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MEDICAL RESEARCH COUNCIL

Special Report Series No. 307

A search for genetic effects of high natural radioactivity in South India

H. Grüneberg, G. S. Bains, R. J. Berry, Linda Riles,
C. A. B. Smith and R. A. Weiss

LONDON: HER MAJESTY'S STATIONERY OFFICE 1966

Contents

Acknowledgements

It is our pleasant duty to record our thanks to the many people who, in one way or another, have helped us to carry out our work. They include Professor H. J. Bhabha, FRS, Director of the Atomic Energy Establishment, Trombay, India; Dr A. R. Gopal-Ayengar, Head of the Biology and Medical Divisions of the same establishment, who also seconded Mr G. S. Bains to our group during the field work in Kerala and again for a year in London to help with the skeletal measurements; Mr A. S. Rao, Head of the Electronics Division, Atomic Energy Establishment, Trombay, and his colleagues, Drs D. Bharatwal and G. H. Vaze, who carried out extensive radiation measurements both on the strip and in the control areas; Drs L. H. Gray, FRS, and J. W. Boag, of the Research Unit in Radiobiology, British Empire Cancer Campaign, Mount Vernon Hospital, Northwood, Middlesex, who advised us in the evaluation of the radiation data; Dr D. S. Falconer for advice on population genetics; Dr Gillian M. Truslove for help in preparing the expedition; Mr A. J. Lee for the text-figures; and Mr W. L. B. Nixon and Miss D. Morgan for assistance with the programming of the data and for working the computer. Our particular thanks are due to Dr M. Sreenivasan, Principal, and Dr S. Sivaprasad, Professor of Zoology, Sree Narayana College, Quilon, whose unselfish hospitality enabled us to set up a temporary laboratory in their college, where all our preparations were made. We had valuable help from Mr V. Ramachandran, the District Collector at Quilon, and many village officers in the field work. Col. Wells, Administrator at Travancore Minerals Factory, Puthenthura, kindly made available to us large-scale topographical maps of the strip, on which the radiation measurements have been based. Dr Arne Martin Klausen, of the Indo-Norwegian Project, Puthenthura, helped us with some of the historical data, and the members of the Indo-Norwegian Project in general helped us in innumerable ways and extended to us their warm-hearted hospitality.

Preface

THE immediate genetic effects of large acute doses of radiation are best studied in the laboratory. By contrast, the laboratory approach to the study of long-term genetic effects of small doses of radiation received at low dose rates over many generations presents great difficulties, at least in mammals. Fortunately, there exist a few areas of high natural radioactivity in the world which lend themselves to field studies. In 1959, the World Health Organization's Expert Committee on Radiation urged the importance of obtaining data on the consequences of prolonged exposure to low doses of radiation in such areas. They wrote:

> 'Such is the status of our knowledge of the somatic and genetic effects of chronic low-level exposures that any proper investigation of areas of high natural radiation is certain to contribute to the fund of biological knowledge and the ultimate specification of the genetic risks accruing from increasing exposure to ionizing radiations.'

The present report deals with such an investigation, carried out in Kerala, South India. In the autumn of 1961, Professor H. Grüneberg, Honorary Director of the Medical Research Council's Experimental Genetics Research Unit at University College London, and his colleagues began a study based on populations of the black rat (*Rattus rattus* L.). The material was collected and skeletal preparations made between November 1961 and January 1962 by Professor Grüneberg, Dr G. S. Bains, Dr R. J. Berry and Mr R. A. Weiss. After their return to this country, dental measurements were carried out by Mr Weiss and skeletal measurements by Dr Bains and Mrs Linda Riles; the classification of non-metrical variants was made by Dr Berry. The statistical treatment of the data was supervised by Professor C. A. B. Smith.

While recognizing the need for meaningful data on the consequences of prolonged exposure, the WHO Expert Committee on Radiation regarded it as rather improbable that the investigation of any of the high-background areas known today would, by itself, lead to the demonstration of significant genetic changes. As will be seen in this report, the work carried out in Kerala by Professor Grüneberg and his colleagues has, in fact, failed to discover positive evidence for genetic effects of low-level radiation in that area. It does not necessarily follow, however, that radiation has no effects at these low dose rates; additional mutations might be masked by an increase in natural selection or a decrease in environmental variance. It might also be that there is an increase in variance so small that it is beyond the reach of statistical method. Further research is clearly required on this general problem of the genetic effects of low-level radiation, but the authors of the report conclude that further studies of this kind in other areas of high-background radiation would be unlikely to yield any more informative data.

MEDICAL RESEARCH COUNCIL
20 Park Crescent London W.1

November 1965

Introduction

WITH the increasing exposure of human populations to various types of radiation, the extent of the risk of radiation-induced somatic and genetic damage has become a question of major importance to both scientific and government authorities. In the past, fundamental work on the mutagenic action of ionizing radiations has largely been carried out on microorganisms, higher plants (the snapdragon *Antirrhinum majus*, maize and others) and insects such as *Drosophila*, which are particularly suitable for such studies. More recently, work on the mouse has shown that mammals behave like other organisms in respect of their response to ionizing radiations, but that there are marked differences in such features as sensitivity to radiation, which could not have been predicted from the facts established for lower organisms. Hence information about the medical problems of radiation damage should come as far as possible from studies on man himself or, failing that, on other mammals.

In mammals the number of individuals that can be scanned in any one experiment is limited, and most research has been concerned with the effect of comparatively high doses of radiation. However, many of the radiation risks (from industrial and other sources) to which man is subjected involve exposure to small doses over long periods and often through successive generations. Under such circumstances the ultimate fate of the mutations induced by radiation becomes an important factor. The genetic structure of the population will largely be determined by the interplay of mutation and natural selection, and ultimately an equilibrium between these opposing forces will establish itself. In the laboratory the study of mammalian populations exposed to low levels of radiation over many generations presents almost insuperable difficulties. It is therefore fortunate that there exist areas of high natural radioactivity where the effects of these radiations on the animals (and humans) living there can be studied. One such locality is to be found on the Malabar coast of South India, in the State of Kerala (formerly Cochin-Travancore) and this report deals with a search for genetic effects of radiation in that area on populations of the black rat (*Rattus rattus* L.), the only mammal from which it seemed likely that critical data could be obtained.

The general approach to the problem

The genetic variance present in all wild populations of animals is replenished partly by the process of mutation. Disregarding random fluctuations of gene frequencies in small populations due to genetic drift, the fate of a mutant gene is determined by its selective value both in the heterozygous and in the homozygous condition. The gene frequency at any one locus thus depends on a dynamic equilibrium between mutation and natural selection. Now if the mutation rate is increased by radiation, what will be the effect on a population thus affected? Will the increased mutation pressure be counterbalanced by increased natural selection so that the level of genetic variance remains unchanged, or will the genetic variance of such a population be greater than that of control populations? This is the question that we are here trying to answer.

In view of the complexity of the situation, it would be difficult to forecast what specific changes in the phenotypic composition of a population would result from of an increased genetic variance. If a comprehensive survey were to show systematic differences between a series of irradiated populations and a similar series of control populations, and if no other causes for such systematic differences could be discovered, a *prima facie* case for the existence of a radiation effect would be established; the nature of the difference would presumably suggest by what other methods the evidence could be further substantiated. If, on the other hand, the results do not show any appreciable difference between the irradiated and the control areas or any consistent pattern of differences which could be confidently attributed to radiation, this negative result will be of value as long as it is realized that it should not be extrapolated to apply to phenomena that cannot be discovered by the present method.

The total amount of radiation to which the inhabitants of the radioactive area are exposed is very small compared with the doses usually administered in laboratory studies of mutagenesis, and in particular the dose rate (dose per unit time) is extremely low. Under these circumstances, virtually all genetic effects of the radiation will be single-hit events—that is, they will result in point mutations and perhaps small deletions. Thus, with the possible exception of non-disjunction, it is very improbable that any changes that could be discovered cytologically will be produced by the radiation. Neither is an analysis of genetic variance by means of breeding experiments practicable in the radioactive area, since the only mammal other than man that occurs in large numbers is the 'black' rat, *Rattus rattus* L.*, which is not a laboratory animal. The only

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* The rats collected by us had a tail/head+body ratio of about 1·30 and, being mainly light-bellied agouti in colour, they fit most closely the subspecies *wroughtoni* Hinton 1919 (Ellerman, 1947). A minority of animals from both strip and control areas had grey or dark bellies. There was no clear dimorphism between dark and light bellies and the difficulties of scoring this character made it valueless for comparing different populations. Polymorphism of coat and particularly of belly colour is common in populations of *Rattus rattus;* by analogy with the mouse, where this also occurs, much of this variation in coat colour is clearly attributable to segregation of alleles at the agouti locus.

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possible approach at present therefore is through phenotypic studies, with all the limitations that these impose.

The material most suitable for phenotypic studies on the rat is the skeleton, preparations of which can be made easily by the papain maceration technique (Luther, 1949). It may be taken for granted that in the rat, as in other animals, metrical variation of the skeleton and of the teeth is largely an expression of multifactorial inheritance and that it can thus be used for the detection of differences between populations. The same applies to the minor skeletal variants studied in some detail by Grüneberg and his colleagues (see review by Grüneberg, 1963).

It had originally been hoped to base this investigation on two species of mammal rather than a single one. When collections were begun in the Neendakara area, it seemed that the large mole rat or bandicoot (*Bandicota indica indica* Bechstein 1800), which is fairly common in that vicinity, might be used; however, the sample obtained was too small for practical purposes, since altogether less than 50 were caught. The only other mammals that went into our traps were *Tatera indica* Hardwick 1807, a kangaroo-like jumping rodent which was taken twice, and a single individual of *Mus musculus* L., the house mouse.

The localities sampled

The radioactive area where we worked is situated on the Malabar coast of South India. The radioactivity is contained in monazite sand, which has been deposited by wave action on a narrow coastal strip that stretches with interruptions from near the southern extremity of India (Cape Comorin) in Madras State for over 100 miles into Kerala State, where it peters out between the towns of Quilon and Alleppey. The distribution of the radioactive sands is very uneven. The most massive deposits occur at Manavalakurichi near Cape Comorin and in an area north of the town of Quilon; in both of these places the sands are being mined.

In genetic studies of this kind, it is essential that the area being sampled should be closed in the sense that the animals to be investigated are prevented by barriers of some kind from migrating readily to and from the radioactive area. Otherwise many individuals captured in the radioactive locality could easily be recent immigrants whose ancestors have not been exposed to the radiation. This consideration ruled out the Manavalakurichi area, which lacks natural frontiers. Migration away from the radioactive area is of no practical importance as control areas can always be chosen that are far away from the test localities. The area we selected (see map—figure 1—and plate I*a*) is a narrow coastal strip that is effectively an island. It starts about 4 miles north of Quilon at the mouth of the Ashtamudi lake (the Loch Lomond of Travancore according to official publications), which is spanned by the 1336 foot long Neendakara Bridge (built between 1920 and 1930) carrying the main Alleppey–Quilon road (National Highway No. 47). This road leaves the strip again about three miles to the north before entering the village of Chavara by a bridge that probably dates back to the end of the 18th century; the remainder of the strip is devoid of roads. The strip extends for about 14 miles north as far as the Kayankulam Bar at the mouth of the Kayankulam lake. Actually this bar is a break in the land during the monsoon only; during most of the year the land is continuous, but only as a bare sandy area several hundred yards wide that probably represents as much of a barrier to rats as the 'backwaters' on the eastward side of the strip. In any case, the adjacent area north of the bar differs little in radiation intensity from that to the south of it. The backwaters of Kerala extend from Trivandrum in the south to well beyond Cochin in the north. This intricate system of canals and shallow lagoons (including the Ashtamudi and Kayankulam lakes) has for many centuries carried much of the traffic in this area. Fringed with groves of coconut trees, flanked by peaceful villages with friendly inhabitants, teeming with many types of characteristic native punts and craft under palmleaf sails, the backwaters of Kerala present indeed most attractive tropical scenery.

