

between the 2 years⁶. In 1970, females had ready access from the well to the ovitraps via an exit trap in the well lid, from which the mosquitos were liberated outside the well daily. However, in 1971, 1972 and 1973 mosquitos could only leave the well with difficulty because the lid was sealed and the only access was through underground channels^{2,6}. The conclusion that the reduced raft collection in 1971, compared with 1970, is not attributable to the effect of the translocation is supported by data⁶ showing approximately constant numbers of rafts collected in the ovitraps in 1971, 1972 and 1973, during which period the proportion of translocated rafts declined from 80% to less than 1% (Figure).

The response to natural selection of a male-linked translocation differs from that of an autosomal or X chromosome translocation with a viable and fertile homozygote, where the translocation frequency would increase spontaneously if a certain equilibrium is exceeded¹²⁻¹⁴. This property arises from negative heterosis (i.e. the heterozygote has less fitness than either homozygote) and it does not apply to the male-linked case where the translocation homozygote cannot exist.

Male-linked translocations could persist in populations, or even spontaneously increase, in the following situations: 1. Permanent association of the translocation with greatly enhanced mating competitiveness¹⁰. Enhanced competitiveness in translocated males was found in a cage experiment¹¹, but this was apparently due to the conditions under which the translocation material for release was reared and would not therefore be expected to apply in the progeny of released males. 2. Linkage of the translocation to a factor causing segregation distortion in favour males¹⁵⁻¹⁷. This system could only lead to increase in the translocation frequency if the translocation caused less than 50% sterility; otherwise the output of male progeny from distorter-translocation fathers would be sub-normal and natural selection would favour the normal male-determining chromosome. However, recent field cage tests at this Unit have shown that integration of sex-ratio distortion with translocations improves their ability to suppress a population¹⁸. 3. Association of the translocation with a 'transport system' based on negative heterosis. Cytoplasmic incompatibility may provide such a system¹⁹, and cage experiments²⁰ have shown the operation of the principle. However, a polymorphism of cyto-

plasmic types in Indian *C. fatigans* populations²¹ and attenuation of incompatibility with ageing of males²² can cause recombination of a translocation and the cytoplasmic transport system²⁰. Further studies are required to determine whether, by minimizing female releases and ensuring that females have mated before release, the system could achieve effective population control.

Summary. Published data on an experimental release of *Culex pipiens* carrying a male-linked translocation are re-examined and it is shown that the steady decline in translocation frequency after termination of releases agrees with theoretical expectations, because of the selective disadvantage of translocation heterozygote males. Systems based on negative heterosis or meiotic drive are considered whereby it might be possible to prolong the population control which would be achieved by a short term release.

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Karyotype of *Geomys pinetis* (Mammalia: Geomyidae), with a Discussion of the Chromosomal Relationships Within the Genus¹

Pocket gophers of the genus *Geomys* are fossorial rodents occurring in the central and southeastern United States and northeastern Mexico. Within the genus, RUSSELL² recognized two species-groups of recent species. Members of the 2 groups are geographically isolated with the Mississippi River and associated lowlands serving as a barrier between them. All members of the *bursarius* species-group (*bursarius*, *arenarius*, *personatus*, and *tropicalis*) have been studied chromosomally. However, none of the members of the *pinetis* species-group (*pinetis*, *colonus*, *cumberlandius*, and *fontanelus*) have been karyotyped. Of the species in this group, only *G. pinetis* occupies a large geographic area in the southeastern United States; the other 3 species are known only from highly restricted areas and their systematic relationships to *G. pinetis* are poorly understood.

We have karyotyped 10 individuals of *Geomys pinetis* using techniques described by BAKER³. Specimens

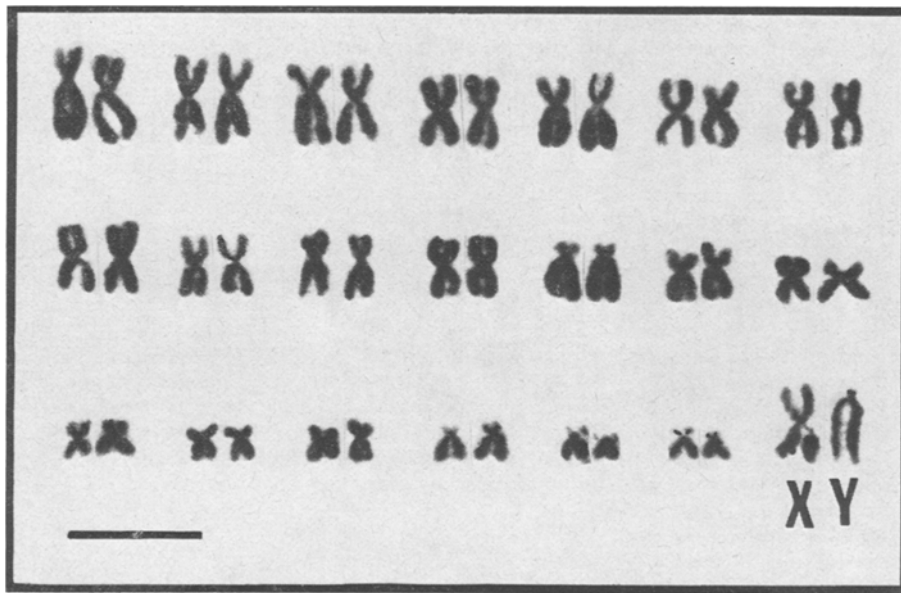
studied represent 4 currently recognized subspecies - *austrinus*, *floridanus*, *mobilhensis*, and *pinetis*. Efforts to obtain the remaining described forms of the *pinetis* species-group were unsuccessful because of scarcity or possible extinction⁴. All individuals that were studied had the same karyotype indicating that there may not be any

