany him during February and March, 1963, on a study trip, through central and southern Chile, which was part of his more extended expedition to collect South American gryllacridoids. Although my primary objective was to obtain acridid testes for caryological study, I took advantage of the opportunity to obtain testes of a series of gryllacridoids, some belonging to undescribed species and genera. In this paper I begin my report on the materials thus obtained. I am very grateful to Dr. Hubbell for the opportunity to participate in the field work, for identification of the specimens, and for his help in preparing this paper for publication. I wish also to express my appreciation of the valuable assistance of the Chilean naturalist and entomologist, Sr. Luis Peña Guzman, who was our companion and guide, and whose unsurpassed knowledge of the geography and environments of his native land contributed so greatly to the success of our work.

MATERIALS AND METHODS.—Testes prepared for chromosome studies were obtained from specimens of the species here reported upon, from the following localities in Chile:

Heteromallus spina Brunner, 5 ♂♂, Prov. Arauco, 4 km N of Río Quidico, 12 February; 4 ♂♂, Prov. Llanquihue, Ensenada, 17 March.

Heteromallus pectinipes Karny, 1 ♂, Prov. Osorno, Pucatrihue, 22 March; 1 ♂, Prov. Malleco, Termas de Río Blanco, 6 March.

Heteromallus spinifer (Blanchard), 7 ♂♂, Prov. Malleco, Cerro Pichinahuel in Sierra de Nahuelbuta, elev. c.1200m, 10 February; 3 ♂♂, Prov. Osorno, Pucatrihue, 22 March.

Heteromallus gracilipes Ander, 2 ♂♂, Prov. Osorno, Pucatrihue, 22 March; 1 ♂, Prov. Llanquihue, Ensenada, 18 March.

The testes were fixed in a mixture of 100 per cent alcohol and acetic acid (3:1). The microscopic slides were made by squashing, after staining by the Feulgen method.

DESCRIPTION OF THE CHROMOSOMES.—All of the four species studied have a diploid chromosome set of 45 in the male, and a sex-determination mechanism of type ♂XO–♀XX. In all four species the X-chromosome, the largest pair of autosomes, and one pair of medium-sized autosomes are metacentric or submetacentric. The remaining chromosomes are acrocentric.

In the first prophases, from the leptotene to the beginning of the pachytene stage, the polarization of the elements occurs as shown in

Plate I, Fig. 3. Throughout these stages the acrocentric chromosomes have their proximal ends positively heteropycnotic, a characteristic which is most accentuated in *H. gracilipes* (Plate I, Fig. 4).

From the end of the pachytene stage onward it is possible to count 22 bivalents and the univalent sex chromosome. The latter is positively heteropycnotic in the entire first prophase, and its arms appear to be united along their whole length, as shown in Plate I, Figs. 5 and 6. The sex chromosome is of approximately the same length as the longest of the autosomes (Plate I, Figs. 1 and 2), and in *H. gracilipes* is longer than in the other three species (cf. Plate IV, Figs. 23, 24, 25 and 26).

The longest pair of autosomes is metacentric or submetacentric, and in the first prophase shows extensive heteropycnotic zones, making it easily recognizable at this stage (Plate IV, Figs. 11, 12, 13, and 14). Its structure is basically similar in *H. spina*, *H. spinifer*, and *H. pectinipes*, with a less heavily stained median zone and a subterminal constriction at each end. The segment between the center and the lower end in Figs. 11, 12 and 13 of Plate IV is more intensively heteropycnotic than the segment that extends from the center to the upper constriction. In *H. gracilipes* the structure of this bivalent seems a little different (Plate IV, Fig. 14). All four species have a metacentric chromosome of medium length (Plate IV, Figs. 19, 20, 21 and 22).

There is one chiasma per bivalent, and the chiasmata generally have an interstitial location. In the metacentric chromosomes two chiasmata are generally observed, one in each arm.

Although it was not possible to determine with certainty the position of the centromere in all the metacentric autosomes of the four species, it is evident that in some instances the lengths of the arms are very unequal. The bivalent shown in Plate IV, Fig. 17 has, for example, one chiasma in the long arm, and that shown in Fig. 21 has one chiasma in the short arm. In both cases the chromosomes are evidently submetacentric.

