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Numerical variations of chromosomes in the natural populations of Indian acridids

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Abstract. Nine natural populations of Indian acridids belonging to seven species were cytologically analysed to study the numerical variations of chromosomes in the male germline cells. Of these, two allopatric populations of *A. humbertianus* and two of *O. nitidula* were chosen for intraspecies interpopulational studies. Both aneuploidy and polyploidy were encountered as intraindividual variations. Two kinds of polyploid cells—one with and another without multivalents—were found to occur. The former signified the occurrence of premeiotic mitotic breakdown of spindle whereas the latter was due to the failure of cytokinesis. While many tetraploid cells without multivalents successfully consummated meiosis producing dimegalous spermatids, tetraploid cells with multivalents and higher polyploids degenerated without completing meiosis. Analysis of quantitative data indicated that failure of cytokinesis is more frequent than spindle in premeiotic mitotic divisions. The frequency of second meiotic polyploid cells was significantly higher than those of first meiosis. The probable reasons for the increased incidence have been discussed. Comparative analysis of qualitative and quantitative data of these anomalies for the allopatric populations of *A. humbertianus* and *O. nitidula* showed that the population structure and breeding systems have an impact on the origin and incidence of the numerical chromosomal variations.

Keywords. Acridids; chromosome variations; *Acrotylus humbertianus*; *Oxya nitidula*.

1. Introduction

The adaptive organisation of a species is partly dictated by the release in time and space of chromosome variations and selection and integration of at least a few into the genetic system. The survival and stabilisation of any karyotypic change, whether it is structural or numerical, depends upon the consequent mechanical and genetic properties that it invokes. Mechanically, the chromosome change must be able to adapt with the dynamics of cell division. Thus, the evolutionary prospect of a newly arisen chromosome variation in the germline, can be assessed by analysing its mitotic and meiotic behaviour. Based on this precept, detailed qualitative and quantitative analyses of polyploid and aneuploid cells occurring in the

germlines of nine natural populations of Indian acridids were carried out. The resultant data on polyploid and aneuploid cells which reflect the relative frequencies of failure of cytokinesis, spindle breakdown and premeiotic mitotic non-disjunctions are presented in this paper. Concomitantly, their cytogenetic implications and their role in population dynamics are discussed.

2. Material and methods

Nine natural populations of short-horned grasshoppers belonging to seven species namely, *Oedaleus senegalensis*, *Trilophidia annulata*, *Acrotylus humbertianus*, *Oxya nitidula*, *Schistocerca gregaria*, *Catantops pinguis innotabilis* and *Chrotogonus oxypterus* were chosen for cytological analysis.

The localities of collection, the symbols used for each population and the number of individuals analysed are shown in table 1. Except for *A. humbertianus* and *O. nitidula*, a total of five populations, one from each of the remaining five species of acridids were examined cytologically. In case of *A. humbertianus*, samples of two populations—one from Mysore and another from Ranganathittu Island—were obtained. The two populations are separated by a distance of 14 km and the latter is bounded on all sides by an aquatic barrier. Similarly, samples of two populations of *O. nitidula*, one from Erode and another from Madras, were collected. These populations are separated by a distance of 317 km.

The testes from each male were removed by vivisection and fixed in 1 : 3 acetic-alcohol. Squash preparations were made using feulagen nucleal stain, Heidenhain's iron haematoxylin and aceto-orcein. All the follicles of the testes were used.

Table 1. Details of the different acridid populations examined.

Name of the species	Locations of collection	Symbols used	No. of individuals examined
Sub-family: *OEDIPODINAE*			
Oedaleus senegalensis Krauss	Manasagangotri, Mysore	OSM	20
Trilophidia annulata Thunb	Srirangapatnam	TAS	22
Acrotylus humbertianus Sauss	Manasagangotri, Mysore	AHM	26
Acrotylus humberianus Sauss	Ranganathittu Island	AHR	27
Sub-family: *CATANTOPINAE*			
Oxya nitidula Walk	Loyola College, Madras	ONM	46
Oxya nitidula Walk	Erode	ONE	23
Schistocerca gregaria Forskal	Bikaner, Rajasthan	SGB	20
Catantops pinguis innotabilis Walk	Manasagangotri, Mysore	CPM	25
Sub-family : *PYRGOMORPHINAE*			
Chrotogounus oxypterus Blanch	Manasagangotri, Mysore	COM	50

Both qualitative and quantitative assay of polyploid and aneuploid cells present in the male germline were done. The frequencies of these anomalies are tabulated independently for all the phases of meiosis and were later categorised under the anomalies of first and second meiotic divisions separately (table 2). Data collected under the last categories were treated as independent classes for biostatistical analysis. Utilising the arc sine transformed data, analysis of variance test was performed to compare the anomalies of the different stages of meiosis (table 3). Similarly, comparison of intraspecies populations of *A. humbertianus* and *O. nitidula* was made, using the test for normal deviate (ND). The resultant values expressed the degree of deviation of the concerned numerical variation between the populations.