The radioactive strip (or 'strip' for short) thus extends from the Neendakara

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Village
1. Neendakara
2. Puthenthura
3. Kovilthottam
4. Ponmana
5. Cheriazhiekal
6. Allapad
7. Shraikadu
8. Azhiekal
Total

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Bridge in the south to the Kayankulam Bar in the north, with the Arabian Sea to the west and the backwaters to the east. The strip varies in width from about 150 yards to half a mile and the backwaters from about 20 to 300 yards or more. The canal system (though crocodile-infested until fairly recently) thus does not present an absolute obstacle to a rat: occasionally one may cross the canal either by swimming or in a native 'vallam'. However, we believe that such leakages are not likely to make much difference to an established rat population of thousands of individuals, and that what leakages there are are unlikely to affect the conclusions reached.

The beach along the western side of the strip consists of black monazite sand mixed in varying proportions with ordinary sand. Most of the strip is covered by almost continuous coconut groves with no undergrowth; there are occasional patches of tapioca and small paddy fields. Typical views are shown in plates II and III. Under the coconut trees stand the huts of the natives, who are mostly fishermen and growers of coconuts (except near the mining areas). The huts are separated from each other irregularly by distances of 10–100 feet or more. Each stands in its own fenced compound. Most of them are built of woven palm leaves; some stand directly on the ground, others upon a brick or concrete base. The rats live in the huts and evidently find no difficulty in getting from one hut into the next. As the human occupation of the strip is virtually continuous, there are few barriers to restrict the movement of the rats from one end of the strip to the other, and over the centuries the ancestors of the rats alive now have presumably occupied the whole strip at random.

As explained in more detail in appendix I, the radiation intensity on the strip is far from uniform. Apart from local irregularities, there are two main gradients. Radiation is highest on the beach and lowest near the backwaters, and it increases from a relatively low level in the north to a maximum near the village of Puthenthura, where the sand is being mined. The mean radiation intensity of the strip as a whole is about 7·5 times that of the control areas.

We sampled eight areas (villages) on the strip, the aim being to take about 50 animals in each (table 1). The position of these localities on the strip is shown in figure 1, and details about the villages will be found in appendix III. Villages that have not been sampled are not shown on the map; but it should be

TABLE 1 Number of rats collected in eight villages on the strip*

Village	♂♂	♀♀	Total
1. Neendakara	31	25	56
2. Puthenthura	33	18	51
3. Kovilthottam	23	30	53
4. Ponmana	23	33	56
5. Cheriazhiekal	25	26	51
6. Allapad	29	30	59
7. Shraikadu	28	22	50
8. Azhiekal	27	35	62
Total	219	219	438

* Subsequent tables do not include all the animals listed in tables 1 and 2. A few old animals with chipped teeth could not be used for dental measurements, and no data on youngsters of less than 45 g body weight have been included in the skeletal measurements. Some skeletons also could not be completely classified on account of damage or loss of individual bones.

noted that the human occupation of the strip is almost continuous. Generally the limits between one village and the next are not sharply delineated and are quite arbitrary.

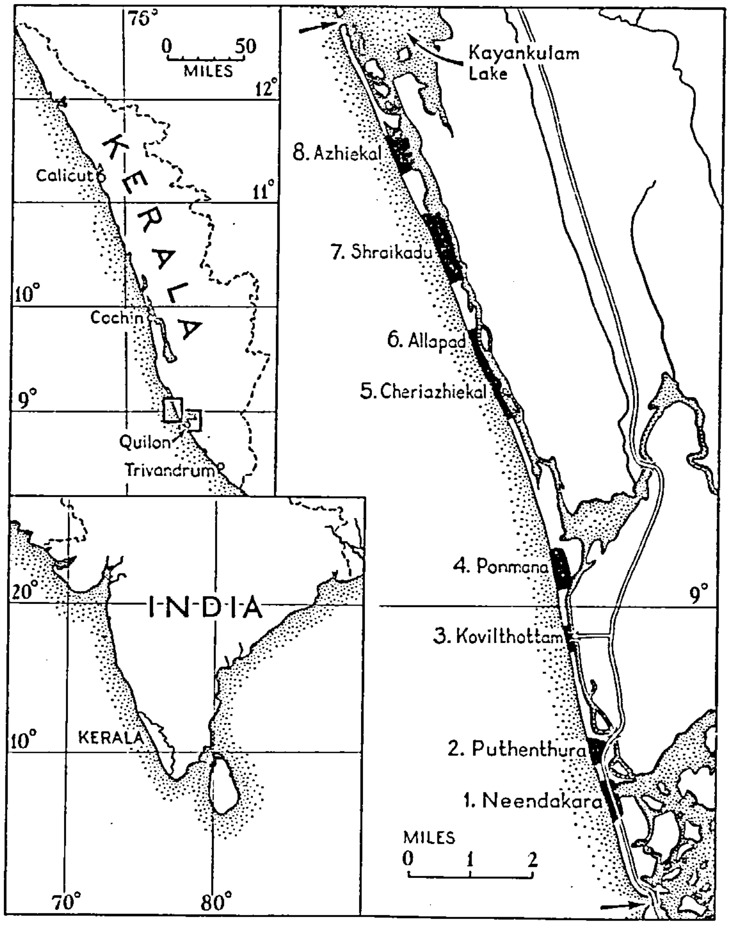

FIGURE 1
Map showing the localities on the strip that were sampled; the Kayankulam bar and the Neendakara bar are indicated by arrows, and the two squares in the upper inset indicate the strip and the control areas.
Note: The spelling of Indian place names is not standardized

The validity of the whole investigation reported here rests on the assumption that the rat population has been on the strip for a sufficient length of time to accumulate an appreciable dose of radiation. Evidence for the antiquity of the human occupation of the strip, and by implication of the commensal rat population, is given in appendix II, where it is shown also that the strip has been an island for a very long time.

The World Health Organization's Expert Committee on Radiation (1959) set out a design of an experiment for investigating the genetic effects of radiation from the monazite sands. They suggested that (human) control populations could most easily be found in the coastal areas adjoining the Neendakara–

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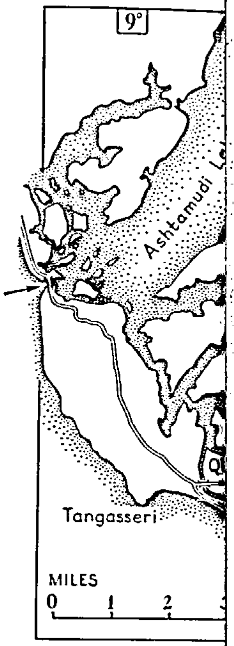

FIGURE 2
Map showing the lo

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localities (table 2) are so fa
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coastal strip is separated fr

TABLE 2 Number of rat

Village
9. Kilikollur
10. Karikode
11. Chandanathoppu
12. Kundara West
13. Kundara East
14. Kottiyam
15. Oomainalur
16. Pallimukku
Total

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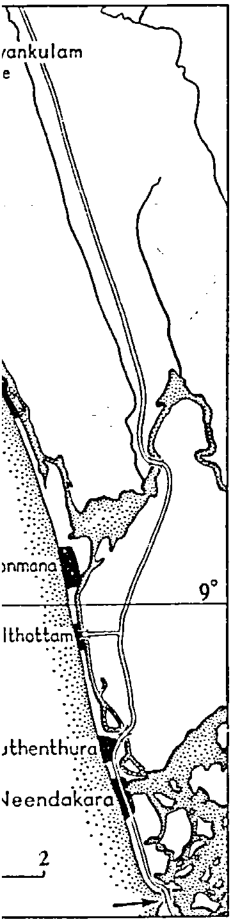

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Kayankulam strip. However, as scattered deposits of radioactive material occur all along the coast, the control rats had to be trapped somewhere away from the immediate coastal areas. For reasons of accessibility it was decided to catch control rats from villages lying along two roads running east and south-east from Quilon and connected by a cross-road six or seven miles from the town. The distance round this triangle (see map, figure 2) was about 24 miles. Unlike the 'experimental' populations on the strip, only a few of the control rats were trapped in dwelling houses; the majority came from shops, and a number from cashew nut and copra factories (for details see appendix III). All the control localities (table 2) are so far from the coastal area that 'contamination' by rats exposed to high radiation levels can be virtually ruled out; in any case, the coastal strip is separated from the inland areas by the moat of the backwaters.

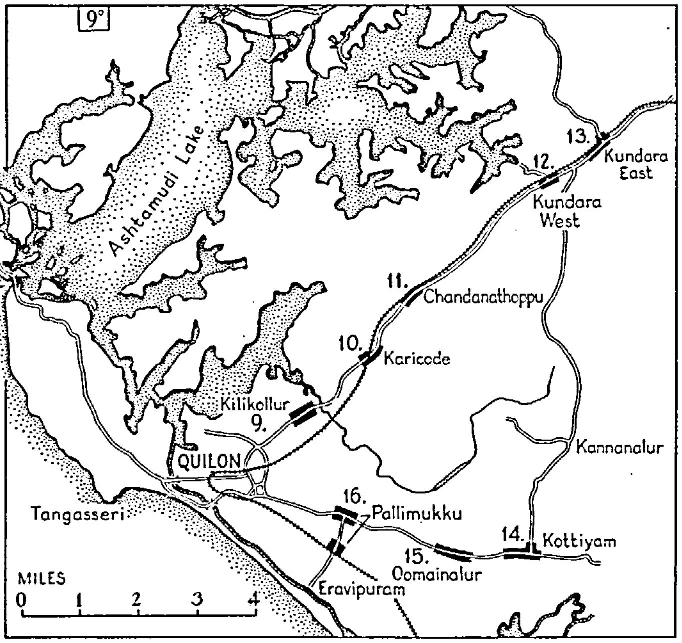

FIGURE 2
Map showing the localities in the control area that were sampled.

TABLE 2 Number of rats collected in eight control villages

Village	♂♂	♀♀	Total
9. Kilikollur	30	27	57
10. Karikode	26	28	54
11. Chandanathoppu	29	39	68
12. Kundara West	26	32	58
13. Kundara East	28	29	57
14. Kottiyam	24	27	51
15. Oomainalur	26	33	59
16. Pallimukku	21	33	54
Total	210	248	458

In fact, the village of Pallimukku is a little more than a mile from the coast, but there was little monazite sand in this region. Our collecting areas on the strip were at least five miles from the nearest control village, and were separated from the control areas by the Ashtamudi Lake and Quilon town. The non-urban areas between strip and control areas and between the control villages were quite intensively cultivated, rice being grown in the low-lying areas and tapioca further inland. There were also numerous stands of palm trees.

The rats were caught in live-traps of local design made and bought in the bazaar of Quilon. These were handed out to individual householders and the houses were visited daily by a member of the team, any rats caught being then removed (plate I*b*). This means that we knew the source from which every rat was obtained. Roasted coconut was used as bait for the earlier trapping on the strip, but plantain was found to be much more effective in the control villages and was therefore used in the last three strip populations, Kovilthottam, Shraikadu and Azhiekal. Some houses substituted dry fish as bait.

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dry fish as bait.