DISCUSSION.—As was suggested above, the "Gryllacridoidea" is a very diverse assemblage. Of the four families comprised in it, according to the classification here followed, one, the Schizodactylidae, is confined to the Old World. The other three are worldwide in distribution and have South American representatives. Caryological studies of this group have been few in number. Our knowledge of chromosome numbers and chromosomal sex-determination mechanisms in gryllacridoids is summarized in Table 1.

According to the data in Table 1, chromosome number varies widely from family to family and even within families. At the generic level

Heteromallus, with $2n = 45$, seems to have stability. In *Dolichopoda*, the only other genus in which more than a single species is known to have been studied, Baccetti (1958) found that one of the five species he examined, *D. schiavazzii*, has $2n = 35$, the other four $2n = 31$. He

TABLE I

SEX-DETERMINATION MECHANISMS AND CHROMOSOME NUMBERS IN GRYLLACRIDOIDEA

	Sex-determ. Mechanism (♂)	2-n Chromo- some Number (♂)	Author and Date
RHAPHIDOPHORIDAE			
Macropathinae			
<i>Heteromallus spina</i> Brunner	XO	45	Mesa (this paper)
<i>H. pectinipes</i> Karny	XO	45	" " "
<i>H. spinifer</i> (Blanchard)	XO	45	" " "
<i>H. gracilipes</i> Ander	XO	45	" " "
Rhaphidophorinae			
Dolichopodini			
<i>Dolichopoda geniculata</i> (Costa)	XO	31	Baccetti, 1958
<i>D. laetitia</i> Menozzi	XO	31	" "
<i>D. baccettii</i> Capra	XO	31	" "
<i>D. ligustica</i> Baccetti & Capra	XO	31	" "
<i>D. schiavazzii</i> Capra	XO	35	" "
<i>D. linderii</i> (Dufour)	XY	28	Saltet, 1959
Ceuthophilini			
<i>Ceuthophilus maculatus</i> (Harris) ²	XO	37-39	Thompson, 1911
<i>Ceuthophilus</i> sp. ³	XO	37	Stevens, 1912
Troglophilini			
<i>Troglophilus cavicola</i> (Kollar)	XO	21	Baccetti, 1961
Rhaphidophorini			
<i>Tachycines asynamorus</i> Adelung ⁴	XO	57	Schelleberg, 1913; Mohr & Eker, 1934
<i>Diestrammena japonica</i> Blatchley	XO	57	Makino, 1931; Omura, 1950
GRYLLACRIDIDAE			
<i>Nippancistroger testaceus</i> (Matsumura & Shiraki) ⁵	XO	17	Ohmachi, 1935
<i>Gryllacris signifera</i> (Stoll)	XO	11	Heberer, 1937
SCHIZODACTYLIDAE			
<i>Schizodactylus monstrosus</i> (Drury)	XY	14	McClung & Asana, 1933
STENOPELMATIDAE			
Stenopelmatinae			
<i>Stenopelmatius</i> spp.	XO	47	Stevens, 1909
Henicinae			
<i>Lutosa brasiliensis</i> Brunner	XO	15	Piza, 1947

²Recorded by Thompson (1911) under the synonymous name *C. latebricola* Scudder (T. H. Hubbell, *in litt.*)

³Very probably *C. maculatus* (Harris) (T. H. Hubbell, *in litt.*)

⁴Recorded by Schelleberg (1913) under the name *Diestrammena marmorata* [not of] de Haan (T. H. Hubbell, *in litt.*)

⁵Recorded by Ohmachi (1935) under the name *Eremus testaceus* Matsumura and Shiraki (T. H. Hubbell, *in litt.*)

observed morphological differences corresponding with the differences in chromosome numbers that enabled him to divide the genus into two easily distinguishable subgenera. Saltet (1959) subsequently found *D. linderii* to have $2n = 28$ and a sex-determination mechanism of type XY.