3. Observations

3.1. *Polyploidy*

This chromosomal variation was found to occur in all the nine populations examined (table 2). Only tetra- and octoploid meiotic cells with a preponderance of the former were observed. Triploid cells were never encountered. Uninucleate tetraploid leptotene cells were recognised by the presence of two sex chromatin masses (figure 1) or a single large mass (figure 2). Octoploid cells did not pass through beyond metaphase I (figures 3 and 4). Without taking into cognisance of the level of ploidy, all these cells were qualitatively categorised as those with multivalents (figures 3 and 5) and those without multivalents (figures 4 and 6). Multivalent formation was restricted to long chromosomes of the complement. The

Table 2. Percentage of meiotic cells showing polyploidy and aneuploidy.

Species/population examined	Meiosis–I					Meiosis–II		
	Total cells counted	Polyploid			Aneu-ploid	Total cells counted	Poly-ploid	Aneu-ploid
		with multi-valents	without multi-valents	Total				
Oedaleus senegalensis	5682	0·14	0·32	0·46	0·33	2627	0·61	..
Trilophidia annulata	6517	0·02	0·15	0·17	0·03	2484	0·52	..
Acrotylus humbertianus (Mysore)	5838	..	0·24	0·24	..	2167	0·42	..
Acrotylus humbertianus (Ranganathittu)	7962	0·05	0·14	0·19	0·03	2198	1·64	..
Oxya nitidula (Madras)	12449	..	0·02	0·02	0·01	4296	0·12	..
Oxya nitidula (Erode)	6654	0·02	0·05	0·06	..	1354	..	..
Schistocerca gregaria	15542	0·03	0·26	0·29	0·14	4389	0·32	..
Catantops pinguis innotabilis	9178	0·01	0·20	0·21	0·10	4272	0·96	0·02
Chrotogonus oxypterus	20612	0·01	0·03	0·04	3·38	14580	0·28	0·23

Table 3. Analysis of variance on the arc sine transformed data for various items of numerical chromosome variations.