The data available for analysis

Animals caught in the wild include all age groups, and no sharp line can be drawn between immature and fully adult individuals. Hence measurements that are independent of age are particularly useful. The dimensions of the crowns of molar teeth do not change following eruption (except for the effects of wear and tear) and means and variances of such dental measurements can thus be used without allowance for age. These measurements formed our first category. All other metrical characters change with age until the rat is fully grown. We have eliminated individuals of less than 45 grams body weight (weanlings) from our skeletal measurements, but even so the samples include many immature animals above 45 grams. Thus for our second category of measurements, age-dependent skeletal dimensions, an adjustment was necessary, and the length of the animal's humerus has been used as the yardstick; the scatter of values round the regression line of a given skeletal measurement on humerus length could then be used as an estimate of the variability of that dimension which allows for the variable size of the individuals (see p. 21). Thirdly, there are the non-metrical (discontinuous) variants of the skeleton. Most of these are laid down early in development and do not undergo significant changes within the age groups of our collections. They have therefore some advantages in the study of wild-caught populations. Finally, we recorded data on fertility and prenatal mortality.

In work of this kind, where the number of individuals available for study is limited, a decision has to be made about the number and kind of measurements to be carried out. Obviously, if too few measurements per animal are made the material is used wastefully and much potential information is left unexploited. An upper limit is set both by the scientific manpower (and time) available to carry out the work and by the fact that biological measurements on the same individual tend to be correlated. The higher the correlation between two measurements, the less economical it is to measure both. The kind of measurement selected depended largely on the availability of well defined measuring points on a given bone. The ultimate compromise reached was partly based on a preliminary study of correlations, carried out on a sample population of rats from Delhi. It included six dental, eight vertebral and two pelvic measurements, one measurement each of the skull, humerus and scapula and two measurements of the mandible—twenty-one in all. If the outcome of the work had proved ambiguous, it would have been easy to make additional measurements. In the event this has not proved necessary.

Dental measurements

The dimensions of the molars are known to be under genetic control in mice (Grüneberg, 1951; Grewal, 1962a). The same genetic control is assumed to be operative in rats. Once the molar teeth have erupted there is no change in their size except that due to progressive wear of the occlusal surfaces with age. Therefore the means and variances for different populations can be evaluated directly from the measurements without adjustment for the size of the animals.

Methods

The molar teeth of the left lower jaw only were measured. The teeth were prepared along with the skeleton by papain digestion. Each tooth (M_1; M_2; M_3) was measured with a Swift travelling microscope to the nearest 0·01 mm. The tooth was orientated so that the cingulum was in a horizontal plane—that is, the occlusal surface faced directly upwards and the objective of the microscope

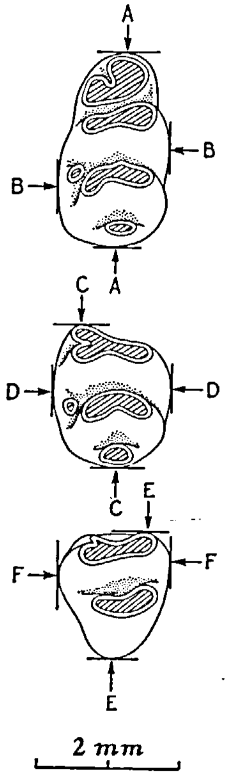

FIGURE 3
The dental measurements taken (symbols defined in text)

TABLE 3 Means (mm) and variances of dental measurements, A–F: males

Population	A		B		C		D		E		F	
	$\bar{A}$	s^2_A	$\bar{B}$	s^2_B	$\bar{C}$	s^2_C	$\bar{D}$	s^2_D	$\bar{E}$	s^2_E	$\bar{F}$	s^2_F
1. Neendakara	2·68	0·0104	1·62	0·0040	1·97	0·0100	1·73	0·0041	1·79	0·0156	1·50	0·0050
2. Puthenthura	2·67	0·0096	1·61	0·0048								

under genetic control in mice
ıetic control is assumed to be
ted there is no change in their
e occlusal surfaces with age.
populations can be evaluated
ːnt for the size of the animals.

re measured. The teeth were
ion. Each tooth (M_1; M_2; M_3)
to the nearest 0·01 mm. The
ı a horizontal plane—that is,
ıe objective of the microscope

TABLE 3 Means (mm) and variances of dental measurements, A–F: males

Population	A		B		C		D		E		F	
	$\bar{A}$	s^2_A	$\bar{B}$	s^2_B	$\bar{C}$	s^2_C	$\bar{D}$	s^2_D	$\bar{E}$	s^2_E	$\bar{F}$	s^2_F
1. Neendakara	2·68	0·0104	1·62	0·0040	1·97	0·0100	1·73	0·0041	1·79	0·0156	1·50	0·0050
2. Puthenthura	2·67	0·0096	1·61	0·0048	1·94	0·0085	1·70	0·0032	1·75	0·0083	1·48	0·0042
3. Kovilthottam	2·66	0·0063	1·60	0·0059	1·91	0·0080	1·68	0·0055	1·74	0·0112	1·47	0·0050
4. Ponmana	2·68	0·0072	1·65	0·0043	1·92	0·0057	1·74	0·0063	1·79	0·0066	1·50	0·0066
5. Cheriazhiekal	2·66	0·0052	1·62	0·0041	1·94	0·0079	1·71	0·0037	1·76	0·0042	1·49	0·0042
6. Allapad	2·69	0·0079	1·64	0·0041	1·94	0·0075	1·73	0·0034	1·76	0·0093	1·50	0·0030
7. Shraikadu	2·64	0·0059	1·59	0·0037	1·92	0·0082	1·67	0·0048	1·77	0·0040	1·48	0·0041
8. Azhiekal	2·65	0·0143	1·61	0·0077	1·91	0·0071	1·69	0·0046	1·71	0·0056	1·47	0·0045
Mean for 1–8	2·67		1·62		1·93		1·71		1·76		1·49	
9. Kilikollur	2·68	0·0064	1·61	0·0049	1·94	0·0051	1·69	0·0039	1·77	0·0108	1·46	0·0048
10. Karikode	2·64	0·0071	1·59	0·0033	1·91	0·0041	1·69	0·0025	1·73	0·0059	1·48	0·0046
11. Chandanathoppu	2·71	0·0147	1·64	0·0044	1·99	0·0118	1·73	0·0039	1·83	0·0086	1·50	0·0036
12. Kundara West	2·65	0·0095	1·61	0·0047	1·92	0·0099	1·71	0·0044	1·78	0·0116	1·52	0·0044
13. Kundara East	2·67	0·0126	1·62	0·0044	1·94	0·0077	1·72	0·0044	1·75	0·0159	1·48	0·0067
14. Kottiyam	2·62	0·0084	1·59	0·0042	1·92	0·0087	1·68	0·0034	1·79	0·0046	1·46	0·0045
15. Oomainalur	2·64	0·0081	1·61	0·0033	1·91	0·0069	1·71	0·0026	1·78	0·0152	1·49	0·0041
16. Pallimukku	2·72	0·0076	1·63	0·0029	1·93	0·0116	1·70	0·0046	1·74	0·0156	1·48	0·0048
Mean for 9–16	2·67		1·61		1·93		1·70		1·77		1·48	

TABLE 4 Means (mm) and variances of dental measurements, A–F: females

Population	A		B		C		D		E		F	
	$\bar{A}$	s^2_A	$\bar{B}$	s^2_B	$\bar{C}$	s^2_C	$\bar{D}$	s^2_D	$\bar{E}$	s^2_E	$\bar{F}$	s^2_F
1. Neendakara	2·66	0·0064	1·61	0·0037	1·93	0·0083	1·72	0·0051	1·76	0·0172	1·49	0·0082
2. Puthenthura	2·67	0·0093	1·66	0·0040	1·98	0·0079	1·74	0·0032	1·82	0·0103	1·51	0·0033
3. Kovilthottam	2·62	0·0053	1·57	0·0034	1·88	0·0089	1·68	0·0026	1·73	0·0096	1·45	0·0033
4. Ponmana	2·67	0·0065	1·62	0·0035	1·90	0·0066	1·72	0·0026	1·76	0·0089	1·50	0·0029
5. Cheriazhiekal	2·65	0·0149	1·59	0·0055	1·91	0·0121	1·69	0·0057	1·74	0·0184	1·46	0·0064
6. Allapad	2·63	0·0104	1·60	0·0043	1·89	0·0066	1·71	0·0043	1·75	0·0132	1·48	0·0065
7. Shraikadu	2·65	0·0062	1·58	0·0024	1·92	0·0080	1·67	0·0034	1·74	0·0058	1·47	0·0039
8. Azhiekal	2·65	0·0102	1·61	0·0047	1·89	0·0100	1·68	0·0042	1·70	0·0105	1·44	0·0052
Mean for 1–8	2·65		1·60		1·91		1·70		1·75		1·48	
9. Kilikollur	2·67	0·0075	1·61	0·0052	1·92	0·0096	1·70	0·0033	1·79	0·0094	1·49	0·0078
10. Karikode	2·66	0·0107	1·62	0·0037	1·90	0·0066	1·72	0·0040	1·77	0·0047	1·48	0·0035
11. Chandanathoppu	2·70	0·0083	1·62	0·0051	1·95	0·0108	1·72	0·0039	1·78	0·0090	1·48	0·0046
12. Kundara West	2·65	0·0102	1·61	0·0028	1·92	0·0080	1·71	0·0039	1·74	0·0107	1·50	0·0054
13. Kundara East	2·65	0·0107	1·62	0·0042	1·91	0·0066	1·71	0·0062	1·74	0·0082	1·49	0·0048
14. Kottiyam	2·61	0·0142	1·60	0·0054	1·90	0·0078	1·68	0·0056	1·76	0·0088	1·48	0·0055
15. Oomainalur	2·60	0·0082	1·60	0·0041	1·89	0·0123	1·69	0·0054	1·74	0·0133	1·47	0·0062
16. Pallimukku	2·68	0·0067	1·61	0·0031	1·91	0·0092	1·69	0·0036	1·73	0·0135	1·46	0·0048
Mean for 9–16	2·65		1·61		1·91		1·70		1·76		1·48	

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faced directly downwards. In
roots embedded in plasticine;
in their sockets, the whole ma
that the cingulum was horizo

As shown in figure 3, the m
along both the antero–posteri
to the terminology adopted b
posterior measurement (A) i
cingulum; in M_2 and M_3 the co
are between the protostylid a
measurements (B, D, and F) a
cingular cusps.

Readings were made with t
and from right to left, and th
nearest 0·01 mm was recorded.
duplicating a series of measur
had a standard error of 0·0077 n
in the orientation of the teeth
observer.

The degree of tooth wear di
the size of the protostylid of M
was slightly reduced (<0·03 m
an almost negligible effect on t
with worn teeth did not differ a
on the comparison of means o
and the exact position of the p
mine. Hence the antero–poste
considered to be as accurate as t

In prolonged procedures of t
be gradual changes in the tech
obviate such tendencies, the o
randomized.

Results

The means and variances for t
sixteen populations are given i
separately, as the measurement
larger than those of the females

TABLE 5 Variance ratio (F)
Values in italic are significant at the
below, depending on the number of t

Measurement	f_2=	♂♂ 210 or
A		1·01
B		1·71
C		1·49
D		*4·21*
E		*2·45*
F		1·34

10. Karikode	2·66	0·0107	1·62	0·0037	1·90	0·0066	1·72	0·0040	1·77	0·0047	1·48	0·0035
11. Chandanathoppu	2·70	0·0083	1·62	0·0051	1·95	0·0108	1·72	0·0039	1·78	0·0090	1·48	0·0046
12. Kundara West	2·65	0·0102	1·61	0·0028	1·92	0·0080	1·71	0·0039	1·74	0·0107	1·50	0·0054
13. Kundara East	2·65	0·0107	1·62	0·0042	1·91	0·0066	1·71	0·0062	1·74	0·0082	1·49	0·0048
14. Kottiyam	2·61	0·0142	1·60	0·0054	1·90	0·0078	1·68	0·0056	1·76	0·0088	1·48	0·0055
15. Oomainalur	2·60	0·0082	1·60	0·0041	1·89	0·0123	1·69	0·0054	1·74	0·0133	1·47	0·0062
16. Pallimukku	2·68	0·0067	1·61	0·0031	1·91	0·0092	1·69	0·0036	1·73	0·0135	1·46	0·0048
Mean for 9–16	2·65		1·61		1·91		1·70		1·76		1·48	

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faced directly downwards. In some cases a tooth had to be orientated with the roots embedded in plasticine; in other cases, when the teeth were still seated in their sockets, the whole mandible was placed in plasticine in such a position that the cingulum was horizontal.