The four species of *Heteromallus* studied agreed not only in chromosome number but also in having the XO type of sex-determination mechanism and an X-chromosome and two autosome pairs with their centromeres in median or submedian position. Furthermore, the longest of the metacentric bivalents is heteropycnotic in the first prophase in all four species, although the details of distribution of heterochromatin suggest that *H. gracilipes* is more highly differentiated than the others. This suggestion is strengthened when we consider other details, such as the great size of the X-chromosome and the more pronounced heteropycnosis in the proximal ends of the acrocentric autosomes in *H. gracilipes*. It would be interesting to determine whether there are morphological or other features in this species that would support the conclusion that it is evolutionarily more advanced than the other three.⁶

SUMMARY.—In the four species of gryllacridoids of the genus *Heteromallus* which were studied, the chromosome number in the male is $2n = 45$, the sex-determination mechanism is of the type ♂ XO–♀ XX, the X-chromosome and two pairs of autosomes are metacentric or submetacentric, and the remaining chromosomes are acrocentric. The longest pair of metacentric autosomes is positively heteropycnotic during the first prophase. *Heteromallus gracilipes* differs from the other three species in details of distribution and intensity of heterochromatin and in size of X-chromosome in a way suggesting that this species is evolutionarily more advanced than the other three.

⁶T. H. Hubbell informs me (*in litt.*) that *Heteromallus gracilipes* differs from the other species in its paler coloration, more slender and less heavily armed legs, straighter and more evenly tapering ovipositor, and other features, but that more detailed morphological study of the species of this genus will be required for evaluation of their relationships.

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Accepted for publication March 4, 1965

PLATE I

Chromosomes of *Heteromallus*

- FIG. 1. *H. spinifer*, first metaphase (m_1 =first metacentric pair; m_2 =second metacentric pair; X=X-chromosome).
- FIG. 2. *H. pectinipes*, first metaphase.
- FIG. 3. *H. gracilipes*, zygotene stage with polarized elements.
- FIG. 4. *H. gracilipes*, pachytene stage.
- FIG. 5. *H. gracilipes*, X-chromosome in pachytene stage.
- FIG. 6. *H. spinifer*, *idem*.