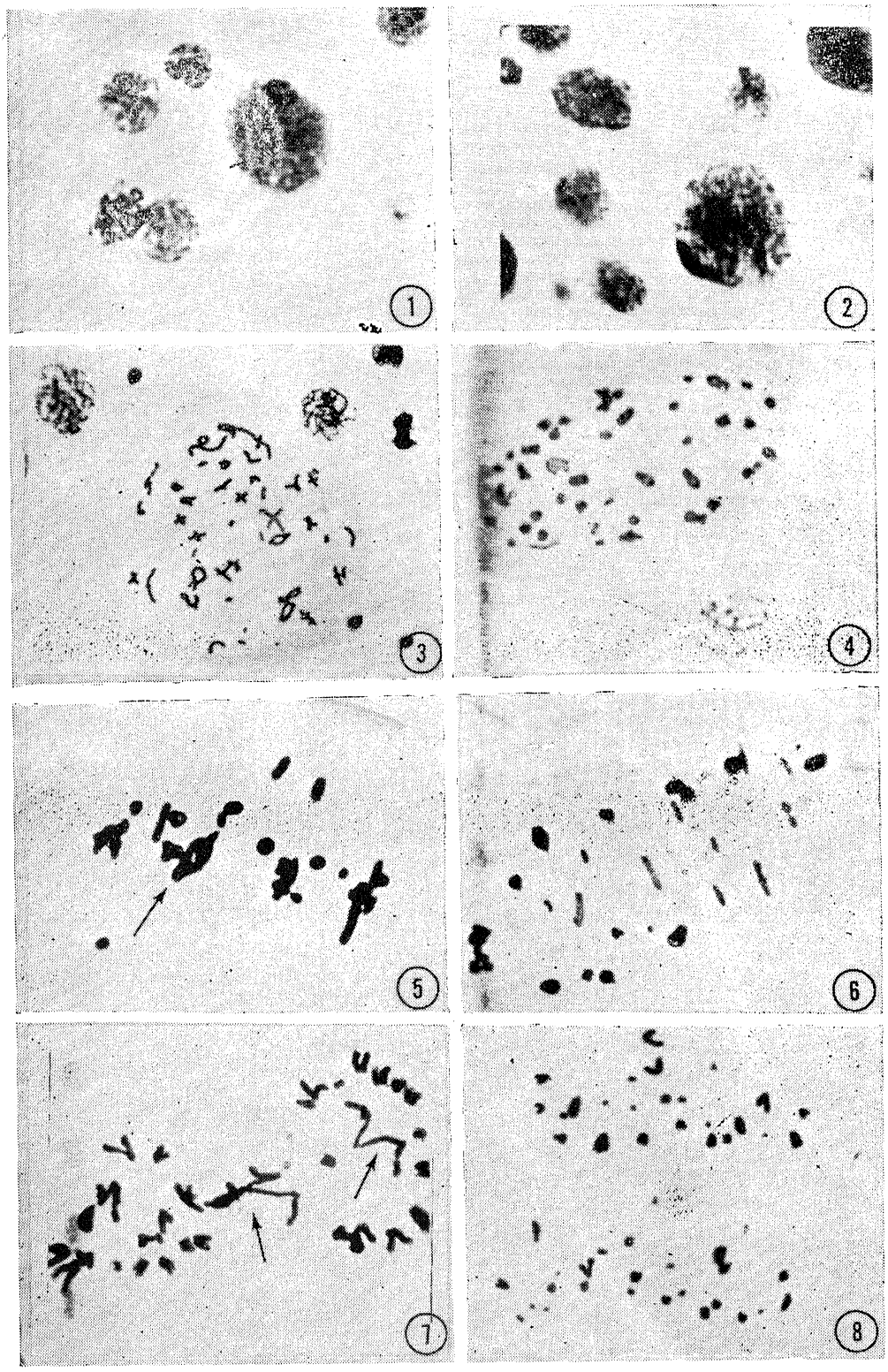
Phase of division and nature of cells	Populations analysed	*df*	*t*	*P*
Meiosis–I: Polyploid cells with multivalents × Meiosis–I: Polyploid cells without multivalents	9	8	4·917	$< 0·005$
Meiosis–I: Total polyploid cells × Meiosis–II: Total polyploid cells	9	8	2·443	$< 0·05$
Meiosis–I: Polyploid cells with multivalents × Meiosis–I: Total aneuploid cells	9	8	1·339	NS
Meiosis–I: Polyploid cells without multivalents × Meiosis–I: Total aneuploid cells	9	8	0·134	NS
Meiosis–I: Total polyploid cells × Meiosis–I: Total aneuploid cells	9	8	0·014	NS

multivalent chromosomes in tetraploid cells often lagged in the middle of the spindle (figure 7). Due to such segregational disorders, tetraploid cells with multivalents never consummated meiosis. On the other hand, many cells which lacked multivalents showed normal orientation and segregation of chromosomes in meiosis I (figures 4, 6 and 8). While most of the metaphase II tetraploid cells possessed diploid number of half bivalents (figure 9), some showed the presence of a bivalent (figure 10), or a reoriented unbroken dicentric bridge (figure 11). Movement of chromosomes in anaphase II tetraploid cells derived from tetraploid primary spermatocytes was normal (figure 12) except in very few instances where one or more elements lagged in the spindle (figure 13). Those which were free from laggards completed meiosis giving rise to diploid spermatids (figure 14). But where there were laggards, the spindle broke down (figure 15) and the resultant cells either underwent degeneration (figure 16) or were converted into tetraploid spermatids (figure 14).