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Karyotype of a male *Geomys pinetis floridanus* from 1 mi. NW Bayard, Duval Co., Florida. The line represents a scale of 10 μ m in length.

geographic variation or polymorphism in chromosomes of this species. The $2N$ is 42 with a FN of 80. All of the autosomes are biarmed elements ranging from metacentrics to submetacentrics. The X -chromosome is a large metacentric chromosome and the Y is a large subtelocentric chromosome (Figure).

Among the members of the *bursarius* species-group, *G. pinetis* most closely resembles *G. tropicalis* karyotypically. *Geomys tropicalis* has a $2N$ of 38 and an FN of 72⁵. Other members of the group have high diploid numbers as follows: *G. bursarius*, $2N = 69-72, 74, FN = 68-100^{6-8}$; *G. personatus*, $2N = 68, 70, 72, FN = 70-76^5$; *G. arenarius*, $2N = 70, FN = 102^5$. In all species of this group except *bursarius*, the X -chromosome is a large biarmed element and the Y -chromosome is a small acrocentric element. In *bursarius*, the Y is the same as in the above species, but the X -chromosome is variable, being a large acrocentric in some populations and a large metacentric in other populations.

The chromosomal relationships of these species may be best understood in light of our knowledge of the fossil history of the genus⁹. The earliest Pleistocene records of the genus are from the Great Plains of the central United States. The southeastern species of *Geomys* were probably derived from this stock in Illinoian (middle Pleistocene) time. RUSSELL¹⁰ believed that the *pinetis* and *bursarius* groups were differentiated by the beginning of the Sangamon (late Pleistocene). Other species within these groups are believed to have differentiated in the late Wisconsin.

MARTIN^{11,12} and MARTIN and WEBB¹³ in a series of papers on Pleistocene mammals from Florida agree with RUSSELL that *G. bursarius* and *G. pinetis* groups have been separated since at least Illinoian time. But they then seem to suggest that *G. personatus* and *G. pinetis* may not be distinct at the specific level. Whether they are suggesting that *G. personatus* be transferred to the *pinetis* group or that the 2 groups are closely related is not clear. However, our karyotypic data definitely indicate that *personatus* and *pinetis* are distinct species. There is no disagreement that the 3 species (*bursarius*, *personatus*, and *pinetis*) evolved from a common ancestor but we believe that *pinetis* has been isolated longer from the *bursarius-personatus* complex than they have been from each other.

As pointed out, the karyotype of *Geomys pinetis* is most similar to, although not identical to, *Geomys tropicalis* of the *bursarius* group. However, the differences in their karyotypes are significant in that *G. pinetis* has 4 chromosomes that are not present in *G. tropicalis*. We believe that these similarities are the result of convergence in centric fusions from a chromosomal complement similar to that of *G. bursarius* or *G. personatus*. This would mean that the karyotype of *Geomys pinetis* was derived by a series of centric fusions and centric shifts, and that of *tropicalis* mainly by centric fusions. *G. arenarius* has a karyotype that was probably derived from a similar primitive karyotype, but mainly by a series of centric shifts. Chromosomally, *G. bursarius* and *G. personatus* are most similar of known members of the genus⁸. They probably also possess a chromosomal complement near that of the ancestral stock. We agree with DAVIS et al.¹⁴ that the ancestral karyotype of *Geomys* probably consisted almost entirely of acrocentric elements with a diploid number of about 70.

Specimens examined: *Geomys pinetis austrinus* - Florida: Hillsborough Co., Tampa, vic. Univ. South Florida, 2 ♂ (TTU 16607, TTU 16610), 1 ♀ (TTU 16613).

Geomys pinetis floridanus - Florida: Alachua Co., 1.9 mi. NW Jct. Hwy. 24 and Hwy. 41 on Hwy. 41, 1 ♀ (TTU 16621); Florida: Alachua Co., 1.4 mi. NW Jct. Hwy. 24 and Hwy. 41 on Hwy. 41, 1 ♂ (TTU 16622);

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¹³ R. A. MARTIN and S. D. WEBB, in *Pleistocene Mammals of Florida* (University Presses of Florida, Gainesville 1974), p. 120.