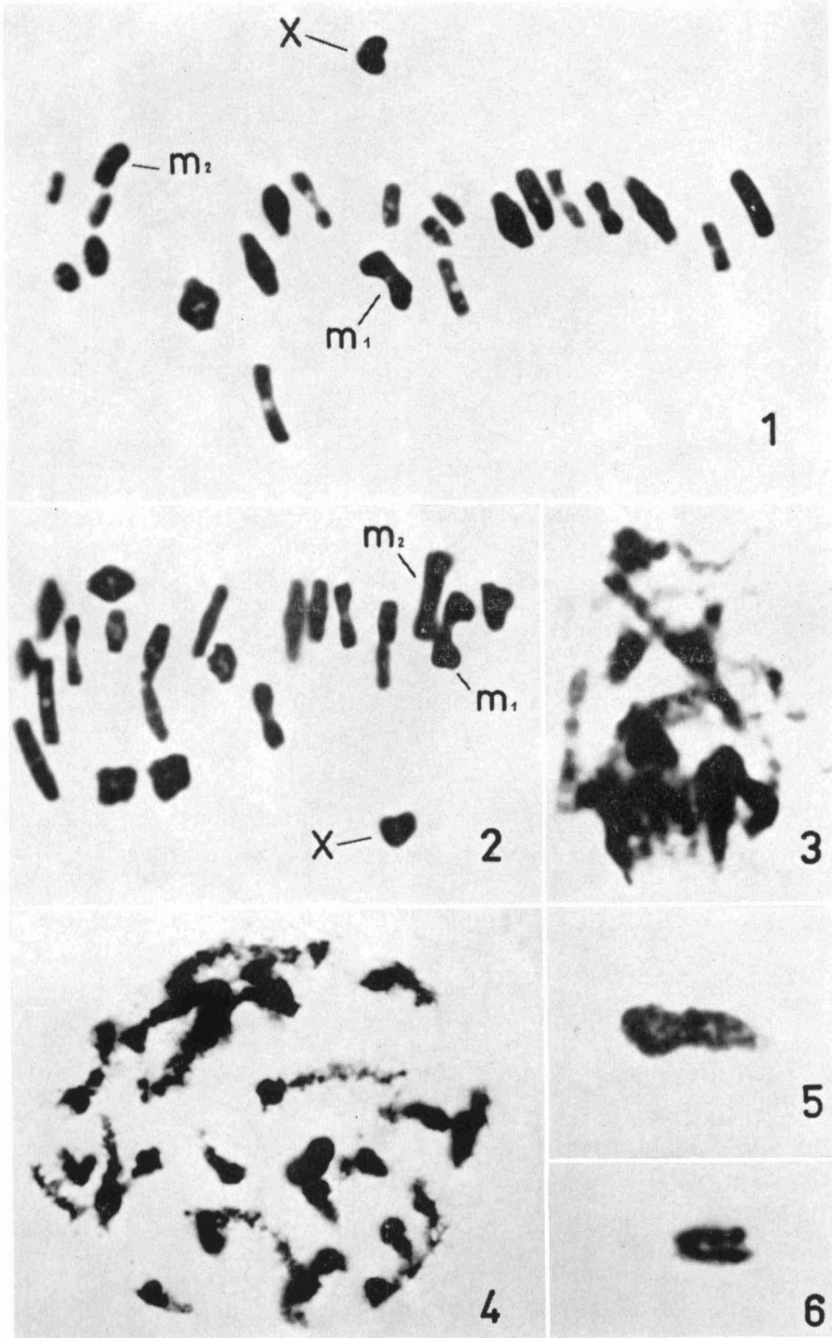


PLATE I

PLATE II

Chromosomes of *Heteromallus*

FIG. 7. *H. pectinipes*, late diplotene stage (m_1 , X as in Pl. I).

FIG. 8. *H. spinifer*, *idem*.

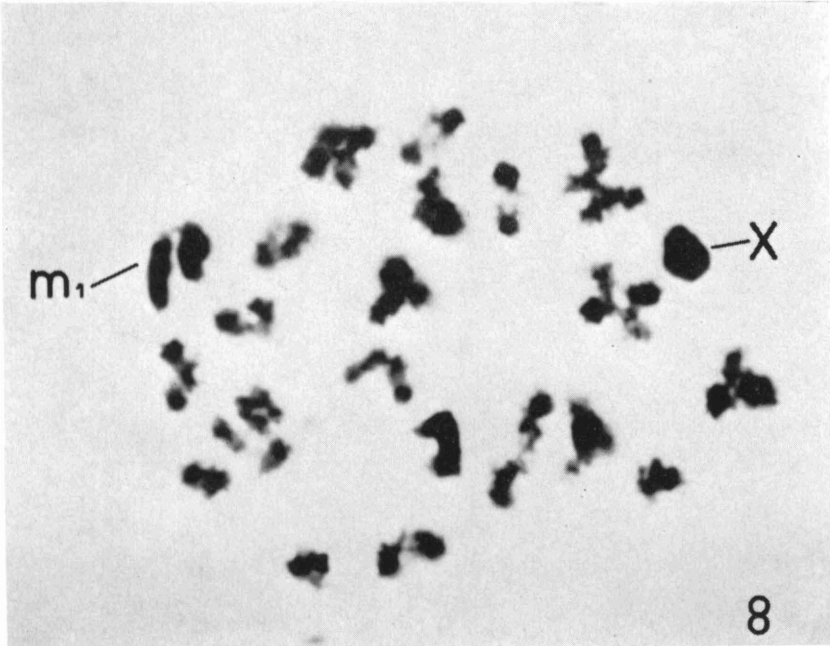
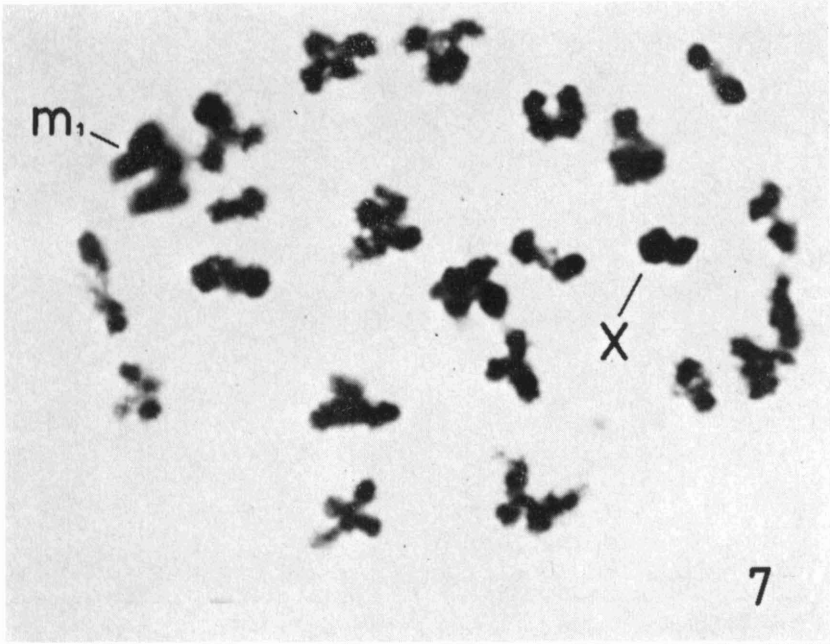


PLATE II

PLATE III

Chromosomes of *Heteromallus*

FIG. 9. *H. spina*, late diplotene stage (m, X as in Pl. I).