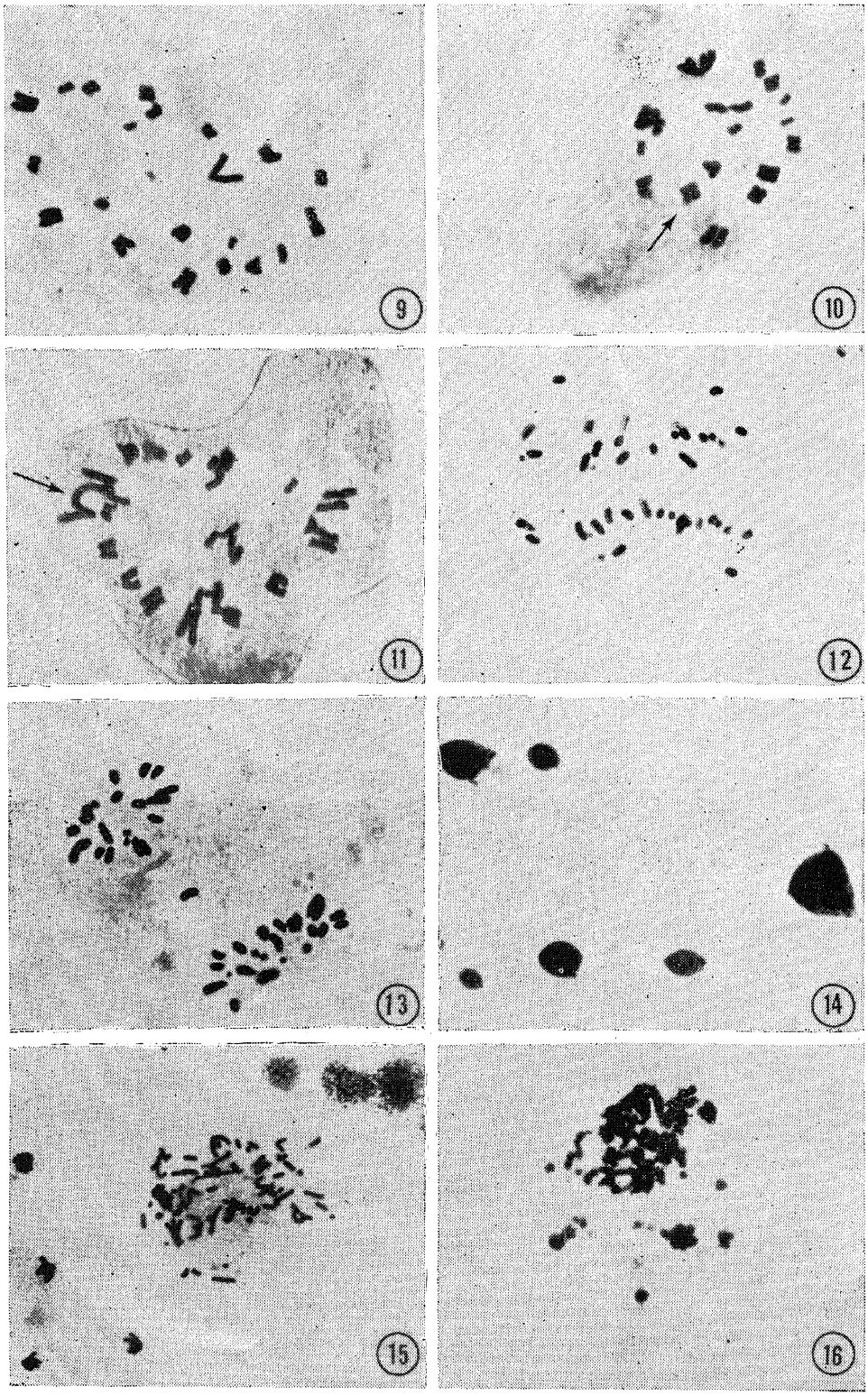
Data from tables 2 and 3 indicate that tetraploid cells with multivalents were significantly fewer than cells without multivalents ($P < 0·005$). They also indicate that the frequency of second meiotic polyploid cells was significantly higher than the frequency of first meiotic polyploid cells ($P < 0·05$).