As shown in figure 3, the maximum dimensions of each tooth were measured along both the antero–posterior and the bucco–lingual axes: that is, according to the terminology adopted by Wood and Wilson (1936), in M_1 the antero–posterior measurement (A) is between the anterolophid and the posterior cingulum; in M_2 and M_3 the corresponding measurements (C and E respectively) are between the protostylid and posterior cingulum; and the bucco–lingual measurements (B, D, and F) are between the widest parts of the cingulum or cingular cusps.

Readings were made with the microscope travelling both from left to right and from right to left, and the mean value of these two measurements to the nearest 0·01 mm was recorded. The accuracy of the measurements was tested by duplicating a series of measurements; the difference between the two readings had a standard error of 0·0077 mm. This error is accounted for both by variations in the orientation of the teeth and by inaccuracies of the microscope and the observer.

The degree of tooth wear did not affect the dimensions measured except that the size of the protostylid of M_2 and hence the antero–posterior measurement C was slightly reduced ($<0{\cdot}03$ mm) in animals with severely worn teeth. This has an almost negligible effect on the variance, and since the proportion of animals with worn teeth did not differ appreciably between populations it had no effect on the comparison of means or variances. The orientation of M_3 was difficult and the exact position of the posterior cingulum was sometimes hard to determine. Hence the antero–posterior measurement of this tooth (E) cannot be considered to be as accurate as the other measurements.

In prolonged procedures of this kind, there is always a danger that there may be gradual changes in the technique or in the accuracy of measurement. To obviate such tendencies, the order in which the animals were measured was randomized.

Results

The means and variances for the six dental measurements for each of the sixteen populations are given in tables 3 and 4. The sexes have been treated separately, as the measurements of the males are slightly but significantly larger than those of the females.

TABLE 5 Variance ratio (F) for dental measurements, A–F

Values in italic are significant at the 0·05 level. The degrees of freedom are $f_1=7$ and f_2 as below, depending on the number of teeth measured.

Measurement		Strip		Control	
	$f_2=$	♂♂ 210 or 211	♀♀ 209 or 210	♂♂ 200 or 202	♀♀ 236 or 237
A		1·01	1·12	*3·06*	*4·18*
B		1·71	*4·48*	*2·12*	0·72
C		1·49	*2·57*	*2·14*	1·16
D		*4·21*	*3·77*	*2·15*	1·17
E		*2·45*	*2·26*	*2·38*	1·60
F		1·34	*3·32*	2·08	1·00

The data of tables 3 and 4 have been subjected to an analysis of variance. Table 5 shows the results of tests for heterogeneity separately for the two groups of eight populations and separately for the sexes. The between-population variance ratio exceeds its expectation significantly in 13 out of 24 cases. On a chance basis (and if the measurements were independent of each other), one or two such cases would have been expected. Actually the measurements are correlated with each other, and for measurements A, B, C and D the various correlation coefficients vary between 0·3 and 0·6. Hence the five significant values of F in the females from the strip and the five significant values in the control males may well reduce to single sources of heterogeneity picked up repeatedly by several correlated measurements. The existence of differences between rat populations from five grain shops in Delhi had previously been demonstrated by Grüneberg (1961), and it is thus not surprising that a similar diversity is also found between the rat populations of Kerala.

Whereas there is thus no doubt that there are differences between populations both on the strip and in the control areas, there is no evidence that the rats in these two areas differ systematically from each other. As shown in tables 3 and 4, the means of the strip means in each case are very close to the means of the control means, and the ratios of the two cluster closely round the value of unity expected if there is no appreciable difference between strip and control (table 6). Four values out of 12 are in excess of unity, the expectation being six; the mean difference between the strip and the control means is about one part in 1000 and clearly not significant. On the other hand, the reality of the sex difference (about one part in 200) cannot be seriously in doubt.

TABLE 6 Values of mean of strip means/mean of control means, separately for the sexes, and similarly male/female ratios, separately for strip and control populations

Measurement	Strip/control		♂♂/♀♀	
	♂♂	♀♀	Strip	Control
A	1·000	·999	1·006	1·006
B	1·002	·996	1·008	1·001
C	·998	·999	1·008	1·010
D	1·001	·999	1·003	1·001
E	·993	·997	1·004	1·008
F	1·004	·996	1·007	·999
Mean	1·000	·998	1·006	1·004

Note: The values given in this table were calculated from those of tables 3 and 4 prior to the rounding off of the last two decimals.

The next step in the analysis is to investigate whether the variances for the six dental measurements and sixteen populations show any signs of heterogeneity. The results are given in table 7. Two only out of 24 values are formally significant. Both of them relate to measurement E, which is known to be less reliable than the others. A more comprehensive test of homogeneity of variances for all six measurements (corresponding to a χ^2 with 42 d.f.) is given in the last line of the table. This test is not strictly valid in the case of measurements that are correlated with each other as it would tend to exaggerate heterogeneity. (It also assumes that the distributions are Gaussian.) Even so, none of the four

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values approaches significant
$=1{\cdot}10$; this corresponds to a
When the values for the se

TABLE 7 Bartlett test for
Each value corresponds to χ^2 with 7
at the 0·005 and 0·05 levels respecti

Measurement	
	♂♂
A	10·32
B	6·13
C	2·24
D	4·81
E	*20·64*
F	4·58
A–F (χ^2_{42})	48·72

population ($\chi^2_{84}=100{\cdot}86$; $P=$
conclude that whereas the me
heterogeneity, this is not the

We have to test next wheth
systematically from those of t
geneity, the residual* variances
compared with each other by

TABLE 8 Comparison of th
for the strip (S) and control (C)
The degrees of freedom are f_1 and
and for the females f_1 is 209 or 210 a

Measurement
A
B
C
D
E
F

expectation of unity in the ab
table 8. Using a formula given
at the 5 per cent point of sign
0·769 to 1·300 for the females.
within these limits. The only v
value for measurement E in m
a *smaller* variance on the strip
one would expect of a radiatio
responding female value, whic

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* I.e. after eliminating that part of th
the means.

to an analysis of variance.
:parately for the two groups
;. The between-population
n 13 out of 24 cases. On a
ıdent of each other), one or
he measurements are correl-
nd D the various correlation
/e significant values of F in
values in the control males
:y picked up repeatedly by
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:rences between populations
no evidence that the rats in
:r. As shown in tables 3 and
ry close to the means of the
;ely round the value of unity
n strip and control (table 6).
ectation being six; the mean

of control means, separately
arately for strip and control

♂♂/♀♀	
Strip	Control
1·006	1·006
1·008	1·001
1·008	1·010
1·003	1·001
1·004	1·008
1·007	·999
1·006	1·004

hose of tables 3 and 4 prior to the

ıs is about one part in 1000
e reality of the sex difference
ubt.
vhether the variances for the
s show any signs of hetero-
out of 24 values are formally
E, which is known to be less
:t of homogeneity of variances
'ith 42 d.f.) is given in the last
he case of measurements that
to exaggerate heterogeneity.
ın.) Even so, none of the four

values approaches significant heterogeneity. For the largest value, $\sqrt{2\chi^2}-\sqrt{2n-1} = 1{\cdot}10$; this corresponds to a normal deviate with unit variance, and $P=0{\cdot}27$. When the values for the sexes are pooled, the (larger) value for the strip population ($\chi^2_{84}=100{\cdot}86$; $P=0{\cdot}20$) again does not suggest heterogeneity. We conclude that whereas the means of the dental measurements show appreciable heterogeneity, this is not the case for the variances.

TABLE 7 Bartlett test for heterogeneity of variances

Each value corresponds to χ^2 with 7 d.f. The two values in italic are significant approximately at the 0·005 and 0·05 levels respectively.

Measurement	Strip		Control	
	♂♂	♀♀	♂♂	♀♀
A	10·32	11·45	8·00	6·44
B	6·13	4·71	3·01	5·61
C	2·24	4·07	11·97	5·06
D	4·81	7·87	4·56	5·30
E	*20·64*	11·16	*14·78*	9·47
F	4·58	12·88	3·25	8·70
A–F (χ^2_{42})	48·72	52·14	45·57	40·58

We have to test next whether the variances of the strip populations differ systematically from those of the control populations. In the absence of heterogeneity, the residual* variances of the two groups can legitimately be pooled and compared with each other by means of the variance ratio $F=s^2_S/s^2_C$, with an expectation of unity in the absence of a difference. The results are given in table 8. Using a formula given by Lindley and Miller (1953), the fiducial limits, at the 5 per cent point of significance, are 0·7607 to 1·315 for the males and 0·769 to 1·300 for the females. It will be seen that 11 out of 12 values are well within these limits. The only value which falls slightly outside this range is the value for measurement E in males. Taken at its face value, it would indicate a *smaller* variance on the strip than in the control areas (which is scarcely what one would expect of a radiation effect). It is, however, contradicted by the corresponding female value, which shows a deviation in the opposite direction.

TABLE 8 Comparison of the residual variances of six dental measurements for the strip (S) and control (C) populations by means of the variance ratio

The degrees of freedom are f_1 and f_2, where for the males f_1 is 210 or 211 and f_2 200 or 202, and for the females f_1 is 209 or 210 and f_2 236 or 237.

Measurement	♂♂	♀♀
A	0·9043	0·9202
B	1·1689	0·9481
C	0·9804	0·9461
D	1·1738	0·8659
E	0·7486	1·1854
F	0·9606	0·9390

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* I.e. after eliminating that part of the variance which is ascribable to the differences between the means.

Actually, the low intrinsic accuracy of measurement E, which has been pointed out above, easily accounts for the slightly increased variance ratio for this measurement. Three of the 12 values exceed unity and thus indicate a greater residual variance of the strip populations; the other 9 values point in the opposite direction. What little difference there is is thus contrary to any expectation and indicates that the strip populations are phenotypically more uniform than their respective controls. However, these differences are trivial and without any statistical significance. The obvious conclusion which must be drawn is that, for the dental measurements discussed in this section, there is no evidence for any consistent and systematic difference between the strip and control populations which might be reasonably attributed to radiation. Both on the strip and in the control areas, some differentiation between populations has taken place, but as this has happened in the same way in both areas it evidently has nothing to do with the radiation differential.

Skeletal measurem

Methods

The 15 skeletal measurements tak
lateral structures the left one was
was damaged. All measurements o
bone were carried out by G.S.B
vertebrae were made by L.R. Wi
the position in which they lay c
was mounted in plasticine to en
the molars, we took the averag
means of the travelling microscope
sequence.

Very occasionally, the shapes o
illustrated (figure 4). For instan
sometimes more lateral than that
thus be larger, a feature which w
for that measurement. Difficulties
spinosus of T2; eight specimens
area were rejected either becaus
showed some obvious pathologic

In tables 9–15, the skeletal m
follows:

Character
Humerus
Innominate b
"
Skull
Mandible: A
" B
Second thorac
" "
" "
" "
" "
Third cervical
Scapula

Statistical analysis and results

The chief purpose of the statisti
evidence of systematic difference
respect of means and variances.

nt E, which has been pointed
ased variance ratio for this
y and thus indicate a greater
other 9 values point in the
is thus contrary to any ex-
ns are phenotypically more
, these differences are trivial
ious conclusion which must
ssed in this section, there is no
rence between the strip and
attributed to radiation. Both
ntiation between populations
e same way in both areas it
erential.