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Florida: Duval Co., 1.0 mi. NW Bayard, 1 ♂ (TTU 16619), 1 ♀ (TTU 16620).

Geomys pinetis mobilensis – Florida: Okaloosa Co., 0.5 mi. W county line on Hwy. 90, 1 ♀ (TTU 16630).

Geomys pinetis pinetis – Georgia: Camden Co., Kingsland, 1 ♀ (TTU 16638); Georgia: Camden Co., 5.9 mi. W St. Marys, 1 ♀ (TTU 16641).

Summary. 4 of the 5 subspecies of *Geomys pinetis* were karyotyped. All specimens examined had a diploid

number of 42 and a fundamental number of 80. This karyotype was compared with the described karyotypes of other species of *Geomys* and was considered to be derived from an ancestral form having a karyotype of about 70 acrocentric elements.

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Mitotic Activity of Endopolyploid Root Cells in *Allium cepa*

The cellular differentiation may be interpreted as a controlled process through which cells with the same genetic charge reach different protein constitutions. In this sense one of the genetic patterns responsible for cyto-differentiation is the differential duplication of the chromosome material. Both in animal and in plant development, somatic polyploidy goes with the differentiation of many cells¹⁻³. In addition, polyploidization of differentiated cells is in many cases produced through an endopolyploid process^{4,5}. In the course of cytological studies on *Allium cepa* meristems, marked differences of size between the cell nuclei in a same root may be observed which might indicate a polyploidization of certain cells as reported in other species of *Allium*⁶.

The aim of the present study is a first approach to the problem of cytodifferentiation by endopolyploidy from diploid meristematic cells, examining the chromosome constitution of polyploid cells of *Allium cepa* roots which have been experimentally induced to divide.

Materials and methods. *Allium cepa* L. root meristems were used. Onion bulbs were grown in the dark at constant temperature (25°C) with tap water renewed every 24 h and continuously aerated. Roots from several bulbs were fixed in 3:1 ethanol-acetic and the specimens were prepared by staining the squashes with acetohydrochloric orcein.

Roots were immersed for 10 min in a solution of thymidine (Schuchardt) diluted with tap water at a concentration of 5 mg/ml and then allowed to recover in renewed tap water. Several roots from each bulb were excised at intervals of 2 h, throughout 4 h recovery from treatments. In order better to separate the metaphase chromosomes, the excised root tips were submerged in a 1 mg/ml colchicine (Sigma) solution for 1 h before fixation. The culture conditions already described were maintained throughout the experiments.

Results and discussion. In all *Allium cepa* bulbs studied, the meristematic cells from the control roots exhibited before the beginning of experiments normal chromosome constitution: $2n = 16$ chromosomes. The root-tips treated, washed and immersed in aerated tap water, show cells with $4n$ nuclei at 3 to 5 h (after colchicine-treatment).

Most of the cells blocked in metaphase – treatment with colchicine – show the typical *Allium cepa* chromosome complement (Figure a) but a small percentage of cells of bigger size in c-metaphase with the dotation $4n = 32$, or with 16 arrangements of 4 chromatids may be observed (Figure b). These metaphases $4n$ display chromosomes forming pairs next to each other or pairs of chromosomes held together at the region adjacent to the kinetochore, which is known under the name of diplochromosomes. The c-anaphases observed in these polyploid cells consisted of groups of 4 very closely allocated chromatids, in the characteristic form of 'ski pairs'.

The existence of endopolyploid cells may be due to a process of differentiation or dedifferentiation⁷, as well as the experimental induction. Concerning the experimental induction of endopolyploidy cited in the literature, one must distinguish between the induction of this state and the mitotic promotion of endopolyploid cells. So, several agents with a stimulating effect on the cell division are known: phytohemaglutinine in lymphocyte cultures⁸ and a variety of growth hormones in plant systems^{9,10}.

Colchicine effect. Regarding the origin of polyploid observed cells, we must reject the possibility of an action of colchicine. C-mitotic agents are known to be able to induce polyploidy and even endopolyploidy^{11,12}, but that polyploidization is produced by the metaphase parade of the cells, causing the formation of restitution nuclei and the achievement of polyploid level with the posterior chromosome replication of these cells. In our case, the fixation of the roots at the end of the treatment with the c-mitotic agent (1 h) excludes the possibility that the metaphases $4n$ blocked by colchicine owe their ploidy level to the action of this drug.

Thymidine effect. As polyploid cells in mitosis were not observed in control roots, it seems evident that some external factor is responsible for this apparent cell-chimera in the meristematic population (cells $2n$ together with others $4n$), so the question arises whether these tetraploid cells owe their polyploid level to the thymidine-induction. The short space of time (3 h) between the treatment with thymidine and the first fixation of the roots which show $4n$ metaphases seems to discard this nucleoside as the inductor of the observed polyploidy in same point of the S period (there is a quantitative study underway of the kinetics of these cellular events).

Endoreduplicated cells. The induction of endoreduplication (interphase endopolyploidy) has been reported in

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