3.2. *Aneuploidy*

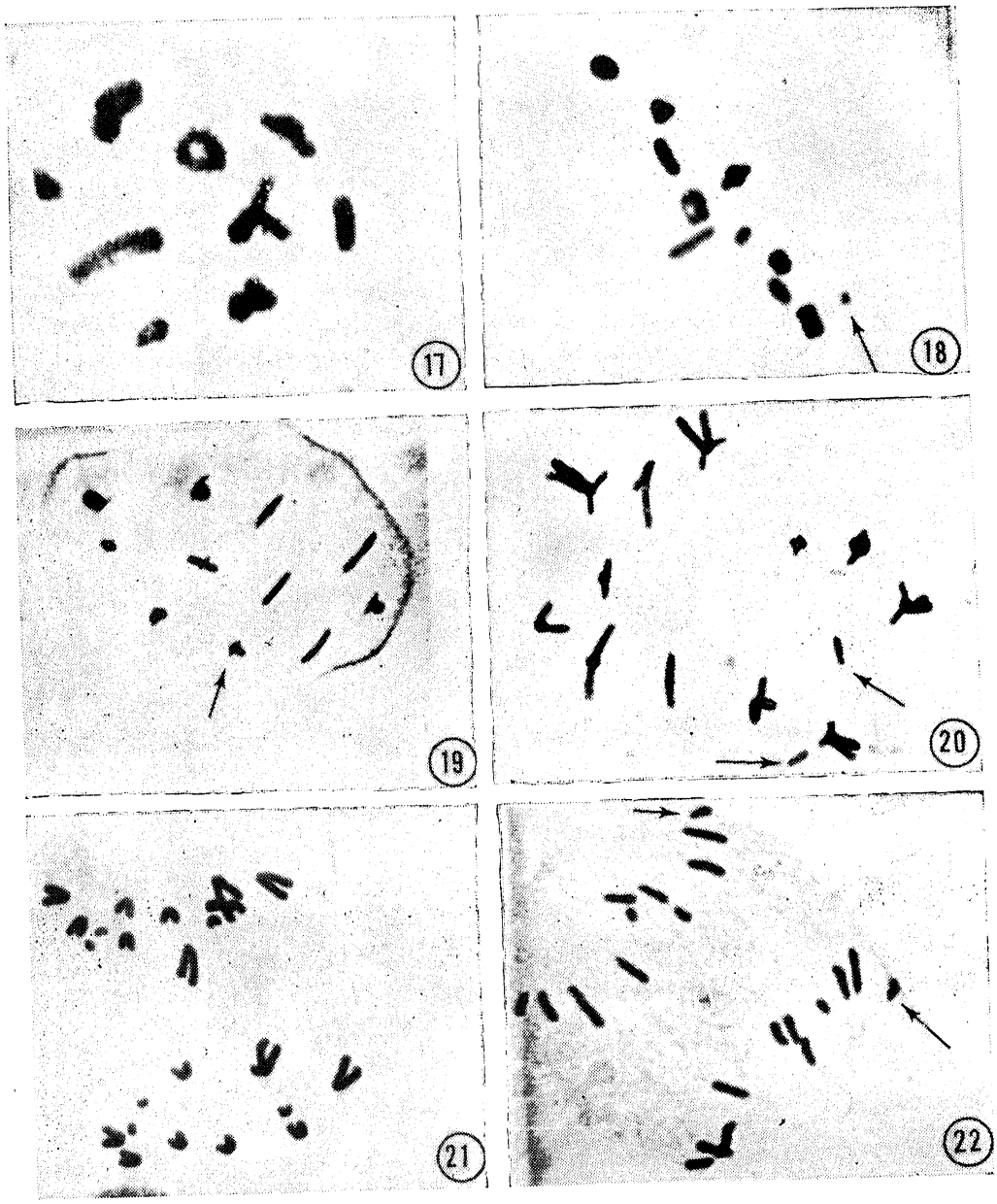
Except the AHM population of *A. humbertianus* collected from Mysore and ONE population of *O. nitidula* collected from Erode, aneuploidy was recorded in the



Figures 1–8. **1–2.** *Catantops pinguis innotabilis* : Tetraploid leptotene cells with two and one sex-chromatin masses. **3.** *A. humbertianus* (Ranganathittu) : Octoploid diplotene cell with multivalents. **4.** *S. gregaria* : Octoploid metaphase–I cell without multivalents. **5.** *A. humbertianus* (Ranganathittu) : Tetraploid metaphase–I cell with a multivalent (arrow). **6.** *A. humbertianus* (Mysore) : Tetraploid metaphase–I cell without multivalents. **7.** *Catantops pinguis innotabilis* : Tetraploid anaphase–I cell with lagging and non-lagging multivalents (arrows). **8.** *A. humbertianus* (Mysore) : Tetraploid anaphase–I cell showing normal segregation.