Skeletal measurements

Methods

The 15 skeletal measurements taken are indicated in figure 4. In the case of bilateral structures the left one was chosen, except in a few instances where that was damaged. All measurements of skull, mandible, humerus and the innominate bone were carried out by G.S.B.; all measurements of scapula and the two vertebrae were made by L.R. With one exception, the bones were measured in the position in which they lay on a flat surface; the third cervical vertebra was mounted in plasticine to ensure its proper orientation. As in the case of the molars, we took the average of duplicate measurements to 0·01 mm by means of the travelling microscope. Again the animals were measured in random sequence.

Very occasionally, the shapes of the bones did not correspond closely to those illustrated (figure 4). For instance, in the scapula the angulus cervicalis was sometimes more lateral than that shown in the figure; the measurement would thus be larger, a feature which would automatically be reflected in the variance for that measurement. Difficulties occasionally arose in the case of the processus spinosus of T2; eight specimens each from the strip and from the control area were rejected either because the processus was damaged or because it showed some obvious pathological lesion.

In tables 9–15, the skeletal measurements are referred to by numbers, as follows:

Character		*Reference number*
Humerus		1
Innominate bone:	A	2
„ „	B	3
Skull		4
Mandible:	A	5
„	B	6
Second thoracic:	A	7
„ „	B	8
„ „	C	9
„ „	D	10
„ „	E	11
Third cervical:	A	12
	B	13
	C	14
Scapula		15

Statistical analysis and results

The chief purpose of the statistical analysis is to find whether there is any evidence of systematic differences between the strip and control populations in respect of means and variances.

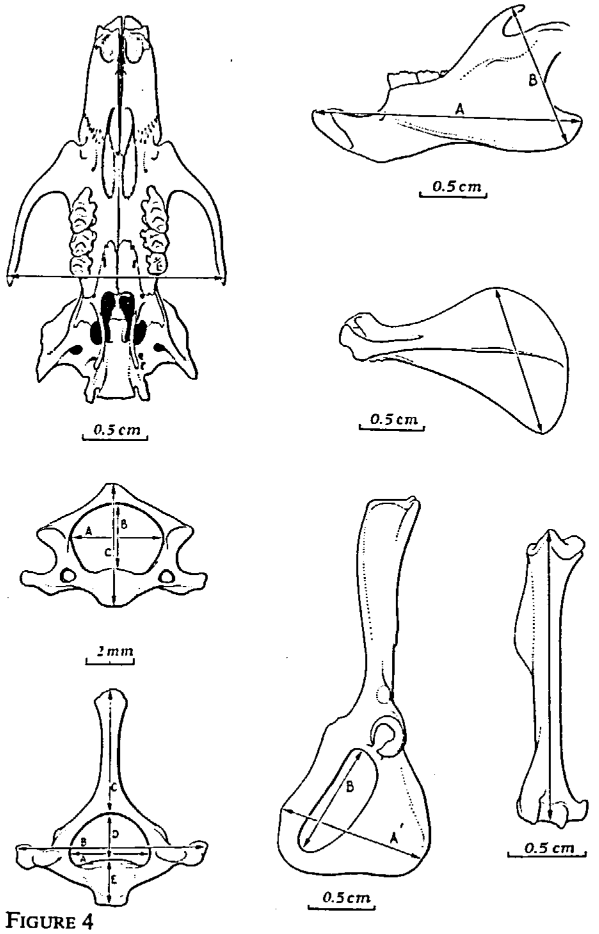

FIGURE 4
The measurements taken on the skull, mandible, scapula, humerus, innominate bone, and the third cervical and second thoracic vertebrae

Table 9 gives the mean measurements obtained in the different populations. As previously stated, some bones were damaged or otherwise unusable; the number of such missing measurements is indicated in the table*. Values for all the variances and covariances were also found for all the control populations. It does not seem worth reproducing these here, but values of the standard deviations, variances and correlations derived from the average within-population covariance matrix are given in table 10. It will be seen from table 10 that there is a high correlation between every pair of measurements, apart from measurements 7 (second thoracic vertebra, measurement A) and 12 (third cervical vertebra, measurement A), which are much less correlated with other measurements though fairly highly correlated with one another.

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* Table 9 is strictly speaking not a simple table of observed means, since in preparing it some adjustment was made for the likely value of the missing measurements; this was based on the general size of the rats concerned, as judged by their humerus lengths. This may increase the accuracy of the means, but it was done chiefly because it happened to be easier to fit into the computer program used in analysing the data. Any difference introduced by this procedure can be expected to be small and of little importance since, as will be explained shortly, the final analysis of the data was not based directly on table 9.

Males TABLE 9 Mean values (mm) of measured characters in the different populations

Population no. No. of rats	1 29	2 32	3 22	4 21	5 25	6 29	7 24	8 24	9 27	10 27	11 34	12 28	13 27	14 25	17 31	16 32
Character no.																
1	19·5	19·2	20·1	21·3	19·5	20·7	21·2	20·0	20·9	19·7	20·4	19·8	20·0	20·1	19·7	20·8
2	12·1	11·7*	12·3	13·2	12·1	12·9	12·9	12·1	13·2	12·3	12·7	12·3	12·0	12·3	12·1	12·9
3	9·03	8·69*	9·29	9·57	8·93	9·53	9·66	9·12	9·58	8·90	9·06	9·01	8·90*	9·14	9·03	9·55
4	17·0*	16·7	17·2*	18·3	16·7*	17·9*	17·8	17·0	17·8	17·1*	17·2	17·1	17·4*	17·2*	17·3†	18·0
5	21·3	20·8	21·7	22·4	21·2	22·2	22·3	21·2	22·3	21·3	21·8	21·2	21·4	21·7	21·4	22·4
6	10·9	10·5	11·0	11·5	10·7	11·2	11·6	10·8	11·5	10·8	10·8	10·7	10·9	10·8	10·9	11·3
7	3·44	3·38	3·41	3·48	3·41	3·39	3·50	3·43	3·49	3·45	3·53	3·41*	3·47	3·49	3·48	3·60
8	7·36	7·18*	7·53	7·88	7·32	7·52	7·73*	7·47	7·52	7·33	7·52	7·31*	7·34	7·47	7·60	7·91
9	4·67*	4·49†	4·81	5·33	4·74*	5·22	5·28*	4·83*	5·29	4·88*	5·24†	4·87*	4·84	4·90	4·86	5·11*
10	2·30	2·21*	2·27	2·32	2·24	2·28	2·32*	2·22	2·24	2·22	2·29	2·26*	2·27	2·24	2·26	2·26
11	1·32	1·31*	1·34	1·45	1·35	1·44	1·42*	1·36	1·43	1·36	1·42	1·34	1·35	1·32	1·39	1·43
12	3·88	3·81	3·79	3·88	3·88	3·84	3·87	3·84	3·93	3·82	3·92	3·85	3·89	3·85	3·91	4·04
13	2·56	2·48	2·60	2·60	2·51	2·57	2·59	2·47	2·54	2·51	2·56	2·58	[illegible]	[illegible]	[illegible]	[illegible]

TABLE 9 Mean values (mm) of measured characters in the different populations

Males

Population no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	16
No. of rats	29	32	22	21	25	29	24	24	27	27	34	28	27	25	31	32
Character no.																
1	19·5	19·2	20·1	21·3	19·5	20·7	21·2	20·0	20·9	19·7	20·4	19·8	20·0	20·1	19·7	20·8
2	12·1	11·7*	12·3	13·2	12·1	12·9	12·9	12·1	13·2	12·3	12·7	12·3	12·0	12·3	12·1	12·9
3	9·03	8·69*	9·29	9·57	8·93	9·53	9·66	9·12	9·58	8·90	9·06	9·01	8·90*	9·14	9·03	9·55
4	17·0*	16·7	17·2*	18·3	16·7*	17·9*	17·8	17·0	17·8	17·1*	17·2	17·1	17·4*	17·2*	17·3†	18·0
5	21·3	20·8	21·7	22·4	21·2	22·2	22·3	21·2	22·3	21·3	21·8	21·2	21·4	21·7	21·4	22·4
6	10·9	10·5	11·0	11·5	10·7	11·2	11·6	10·8	11·5	10·8	10·8	10·7	10·9	10·8	10·9	11·3
7	3·44	3·38	3·41	3·48	3·41	3·39	3·50	3·43	3·49	3·45	3·53	3·41*	3·47	3·49	3·48	3·60
8	7·36	7·18*	7·53	7·88	7·32	7·52	7·73*	7·47	7·52	7·33	7·52	7·31*	7·34	7·47	7·60	7·91
9	4·67*	4·49†	4·81	5·33	4·74*	5·22	5·28*	4·83*	5·29	4·88*	5·24†	4·87*	4·84	4·90	4·86	5·11*
10	2·30	2·21*	2·27	2·32	2·24	2·28	2·32*	2·22	2·24	2·22	2·29	2·26*	2·27	2·24	2·26	2·26
11	1·32	1·31*	1·34	1·45	1·35	1·44	1·42*	1·36	1·43	1·36	1·42	1·34	1·35	1·32	1·39	1·43
12	3·88	3·81	3·79	3·88	3·88	3·84	3·87	3·84	3·93	3·82	3·92	3·85	3·89	3·85	3·91	4·04
13	2·56	2·48	2·60	2·60	2·51	2·57	2·59	2·47	2·54	2·51	2·56	2·58	2·54	2·52	2·50	2·52
14	4·84	4·83*	4·93	5·17	4·80	5·02	5·20	4·83	5·05	4·84*	4·99	4·98	4·88*	4·89	4·94	5·06
15	12·8	12·4	13·2	14·1	12·5	13·8	13·9	12·8	13·9	12·8	13·1	12·8	12·8	12·7	13·0	13·6

Females

Population no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
No. of rats	23	16	29	28	25	30	20	35	27	27	34	28	27	25	31	32
Character no.																
1	18·7	20·8	19·7	20·5	19·3	19·3	19·3	19·8	20·4	19·8	20·7	19·2	19·5	20·3	10·2	20·0
2	11·8	13·1	12·4	12·8	12·1*	12·2*	12·1	12·3	13·2	12·4†	13·0	12·2*	12·4	12·7	12·0*	12·8*
3	8·96	10·2	9·84	9·81	9·40*	9·46*	9·68	9·72	10·02	9·71†	9·55	9·38*	9·36	9·90	9·30*	9·91*
4	16·7*	18·1	17·2	17·9	17·0	17·4	17·3*	17·3	18·0*	17·4*	17·4	17·1*	17·4	18·0	17·2	17·8†
5	21·0	22·4	21·7	22·1	21·3	21·5	21·5	21·5	22·5	21·6	22·0	21·1	21·5	22·2	21·2	22·1
6	10·7	11·5	11·0	11·3	10·7	10·9	11·0	11·0	11·5	11·1	11·1	10·8	11·0	11·1	10·7	11·2
7	3·41	3·43*	3·40	3·40	3·41	3·38	3·38	3·47	3·48*	3·44	3·44	3·39	3·37	3·46*	3·45	3·49
8	7·20	7·76	7·48	7·60*	7·28	7·35	7·27	7·45	7·53*	7·38	7·55	7·31	7·38	7·54*	7·38	7·61
9	4·42*	5·17*	4·90	5·10	4·76	4·70	4·74	4·76	5·44*	4·94	5·17†	4·63†	4·94	5·23*	4·66	4·91
10	2·20	2·29*	2·29	2·33	2·24	2·22	2·26	2·26	2·26*	2·27	2·26	2·24	2·25	2·33*	2·23	2·26
11	1·27	1·39*	1·29	1·35	1·34	1·40	1·35	1·32	1·45*	1 35	1 50	1·34	1·35	1·35*	1·32	1·37
12	3·82	3·87	3·86	3·86	3·83*	3·85*	3·76	3·90	3·89	3·85*	3·88	3·84	3·80	2·89	3·84	3·93
13	2·48	2·57	2·54	2·54	2·54*	2·48*	2·51	2·49	2·54	2·49*	2·58	2·57	2·54	2·54	2·46	2·52
14	4·67	5·14	4·90	4·93	4·81*	4·89*	4·91	4·89	5·07	4·84*	5·00*	4·84	4·96	5·07	4·83	4·94
15	12·1	13·7	13·0	13·6	12·7	12·9	12·9	12·8	13·7	12·9	13·4	12·5	12·8	13·1	12·3	13·2

* One measurement missing because bone was damaged or unmeasurable. † Two measurements missing because bone was damaged or unmeasurable.