FIG. 10. *H. gracilipes*, *idem*.

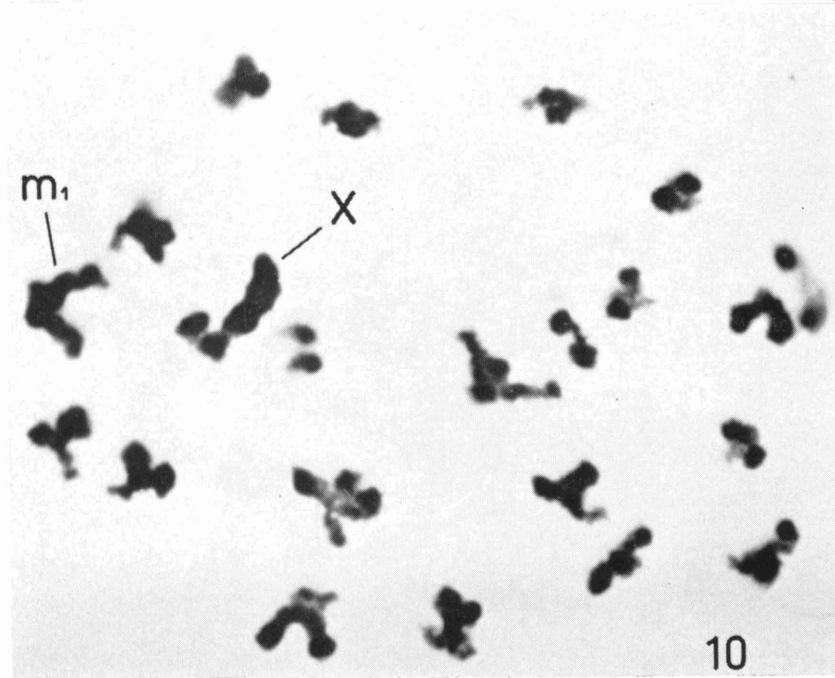
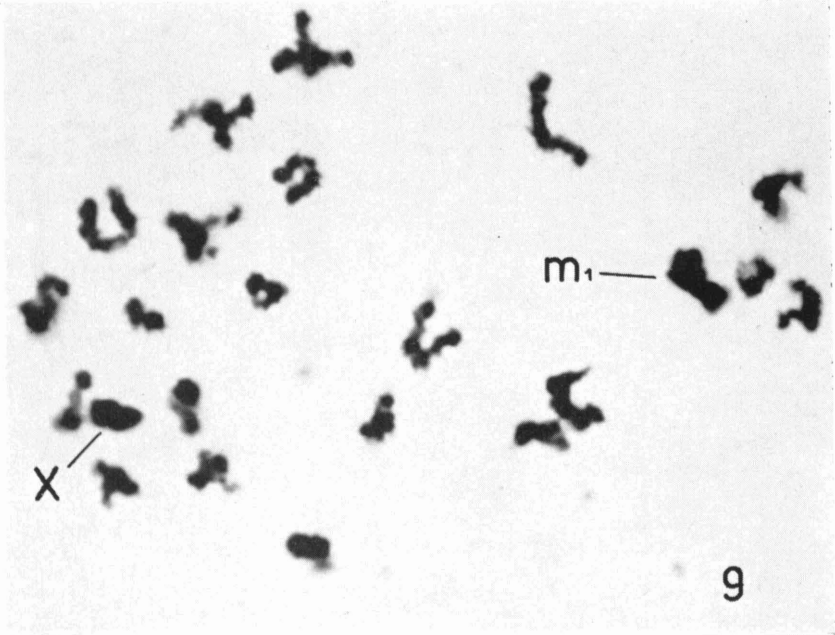