Figures 9–16. **9.** *Catantops pinguis innotabilis* : Metaphase–II tetraploid cell. **10.** *Catantops pinguis innotabilis* : Metaphase–II tetraploid cell with a bivalent (arrow). **11.** *Catantops pinguis innotabilis :* Metaphase–II tetraploid cell with a reoriented unbroken dicentric chromatid bridge. **12.** *A. humbertianus* (Mysore): Anaphase–II tetraploid cell showing normal segregation. **13.** *A. humbertianus* (Ranganathittu) : Anaphase–II tetraploid cell with a laggard. **14.** *S. gregaria :* Haploid, diploid and tetraploid spermatids in mid-spermiogenesis. **15–16.** *A. humbertianus* (Mysore) : Degenerating second meiotic polyploid cells after spindle breakdown.



Figures 17–22. Aneuploid cells. **17.** *C. oxypterus* : Nullisomic diplotene cell $2n = 8AA + X$. **18.** *Ch. oxypterus* : Trisomic metaphase–I cell $2n = 9AA + X +$ one univalent (arrow). **19.** *C. oxypterus :* Tetrasomic metaphase–I cell with an additional bivalent $2n = 9AA + 1AA + X$ (arrow). **20.** *Catantops pinguis innotabilis :* Tetrasomic metaphase–I cell with $2n = 9AA + X +$ two univalents (arrows). **21.** *A. humbertianus* (Mysore) : Anaphase–I cell showing normal segregation of the extra bivalent. **22.** *C. oxypterus :* Anaphase–II cell with an extra chromosome in each pole (arrows).

remaining populations. The highest frequency of aneuploidy was found in *C. oxypterus* (3·38% and 0·23% in I and II meiotic cells respectively). Aneuploids of various grades from nullisomy to tetrasomy were observed (figures 17–22). Multivalent formation in trisomic and tetrasomic cells was never observed. In trisomic cells, the extra chromosome remained as an unpaired univalent (figure 18). During anaphase I, the odd chromosome either lagged in the spindle or moved to one of the poles undivided. In the latter case, it divided in the second meiotic division. The two additional chromosomes in tetrasomic cells frequently paired to form a bivalent (figure 19). But, occasionally they failed to pair and therefore remained as univalents (figure 20). The movement and segregational pattern of the extra bivalent synchronised with those of the normal bivalents in anaphase I (figure 21) and anaphase II (figure 22). Perusal of table 2 shows that apparently the frequency of total polyploidy was higher than that of aneuploidy in all the populations except in *C. oxypterus*. However, analysis of data in table 3 indicated that this difference was not significant. A similar pattern emerged when we compared the frequency of aneuploid cells and polyploid cells with and without multivalents.

4. Comparison of intraspecies populations

When comparisons of the frequencies of (i) first meiotic polyploid cells, (ii) second meiotic polyploid cells, (iii) total polyploid cells and (iv) total polyploid and aneuploid cells between AHM (Mysore) and AHR (Ranganathittu Island) populations of *A. humbertianus* were made (tables 2 and 4), it was found that the AHR population showed significant higher frequencies for all categories except for first meiotic polyploidy. It was further noticed that the metaphase II polyploid cells had mainly contributed to these increased frequencies.

Likewise, comparison of the two populations of *O. nitidula* indicated that although there were significant differences in the incidence of first meiotic polyploid cells and second meiotic polyploid cells between the populations, the differences for the frequency of total polyploid cells of both divisions and for the frequency of polyploid and aneuploid cells of both divisions of meiosis were not significant (tables 2 and 4).

5. Discussion

Polyploidy as a form of numerical chromosomal deviant has been recorded in several Indian short-horned grasshoppers (Ramachandra Rao 1933; Ray-Chaudhuri and Bose 1948; Dutt 1951; Sharma *et al* 1962; Rahiman and Rajasekarasetty 1967). Analysis of tetraploid cells in meiosis I made it possible to discern two categories of cells—one with and another without multivalents. This difference reflects their different modes of origin. Multivalent formation is characteristic of uninucleate tetraploid primary spermatocytes which originate as a result of spindle breakdown in premeiotic mitotic division. In contrast, absence of multivalents is distinctive to binucleate tetraploid primary spermatocytes. These arise from failure of cytokinesis in the premeiotic mitotic division.

It is interesting to note that only long chromosomes are involved in multivalent formation and the number of multivalents noticed in tetraploid cells never exceeded

Table 4. Comparison of intraspecies populations of *Acrotylus humbertianus* (AHM and AHR) and *Oxya nitidula* (ONM and ONE).