TABLE 10 Standard deviations, variances and correlations between unadjusted characters (averaged over all control populations)

Females

Character no.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Standard deviation		1·80	1·37	1·06	1·42	1·46	·931	·152	·552	·880	·144	·160	·145	·167	·473	1·64
Variance		3·23	1·89	1·12	2·02	2·12	·87	·023	·30	·77	·021	·026	·021	·028	·23	2·68
Correlations with character no.:	1	—	·89	·87	·91	·92	·90	·35	·78	·81	·70	·70	·29	·63	·79	·93
	2	—	—	·83	·88	·90	·90	·26	·76	·76	·62	·77	·29	·60	·82	·92
	3	—	—	—	·84	·85	·85	·37	·73	·76	·65	·63	·27	·60	·76	·83
	4	—	—	—	—	·91	·91	·32	·71	·81	·70	·74	·24	·63	·82	·92
	5	—	—	—	—	—	·95	·36	·76	·79	·72	·74	·31	·67	·83	·91
	6	—	—	—	—	—	—	·35	·76	·81	·67	·75	·31	·65	·83	·91
	7	—	—	—	—	—	—	—	·44	·25	·20	·17	·54	·21	·26	·24
	8	—	—	—	—	—	—	—	—	·70	·50	·67	·28	·45	·65	·75
	9	—	—	—	—	—	—	—	—	—	·61	·64	·12	·54	·72	·81
	10	—	—	—	—	—	—	—	—	—	—	·40	·26	·77	·70	·67
	11	—	—	—	—	—	—	—	—	—	—	—	·28	·47	·73	·74
	12	—	—	—	—	—	—	—	—	—	—	—	—	·19	·20	·25
	13	—	—	—	—	—	—	—	—	—	—	—	—	—	·76	·62
	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	·84
	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Males

Character no.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Standard deviation		2·23	1·51	1·15	1·66	1·59	1·03	·154	·604	·989	·165	·176	·143	·169	·567	2·02
Variance		4·96	2·88	1·32	2·76	2·53	1·07	·024	·36	·98	·027	·031	·020	·028	·32	4·09
Correlations with character no.:	1	—	·94	·92	·93	·92	·92	·50	·84	·89	·63	·81	·50	·71	·83	·94
	2	—	—	·92	·92	·93	·92	·44	·82	·87	·64	·84	·50	·72	·82	·94
	3	—	—	—	·90	·90	·90	·48	·80	·88	·56	·76	·50	·65	·78	·92
	4	—	—	—	—	·93	·94	·52	·82	·89	·63	·85	·51	·70	·87	·94
	5	—	—	—	—	—	·96	·51	·83	·91	·61	·84	·53	·68	·84	·93
	6	—	—	—	—	—	—	·48	·81	·90	·62	·83	·52	·68	·84	·93
	7	—	—	—	—	—	—	—	·62	·46	·23	·38	·59	·37	·42	·49
	8	—	—	—	—	—	—	—	—	·82	·56	·74	·47	·63	·76	·83
	9	—	—	—	—	—	—	—	—	—	·57	·79	·46	·62	·80	·89
	10	—	—	—	—	—	—	—	—	—	—	·55	·41	·67	·64	·60
	11	—	—	—	—	—	—	—	—	—	—	—	·44	·64	·84	·86
	12	—	—	—	—	—	—	—	—	—	—	—	—	·43	·42	·48
	13	—	—	—	—	—	—	—	—	—	—	—	—	—	·74	·69
	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	·86
	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

One complicating factor
differs from one population
differences in means and va
have been rejected from the
arise in many ways other tha
to make some adjustment f
accurate estimate of the ag
it was decided to make so
convenient measure of the
was present undamaged an
method was to subtract
determined by the regressio
in the control populations.
appreciable non-linearity, i
gression. The values of the '

TABLE 11 Formulae for
on length of humerus

Males

Character no.	Ori measu
1	x
2	x
3	x
4	x
5	x
6	x
7	x
8	x
9	x
10	x
11	x
12	x
13	x
14	x
15	x

Females

Character no.	Ori measu
1	x_1
2	x_2
3	x_3
4	x_4
5	x_5
6	x_6
7	x_7
8	x_8
9	x_9
10	x_1
11	x_1
12	x_1
13	x_1
14	x_1
15	x_1

Correlations with character no.:															
1	—	·94	·92	·93	·92	·92	·50	·84	·89	·63	·81	·50	·71	·83	·94
2	—	—	·92	·92	·93	·92	·44	·82	·87	·64	·84	·50	·72	·82	·94
3	—	—	—	·90	·90	·90	·48	·80	·88	·56	·76	·50	·65	·78	·92
4	—	—	—	—	·93	·94	·52	·82	·89	·63	·85	·51	·70	·87	·94
5	—	—	—	—	—	·96	·51	·83	·91	·61	·84	·53	·68	·84	·93
6	—	—	—	—	—	—	·48	·81	·90	·62	·83	·52	·68	·84	·93
7	—	—	—	—	—	—	—	·62	·46	·23	·38	·59	·37	·42	·49
8	—	—	—	—	—	—	—	—	·82	·56	·74	·47	·63	·76	·83
9	—	—	—	—	—	—	—	—	—	·57	·79	·46	·62	·80	·89
10	—	—	—	—	—	—	—	—	—	—	·55	·41	·67	·64	·60
11	—	—	—	—	—	—	—	—	—	—	—	·44	·64	·84	·86
12	—	—	—	—	—	—	—	—	—	—	—	—	·43	·42	·48
13	—	—	—	—	—	—	—	—	—	—	—	—	—	·74	·69
14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	·86
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

One complicating factor is that, if the proportion of young immature rats differs from one population to another, this of itself would be enough to produce differences in means and variances, even though all rats below a certain weight have been rejected from the sample. Such differences in age distributions might arise in many ways other than by the effects of radiation. Hence it seems essential to make some adjustment for them. Now in general it is impossible to make an accurate estimate of the age of a wild rat. Thus, instead of adjusting for age it was decided to make some adjustment for the general size of the rat. As a convenient measure of the size, the length of the humerus was chosen, since it was present undamaged and measurable in almost all the rat skeletons. The method was to subtract from each measurement an 'adjustment for size' determined by the regression of the measurement on the length of the humerus in the control populations. Although some scatter diagrams did not show any appreciable non-linearity, it was felt safer to add a quadratic term to the regression. The values of the 'adjusted characters' used are given by the formulae

TABLE 11 Formulae for adjustment of characters by quadratic regression on length of humerus

	Character no.	*Original measurement*	*Adjusted measurement*
Males			
	1	x_1	
	2	x_2	$y_2 = x_2 + {\cdot}02090\, x_1^2 - 1{\cdot}461\, x_1 + 20{\cdot}85$
	3	x_3	$y_3 = x_3 + {\cdot}01673\, x_1^2 - 1{\cdot}134\, x_1 + 15{\cdot}85$
	4	x_4	$y_4 = x_4 - {\cdot}00200\, x_1^2 - {\cdot}615\, x_1 + 13{\cdot}23$
	5	x_5	$y_5 = x_5 + {\cdot}00605\, x_1^2 - {\cdot}896\, x_1 + 15{\cdot}61$
	6	x_6	$y_6 = x_6 - {\cdot}00315\, x_1^2 - {\cdot}304\, x_1 + 7{\cdot}42$
	7	x_7	$y_7 = x_7 - {\cdot}00081\, x_1^2 - {\cdot}002\, x_1 + {\cdot}36$
	8	x_8	$y_8 = x_8 + {\cdot}00044\, x_1^2 - {\cdot}246\, x_1 + 4{\cdot}77$
	9	x_9	$y_9 = x_9 - {\cdot}00968\, x_1^2 - {\cdot}012\, x_1 + 4{\cdot}23$
	10	x_{10}	$y_{10} = x_{10} + {\cdot}00211\, x_1^2 - {\cdot}130\, x_1 + 1{\cdot}74$
	11	x_{11}	$y_{11} = x_{11} - {\cdot}00105\, x_1^2 - {\cdot}027\, x_1 + {\cdot}89$
	12	x_{12}	$y_{12} = x_{12} + {\cdot}00436\, x_1^2 - {\cdot}204\, x_1 + 2{\cdot}31$
	13	x_{13}	$y_{13} = x_{13} + {\cdot}00378\, x_1^2 - {\cdot}203\, x_1 + 2{\cdot}54$
	14	x_{14}	$y_{14} = x_{14} - {\cdot}00040\, x_1^2 - {\cdot}195\, x_1 + 4{\cdot}09$
	15	x_{15}	$y_{15} = x_{15} + {\cdot}01251\, x_1^2 - 1{\cdot}345\, x_1 + 21{\cdot}98$
Females			
	1	x_1	
	2	x_2	$y_2 = x_2 + {\cdot}01857\, x_1^2 - 1{\cdot}401\, x_1 + 20{\cdot}43$
	3	x_3	$y_3 = x_3 + {\cdot}00428\, x_1^3 - {\cdot}679\, x_1 + 11{\cdot}75$
	4	x_4	$y_4 = x_4 + {\cdot}01070\, x_1^2 - 1{\cdot}135\, x_1 + 18{\cdot}29$
	5	x_5	$y_5 = x_5 + {\cdot}00288\, x_1^2 - {\cdot}859\, x_1 + 15{\cdot}91$
	6	x_6	$y_6 = x_6 + {\cdot}00817\, x_1^2 - {\cdot}786\, x_1 + 12{\cdot}32$
	7	x_7	$y_7 = x_7 - {\cdot}00426\, x_1^2 + {\cdot}136\, x_1 - 1{\cdot}00$
	8	x_8	$y_8 = x_8 - {\cdot}00634\, x_1^2 - {\cdot}487\, x_1 + 7{\cdot}13$
	9	x_9	$y_9 = x_9 + {\cdot}01079\, x_1^2 - {\cdot}814\, x_1 + 11{\cdot}86$
	10	x_{10}	$y_{10} = x_{10} + {\cdot}00296\, x_1^2 - {\cdot}171\, x_1 + 2{\cdot}22$
	11	x_{11}	$y_{11} = x_{11} - {\cdot}00088\, x_1^2 - {\cdot}028\, x_1 + {\cdot}89$
	12	x_{12}	$y_{12} = x_{12} + {\cdot}00047\, x_1^2 - {\cdot}042\, x_1 + {\cdot}64$
	13	x_{13}	$y_{13} = x_{13} + {\cdot}00086\, x_1^2 - {\cdot}092\, x_1 + 1{\cdot}48$
	14	x_{14}	$y_{14} = x_{14} + {\cdot}00473\, x_1^2 - {\cdot}392\, x_1 + 5{\cdot}88$
	15	x_{15}	$y_{15} = x_{15} + {\cdot}02388\, x_1^2 - 1{\cdot}771\, x_1 + 25{\cdot}63$