PLATE III

PLATE IV

Chromosomes of *Heteromallus*

- FIG. 11. *H. pectinipes*, first metacentric pair in pachytene stage.
- FIG. 12. *H. spina*, *idem*.
- FIG. 13. *H. spinifer*, *idem*.
- FIG. 14. *H. gracilipes*, *idem*.
- FIG. 15. *H. pectinipes*, first metacentric pair in first metaphase.
- FIG. 16. *H. spina*, *idem*.
- FIG. 17. *H. spinifer*, *idem*.
- FIG. 18. *H. gracilipes*, *idem*.
- FIG. 19. *H. pectinipes*, second metacentric pair in first metaphase.
- FIG. 20. *H. spina*, *idem*.
- FIG. 21. *H. spinifer*, *idem*.
- FIG. 22. *H. gracilipes*, *idem*.
- FIG. 23. *H. pectinipes*, X-chromosome in first metaphase.
- FIG. 24. *H. spina*, *idem*.
- FIG. 25. *H. spinifer*, *idem*.
- FIG. 26. *H. gracilipes*, *idem*.

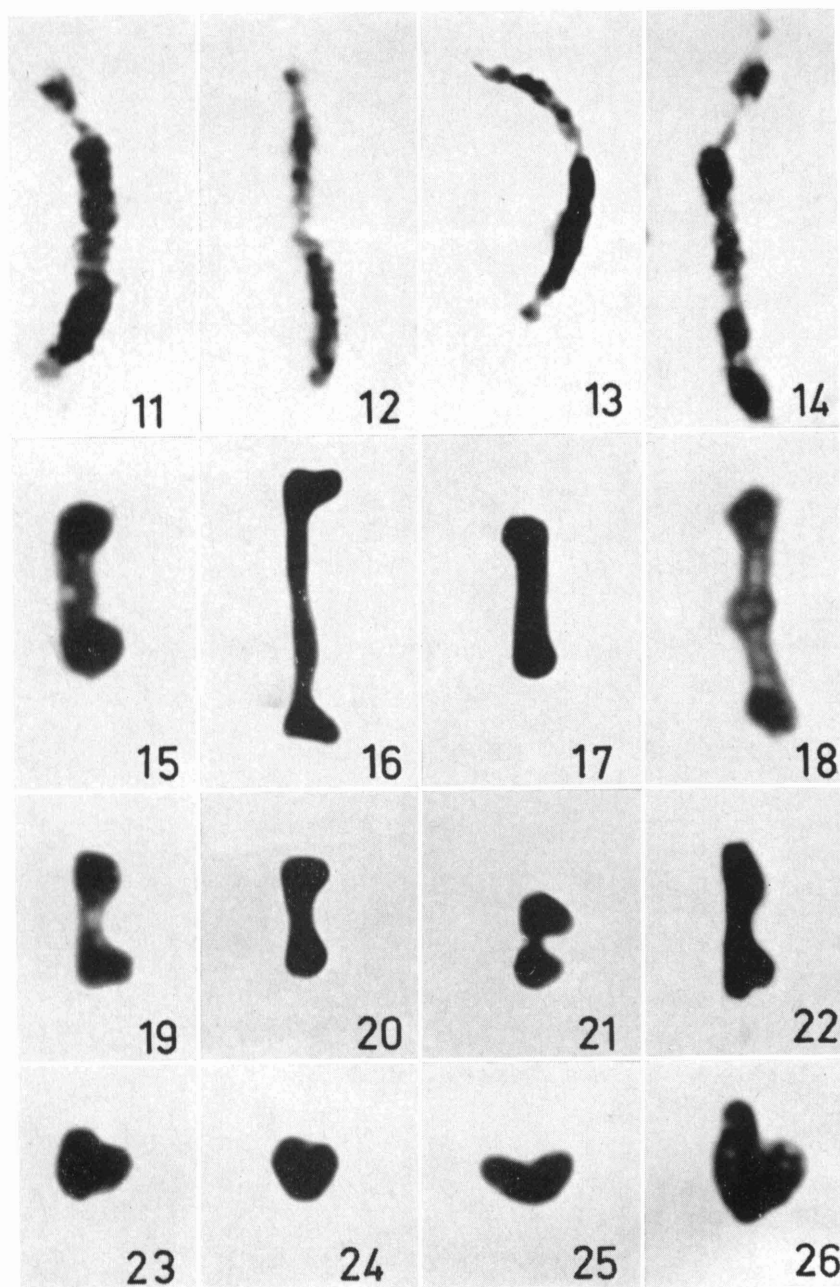


PLATE IV