Phase of division and nature of cells	Frequency (%)		ND	*P*
Meiosis-I: Polyploidy	0·24 (AHM)	0·19 (AHR)	1·283	NS
Meiosis-II: Polyploidy	0·42 (AHM)	1·64 (AHR)	2·765	$< 0·01$
Meiosis-I and II: Polyploidy	0·29 (AHM)	0·50 (AHR)	4·484	$< 0·001$
Meiosis-I and II: Total polyploidy and aneuploidy	0·29 (AHM)	0·52 (AHR)	4·793	$< 0·001$
Meiosis-I: Polyploidy	0·06 (ONE)	0·02 (ONM)	7·986	$< 0·001$
Meiosis-II: Polyploidy	0·00 (ONE)	0·12 (ONM)	3·008	$< 0·005$
Meiosis-I and II: Polyploidy	0·0499 (ONE)	0·0477 (ONM)	0·157	NS
Meiosis-I and II: Total polyploidy and aneuploidy	0·0499 (ONE)	0·5374 (ONM)	0·261	NS

two at the maximum. This is in contrast to the findings of White (1934) in *Schistocerca gregaria* and John and Henderson (1962) in *Schistocerca paranensis*. While White found a maximum of six multivalents, John and Henderson observed that all classes of chromosomes were involved in multivalent formation. Thus, it may be inferred that the interference caused by the presence of multivalents in the completion of cell division is comparatively minimised in the populations under study by reducing the total number of multivalents. In spite of this reduction in the number of multivalents, the present observations showed that cells with multivalents never completed meiosis due to segregational disorders. Thus a tetraploid cell which originates as a consequence of spindle breakdown has no evolutionary scope, since selection will eliminate it prior to the completion of meiosis. On the other hand, tetraploid cells without multivalents generally consummate meiosis producing diploid spermatids. It will, however, be shown in the later part of this discussion that these will also be selected against at the zygotic level. Therefore, both kinds of tetraploid cells lack any evolutionary potential in the acridid populations examined. The fate of higher polyploid cells simulate that of tetraploid cells with multivalents in that they never progress beyond metaphase I and undergo degeneration subsequently. This is due to spatio-temporal disturbances caused by the high polyploid condition, ultimately leading to blockage of cell division.

Comparison of data (tables 2 and 3) with regard to the frequencies of tetraploid cells with and without multivalents indicates that the frequency of the former is significantly lower than the latter in all the populations. This in turn implies a higher frequency of failure of cytokinesis than spindle breakdown. The presence of higher ploidy cells like octoploids without multivalents suggests the existence of tetranucleate spermatocytes. They seem to have arisen by two consecutive failures of cytokinesis at premeiotic mitoses. White (1973) has proposed that multinucleate cells can be derived by the fusion of spermatocytes. Such spermatocyte fusion has not been encountered in the present analysis. Further, if this process

is operative, a few hexaploids must have been observed in addition to tetra- and octoploids since the chances of fusion of three spermatocytes should be in par with the fusion of two and four spermatocytes. The rarity of octoploid cells in comparison to tetraploid cells point that failure of cytokinesis in two successive mitotic divisions of spermatogonia is an occasional event.

When the frequencies of polyploids between the first and second meiotic cells are compared, it is found that the latter always exceeds the former significantly in every population of the species studied. Qualitative analysis has shown that some of the tetraploid metaphases in second division represent restitution nuclei. This demonstrates that cleavage suppression subsequent to anaphase I results in metaphase II polyploidy. The presence of bivalents and unbroken dicentric bridges in some metaphase II tetraploid cells indicates that cleavage suppression must have been brought about by either laggards or by the persistent dicentric bridges.

Production of large diploid spermatids as a consequence of successful completion of meiosis by tetraploid cells has been reported in acridids (Callan 1941; Mickey 1942; Lewis and John 1959; Rajasekarasetty 1965; Nur 1969). Paulmiers (1899) and Creighton and Evans (1941) (as quoted by Ray-Chaudhuri and Bose 1948) postulated direct transformation of primary spermatocytes as a way of diploid spermatid production. The dimegalous spermatids studied in all the populations presently, however, are the end products of meiosis of tetraploid cells. No evidence can be adduced to show that spermatocytes are directly transformed into spermatids. Thus far no report has forthcome with regard to the existence of polyploid grasshoppers. This, as Lewis and John (1959) pointed out, may be due to a failure on the part of diploid sperms to compete successfully with haploid sperms at fertilisation or having succeeded at fertilisation may produce inviable zygotes.