TABLE 12a Observed means (mm) of various measurements (corrected for regression on humerus) with standard errors

Population no.	CHARACTER NO.								
	2	3	4	5	6	7	8	9	10
	FEMALES								
1	12·57±·085	9·54±·089	17·52±·084	21·87±·122	11·21±·086	3·44±·092	7·48±·068	4·88±·090	2·27±·029
2	12·43 ·100	9·71 ·104	17·48 ·131	21·73 ·160	11·05 ·092	3·40 ·041	7·53 ·071	4·79 ·093	2·24 ·039
3	12·44 ·085	9·89 ·094	17·39 ·128	21·85 ·097	11·06 ·072	3·41 ·029	7·50 ·051	4·93 ·093	2·30 ·030
4	12·35 ·118	9·46 ·094	17·45 ·111	21·56 ·123	10·93 ·083	3·37 ·026	7·44 ·060	4·85 ·068	2·30 ·023
5	12·52 ·077	9·66 ·065	17·45 ·108	21·74 ·078	10·95 ·064	3·42 ·024	7·41 ·071	4·97 ·050	2·27 ·025
6	12·59 ·108	9·72 ·097	17·83 ·114	21·88 ·093	11·17 ·071	3·38 ·023	7·48 ·042	4·91 ·057	2·26 ·024
7	12·03 ·127	9·59 ·101	17·20 ·105	21·40 ·125	10·97 ·092	3·36 ·032	7·24 ·067	4·69 ·075	2·26 ·032
8	12·30 ·069	9·73 ·071	17·31 ·101	21·56 ·084	11·00 ·069	3·47 ·027	7·45 ·053	4·77 ·095	2·27 ·020
9	12·80 ·131	9·73 ·085	17·60 ·144	22·06 ·151	11·26 ·100	3·46 ·022	7·40 ·073	5·22 ·077	2·23 ·016
10	12·40 ·120	9·72 ·086	17·42 ·105	21·61 ·105	11·09 ·071	3·44 ·031	7·39 ·074	4·96 ·134	2·23 ·022
11	12·82 ·128	9·41 ·108	17·28 ·124	21·83 ·112	10·95 ·083	3·43 ·024	7·49 ·046	5·08 ·074	2·25 ·018
12	12·61 ·095	9·68 ·096	17·54 ·140	21·55 ·106	11·04 ·076	3·41 ·038	7·48 ·066	4·86 ·076	2·26 ·023
13	12·58 ·104	9·50 ·079	17·63 ·111	21·73 ·134	11·16 ·080	3·38 ·023	7·42 ·051	5·05 ·088	2·26 ·020
14	12·41 ·157	9·65 ·099	17·64 ·102	21·81 ·106	10·84 ·083	3·44 ·032	7·42 ·059	5·04 ·089	2·30 ·018
15	12·42 ·106	9·60 ·095	17·63 ·111	21·68 ·061	10·99 ·047	3·46 ·021	7·53 ·073	4·90 ·070	2·27 ·018
16	12·54 ·113	9·79 ·084	17·64 ·087	21·91 ·079	11·10 ·059	3·48 ·020	7·56 ·062	4·82 ·059	2·24 ·021
	MALES								
1	12·51±·075	9·19±·092	17·34±·107	21·79±·092	11·18±·079	3·45±·027	5·044±·063	4·94±·062	2·32±·022
2	12·37 ·087	9·03 ·086	17·35 ·088	21·47 ·085	10·89 ·069	3·39 ·023	5·032 ·060	4·84 ·050	2·26 ·020
3	12·27 ·080	9·15 ·077	17·28 ·109	21·74 ·122	10·98 ·106	3·40 ·038	5·037 ·072	4·85 ·095	2·27 ·024
4	12·49 ·130	8·95 ·108	17·56 ·155	21·70 ·169	10·98 ·105	3·42 ·033	5·056 ·082	4·87 ·056	2·27 ·030
5	12·52 ·138	9·13 ·084	17·11 ·106	21·62 ·083	10·92 ·062	3·41 ·038	5·039 ·068	4·98 ·088	2·26 ·024
6	12·59 ·108	9·20 ·094	17·48 ·099	21·89 ·119	10·99 ·078	3·35 ·027	5·033 ·057	4·98 ·082	2·26 ·018
7	12·21 ·098	9·05 ·097	17·08 ·103	21·63 ·086	11·09 ·071	3·45 ·024	5·043 ·064	4·87 ·075	2·27 ·020
8	12·22 ·100	9·07 ·086	17·05 ·093	21·38 ·081	10·89 ·086	3·41 ·038	5·043 ·064	4·87 ·093	2·23 ·020
9	12·74 ·127	9·09 ·105	17·31 ·150	21·86 ·169	11·15 ·091	3·45 ·025	5·028 ·072	5·02 ·136	2·21 ·020
10	12·63 ·087	9·00 ·077	17·42 ·099	21·63 ·107	11·05 ·078	3·45 ·028	5·038 ·075	5·09 ·065	2·23 ·017
11	12·52 ·109	8·81 ·115	17·08 ·098	21·64 ·113	10·72 ·065	3·50 ·026	5·039 ·065	5·14 ·089	2·28 ·019
12	12·58 ·107	9·06 ·091	17·37 ·123	21·47 ·128	10·84 ·082	3·40 ·034	5·033 ·054	5·03 ·073	2·28 ·028
13	12·13 ·105	8·84 ·098	17·48 ·130	21·51 ·140	10·98 ·097	3·46 ·024	5·031 ·061	4·89 ·081	2·28 ·017
14	12·31 ·085	9·04 ·081	17·24 ·139	21·74 ·090	10·88 ·080	3·47 ·029	5·042 ·054	4·95 ·059	2·24 ·023
15	12·47 ·086	9·16 ·080	17·65 ·135	21·70 ·111	11·03 ·080	3·47 ·021	5·064 ·070	5·02 ·069	2·28 ·020
16	12·44 ·120	9·10 ·072	17·54 ·080	21·95 ·103	11·04 ·065	3·56 ·033	5·069 ·085	4·88 ·088	2·22 ·029

measurements (corrected for

NO.		
5	6	7
7±·122	11·21±·086	3·44±·092
3 ·160	11·05 ·092	3·40 ·041
5 ·097	11·06 ·072	3·41 ·029
6 ·123	10·93 ·083	3·37 ·026
4 ·078	10·95 ·064	3·42 ·024
3 ·093	11·17 ·071	3·38 ·023
·125	10·97 ·092	3·36 ·032
5 ·084	11·00 ·069	3·47 ·027
5 ·151	11·26 ·100	3·46 ·022
·105	11·09 ·071	3·44 ·031
·112	10·95 ·083	3·43 ·024
5 ·106	11·04 ·076	3·41 ·038
·134	11·16 ·080	3·38 ·023
·106	10·84 ·083	3·44 ·032
·061	10·99 ·047	3·46 ·021
·079	11·10 ·059	3·48 ·020
±·092	11·18±·079	3·45±·027
·085	10·89 ·069	3·39 ·023
·122	10·98 ·106	3·40 ·038
·169	10·98 ·105	3·42 ·033
·083	10·92 ·062	3·41 ·038
·119	10·99 ·078	3·35 ·027
·086	11·09 ·071	3·45 ·024
·081	10·89 ·086	3·41 ·038
·169	11·15 ·091	3·45 ·025
·107	11·05 ·078	3·45 ·028
·113	10·72 ·065	3·50 ·026
·128	10·84 ·082	3·40 ·034
·140	10·98 ·097	3·46 ·024
·090	10·88 ·080	3·47 ·029
·111	11·03 ·080	3·47 ·021
·103	11·04 ·065	3·56 ·033

CHARACTER NO.							
8	9	10	11	12	13	14	15
7·48±·068	4·88±·090	2·27±·029	1·33±·016	3·85±·031	2·54±·024	4·91±·055	13·10±·107
7·53 ·071	4·79 ·093	2·24 ·039	1·32 ·020	3·85 ·027	2·51 ·106	4·94 ·115	12·93 ·135
7·50 ·051	4·93 ·093	2·30 ·030	1·29 ·016	3·83 ·026	2·54 ·025	4·91 ·041	13·08 ·104
7·44 ·060	4·85 ·068	2·30 ·023	1·30 ·019	3·84 ·032	2·50 ·029	4·79 ·051	13·09 ·139
7·41 ·071	4·97 ·050	2·27 ·025	1·37 ·019	3·85 ·031	2·57 ·023	4·92 ·067	13·12 ·104
7·48 ·042	4·91 ·057	2·26 ·024	1·42 ·016	3·86 ·027	2·50 ·023	5·00 ·042	13·34 ·090
7·24 ·067	4·69 ·075	2·26 ·032	1·33 ·019	3·76 ·035	2·50 ·026	4·88 ·063	12·77 ·128
7·45 ·053	4·77 ·095	2·27 ·020	1·32 ·012	3·90 ·029	2·49 ·020	4·88 ·041	12·84 ·081
7·40 ·073	5·22 ·077	2·23 ·016	1·41 ·023	3·88 ·023	2·51 ·018	4·92 ·056	13·18 ·127
7·39 ·074	4·96 ·134	2·23 ·022	1·34 ·019	3·85 ·025	2·49 ·024	4·84 ·045	12·92 ·112
7·49 ·046	5·08 ·074	2·25 ·018	1·48 ·027	3·88 ·022	2·56 ·025	4·94 ·059	13·21 ·109
7·48 ·066	4·86 ·076	2·26 ·023	1·38 ·023	3·86 ·029	2·60 ·028	4·96 ·064	12·95 ·107
7·42 ·051	5·05 ·088	2·26 ·020	1·37 ·019	3·82 ·021	2·50 ·025	5·01 ·052	13·06 ·118
7·42 ·059	5·04 ·089	2·30 ·018	1·31 ·026	3·88 ·032	2·51 ·023	4·96 ·068	12·72 ·135
7·53 ·073	4·90 ·070	2·27 ·018	1·35 ·018	3·86 ·023	2·50 ·027	4·95 ·044	12·79 ·101
7·56 ·062	4·82 ·059	2·24 ·021	1·35 ·018	3·93 ·030	2·50 ·020	4·89 ·036	13·01 ·099
5·044±·063	4·94±·062	2·32±·022	1·36±·017	3·89±·025	2·59±·017	4·98±·044	13·31±·099
5·032 ·060	4·84 ·050	2·26 ·020	1·37 ·013	3·84 ·027	2·54 ·019	5·03 ·056	13·28 ·088
5·037 ·072	4·85 ·095	2·27 ·024	1·35 ·022	3·78 ·030	2·59 ·026	4·94 ·050	13·26 ·126
5·056 ·082	4·87 ·056	2·27 ·030	1·37 ·014	3·89 ·032	2·55 ·030	4·94 ·074	13·17 ·167
5·039 ·068	4·98 ·088	2·26 ·024	1·39 ·018	3·90 ·033	2·55 ·026	4·93 ·045	13·08 ·080
5·033 ·057	4·98 ·082	2·26 ·018	1·40 ·018	3·83 ·024	2·55 ·019	4·90 ·039	13·35 ·144
5·043 ·064	4·87 ·075	2·27 ·020	1·36 ·017	3·83 ·017	2·54 ·027	4·98 ·060	13·07 ·111
5·043 ·064	4·87 ·093	2·23 ·020	1·36 ·013	3·84 ·025	2·48 ·022	4·86 ·045	12·93 ·103
5·028 ·072	5·02 ·136	2·21 ·020	1·38 ·025	3·90 ·101	2·50 ·025	4·90 ·066	13·28 ·192
5·038 ·075	5·09 ·065	2·23 ·017	1·39 ·020	3·83 ·026	2·54 ·024	4·95 ·057	13·18 ·114
5·039 ·065	5·14 ·089	2·28 ·019	1·40 ·021	3·93 ·020	2·54 ·024	4·94 ·050	12·92 ·127
5·033 ·054	5·03 ·073	2·28 ·028	1·37 ·017	3·85 ·028	2·60 ·024	5·06 ·075	13·19 ·108
5·031 ·061	4·89 ·081	2·28 ·017	1·36 ·019	3·85 ·024	2·55 ·023	4·91 ·072	12·90 ·141
5·042 ·054	4·95 ·059	2·24 ·023	1·33 ·019	3·88 ·024	2·53 ·020	4·91 ·034	12·73 ·106
5·064 ·070	5·02 ·069	2·28 ·020	1·42 ·023	3·93 ·025	2·53 ·023	5·03 ·068	13·45 ·215
5·069 ·085	4·88 ·088	2·22 ·029	1·39 ·021	4·00 ·026	2·48 ·029	4·93 ·046	13·03 ·133

TABLE 12b Observed variances of various measurements (corrected for regression on humerus) with standard errors.