Prevalence of aneuploid cells in the germline of short-horned grasshoppers was reported previously by Callan (1941), Lewis and John (1959), John and Naylor (1961) and Hewitt (1963). This anomaly originates by the process of mitotic non-disjunction. Existence of tetra- and nullisomic cells suggests successive non-disjunction of chromosomes in the premeiotic mitotic divisions. Present analysis corroborates the previous findings that aneuploidy in the majority of acridid populations prevails as an intraindividual chromosomal variation. Development of individuals from polysomic zygotes is an extremely rare event in nature (Callan 1941; Hewitt and John 1965). The studies of Callan (1941) and Hewitt (1963) have shown that the presence of extra chromosomes frequently causes breakdown of meiosis and imposes genetic instability at the gametic level. Failure to record polysomic individuals in the populations under study in spite of wide occurrence of aneuploidy in the germline, must be attributed to the production of genetically imbalanced and non-viable zygotes.

Comparison of the frequencies between first meiotic aneuploid and polyploid cells with and without multivalents is instructive in appraising the relative rates of premeiotic mitotic non-disjunction on the one hand and failure of spindle and cytokinesis on the other respectively. Perusal of quantitative data in table 2 and statistical analysis in table 3 reveals that even though the frequency of premeiotic non-disjunction is higher than spindle breakdown, it is not significant. A similar result is obtained when the frequencies of non-disjunction and failure of cytokinesis are compared. Quantitative data of table 2 further show that the incidence of

aneuploid cells in *C. oxypterus* is several folds higher than the incidence of polyploid cells. It can be inferred that only in the population of this species, the rate of non-disjunction is higher in relation to spindle and cytokinetic failures. The fundamental difference between this population and the remaining eight populations may be a reflection of the two interlinked attributes of a natural population namely, the breeding system and genotypic control of cell division.

Statistical comparison of the intraspecies populations of *A. humbertianus* and *O. nitidula* (table 4) has thrown light to a certain extent on the relationship between the frequencies of anomalies and population structure.

Except for the incidence of first meiotic polyploid cells, the AHR population shows high frequencies of both first meiotic aneuploid cells and second meiotic polyploid cells. This means that the incidence of non-disjunction and breakdown of first meiotic spindle is much more frequent in AHR population. This population is restricted to Ranganathittu Island with an effective barrier and thus constitutes a small population. Concomitantly, inbreeding must be prevailing in this population. Thus, the population structure and breeding systems of the two populations vary. It is opined that both attributes namely, the size of the population and the consequent high degree of inbreeding are responsible for the partial breakdown of the genotypic control over cell division. This view derives its support by the work of Lewis and John (1959) who found that there is a breakdown of chromosome stability during cell division following inbreeding of the grasshopper *Pyrgomorpha kraussi.*

The ONM and ONE populations of *O. nitidula* are also allopatric since they are geographically isolated from each other by a distance of 314 km. Data from tables 2 and 4 indicate that the frequency of first meiotic polyploid cells in ONE is significantly higher than ONM population whereas the frequency of second meiotic polyploid cells in ONM population is significantly higher than ONE population. The individuals of ONE population were collected from open paddy fields. The individuals of the ONM population were collected from the specially grown grass field of Loyola College, Madras, which is encircled by a compound wall. Although this cannot be construed as an effective barrier, the outer surrounding area is not found to be very favourable for the inhabitation of the grasshoppers. Hence it is reasonable to surmise that most of the individuals tend to remain within the confines of the college which provide ideal conditions for inhabitation. Thus, ONE populations is a large and outbreeding unit and ONM population is a small, relatively inbreeding one. As in the case of *A. humbertianus,* there is divergence both in the population structure and breeding system. Similarly, it is also a case where inbreeding has upset the genotypic control over cell division.

The discussion on karyotypic stability as related to population structure and breeding system in the populations of *A. humbertianus* and *O. nitidula* brings out a pertinent fact. In the small populations of both species where inbreeding is practiced, there is relative breakdown of genotypic control affecting adversely the premeiotic mitotic disjunctional behaviour of chromosomes and stability of first meiotic spindle. Hence, the high incidence of first meiotic aneuploidy and second meiotic polyploidy.

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