Population no.	CHARACTER NO. 2	3	4	5	6	7
	FEMALES					
1	·17±·043	·18±·056	·15±·032	·34±·201	·17±·052	·020±·0054
2	·16 ·049	·17 ·046	·28 ·106	·41 ·182	·14 ·036	·025 ·0056
3	·22 ·058	·25 ·063	·46 ·107	·27 ·096	·15 ·075	·024 ·0066
4	·39 ·102	·25 ·063	·35 ·061	·42 ·113	·19 ·044	·019 ·0049
5	·14 ·038	·10 ·031	·29 ·087	·15 ·030	·10 ·033	·015 ·0036
6	·34 ·075	·27 ·086	·39 ·089	·26 ·078	·15 ·052	·015 ·0048
7	·32 ·108	·20 ·059	·25 ·042	·31 ·187	·17 ·055	·021 ·0101
8	·11 ·052	·20 ·045	·35 ·074	·25 ·037	·17 ·039	·026 ·0066
9	·44 ·141	·39 ·119	·40 ·101	·61 ·164	·27 ·083	·012 ·0032
10	·36 ·102	·18 ·052	·34 ·115	·30 ·073	·14 ·027	·027 ·0075
11	·54 ·109	·40 ·115	·53 ·098	·43 ·113	·24 ·065	·020 ·027
12	·24 ·063	·25 ·061	·52 ·051	·32 ·067	·16 ·044	·036 ·0121
13	·29 ·077	·17 ·035	·33 ·079	·48 ·133	·17 ·058	·015 ·0029
14	·61 ·210	·24 ·078	·26 ·056	·28 ·072	·17 ·050	·025 ·0100
15	·34 ·067	·27 ·062	·37 ·097	·11 ·034	·07 ·017	·014 ·0055
16	·40 ·081	·22 ·048	·23 ·049	·20 ·040	·11 ·029	·013 ·0043
	MALES					
1	·16±·044	·24±·059	·32±·078	·24±·062	·18±·013	·021±·0060
2	·24 ·049	·23 ·053	·25 ·078	·23 ·052	·15 ·028	·018 ·0042
3	·14 ·045	·13 ·026	·25 ·064	·33 ·098	·25 ·070	·032 ·0111
4	·30 ·098	·25 ·061	·51 ·049	·60 ·224	·23 ·055	·023 ·0062
5	·38 ·100	·18 ·071	·27 ·069	·17 ·037	·10 ·005	·036 ·0086
6	·34 ·071	·26 ·061	·28 ·062	·41 ·108	·18 ·042	·021 ·0050
7	·25 ·067	·24 ·055	·28 ·055	·19 ·016	·13 ·032	·015 ·0043
8	·24 ·091	·18 ·042	·22 ·062	·16 ·013	·17 ·049	·034 ·0090
9	·42 ·097	·29 ·077	·59 ·292	·74 ·232	·21 ·053	·017 ·0044
10	·18 ·044	·15 ·048	·23 ·054	·28 ·084	·15 ·055	·019 ·0086
11	·31 ·063	·34 ·096	·25 ·053	·33 ·105	·11 ·024	·018 ·0043
12	·29 ·098	·21 ·057	·38 ·124	·41 ·139	·17 ·051	·028 ·0066
13	·24 ·091	·21 ·047	·39 ·114	·45 ·126	·22 ·062	·013 ·0074
14	·17 ·049	·16 ·045	·44 ·147	·19 ·064	·15 ·059	·020 ·0043
15	·18 ·038	·16 ·037	·42 ·245	·31 ·151	·16 ·050	·011 ·0028
16	·28 ·096	·10 ·030	·14 ·056	·20 ·077	·08 ·024	·020 ·0044

8	9	10
·106±·032	·18±·081	·019±·0069
·073 ·033	·13 ·049	·023 ·0029
·076 ·027	·20 ·066	·026 ·0062
·098 ·029	·13 ·043	·015 ·0047
·119 ·028	·06 ·025	·015 ·0031
·053 ·015	·10 ·018	·017 ·0033
·089 ·033	·11 ·028	·020 ·0053
·097 ·023	·32 ·187	·014 ·0043
·140 ·037	·16 ·043	·007 ·0017
·148 ·043	·49 ·406	·013 ·0028
·073 ·066	·17 ·089	·011 ·0188
·120 ·032	·15 ·053	·015 ·0037
·066 ·027	·21 ·090	·010 ·0025
·082 ·022	·19 ·052	·008 ·0039
·165 ·034	·15 ·061	·010 ·0021
·125 ·026	·11 ·040	·015 ·0037
·115±·026	·11±·027	·014±·0031
·113 ·022	·08 ·020	·013 ·0031
·113 ·031	·20 ·059	·013 ·0059
·141 ·033	·07 ·022	·018 ·0057
·116 ·031	·19 ·060	·014 ·0028
·093 ·025	·19 ·053	·010 ·0020
·103 ·036	·14 ·030	·010 ·0028
·097 ·037	·20 ·095	·010 ·0037
·137 ·051	·48 ·210	·010 ·0028
·135 ·038	·10 ·022	·007 ·0023
·111 ·020	·19 ·058	·009 ·0025
·070 ·020	·13 ·036	·018 ·0049
·084 ·020	·15 ·041	·007 ·0013
·070 ·020	·08 ·069	·012 ·0044
·123 ·030	·12 ·041	·010 ·0063
·098 ·029	·14 ·051	·016 ·0074

asurements (corrected for

	6	7
201	·17±·052	·020±·0054
182	·14 ·036	·025 ·0056
96	·15 ·075	·024 ·0066
113	·19 ·044	·019 ·0049
030	·10 ·033	·015 ·0036
078	·15 ·052	·015 ·0048
187	·17 ·055	·021 ·0101
037	·17 ·039	·026 ·0066
164	·27 ·083	·012 ·0032
073	·14 ·027	·027 ·0075
113	·24 ·065	·020 ·027
067	·16 ·044	·036 ·0121
·133	·17 ·058	·015 ·0029
·072	·17 ·050	·025 ·0100
·034	·07 ·017	·014 ·0055
·040	·11 ·029	·013 ·0043
·062	·18±·013	·021±·0060
·052	·15 ·028	·018 ·0042
·098	·25 ·070	·032 ·0111
·224	·23 ·055	·023 ·0062
·037	·10 ·005	·036 ·0086
·108	·18 ·042	·021 ·0050
·016	·13 ·032	·015 ·0043
·013	·17 ·049	·034 ·0090
·232	·21 ·053	·017 ·0044
·084	·15 ·055	·019 ·0086
·105	·11 ·024	·018 ·0043
·139	·17 ·051	·028 ·0066
·126	·22 ·062	·013 ·0074
·064	·15 ·059	·020 ·0043
·151	·16 ·050	·011 ·0028
·077	·08 ·024	·020 ·0044

CHARACTER NO.							
8	9	10	11	12	13	14	15
·106±·032	·18±·081	·019±·0069	·0056±·0014	·022±·0063	·014±·0045	·070±·016	·26±·222
·073 ·033	·13 ·049	·023 ·0029	·0063 ·0023	·012 ·0030	·018 ·0023	·212 ·159	·29 ·066
·076 ·027	·20 ·066	·026 ·0062	·0075 ·0019	·020 ·0041	·018 ·0036	·048 ·014	·32 ·066
·098 ·029	·13 ·043	·015 ·0047	·0104 ·0033	·029 ·0074	·015 ·0034	·072 ·025	·55 ·138
·119 ·028	·06 ·025	·015 ·0031	·0089 ·0026	·024 ·0113	·013 ·0030	·107 ·033	·27 ·075
·053 ·015	·10 ·018	·017 ·0033	·0078 ·0018	·021 ·0048	·015 ·0056	·052 ·019	·24 ·538
·089 ·033	·11 ·028	·020 ·0053	·0074 ·0024	·025 ·0076	·013 ·0030	·069 ·021	·33 ·118
·097 ·023	·32 ·187	·014 ·0043	·0053 ·0013	·029 ·0075	·014 ·0032	·060 ·011	·23 ·169
·140 ·037	·16 ·043	·007 ·0017	·0139 ·0042	·014 ·0046	·009 ·0028	·085 ·025	·44 ·123
·148 ·043	·49 ·406	·013 ·0028	·0098 ·0024	·016 ·0043	·014 ·0037	·052 ·015	·34 ·111
·073 ·066	·17 ·089	·011 ·0188	·0235 ·021	·016 ·020	·021 ·023	·120 ·050	·40 ·127
·120 ·032	·15 ·053	·015 ·0037	·0147 ·0040	·023 ·0051	·022 ·0043	·113 ·024	·32 ·077
·066 ·027	·21 ·090	·010 ·0025	·0093 ·0024	·012 ·0027	·017 ·0058	·073 ·016	·38 ·090
·082 ·022	·19 ·052	·008 ·0039	·0151 ·0042	·025 ·0069	·013 ·0030	·117 ·038	·46 ·166
·165 ·034	·15 ·061	·010 ·0021	·0104 ·0023	·017 ·0030	·022 ·0048	·061 ·014	·32 ·088
·125 ·026	·11 ·040	·015 ·0037	·0108 ·0024	·028 ·0071	·012 ·0038	·040 ·009	·32 ·075
·115±·026	·11±·027	·014±·0031	·0082±·0019	·018±·0058	·008±·0021	·059±·018	·28±·069
·113 ·022	·08 ·020	·013 ·0031	·0054 ·0013	·023 ·0054	·011 ·0033	·098 ·037	·23 ·064
·113 ·031	·20 ·059	·013 ·0059	·0074 ·0037	·029 ·0082	·015 ·0053	·055 ·020	·35 ·086
·141 ·033	·07 ·022	·018 ·0057	·0044 ·0011	·021 ·0053	·019 ·0055	·114 ·041	·58 ·136
·116 ·031	·19 ·060	·014 ·0028	·0084 ·0028	·028 ·0095	·016 ·0055	·051 ·017	·16 ·040
·093 ·025	·19 ·053	·010 ·0020	·0089 ·0028	·016 ·0061	·011 ·0026	·044 ·012	·60 ·197
·103 ·036	·14 ·030	·010 ·0028	·0069 ·0015	·007 ·0021	·018 ·0054	·094 ·048	·32 ·111
·097 ·037	·20 ·095	·010 ·0037	·0039 ·0016	·015 ·0036	·012 ·0029	·050 ·014	·25 ·068
·137 ·051	·48 ·210	·010 ·0028	·0158 ·0052	·027 ·0067	·016 ·0029	·114 ·046	·95 ·515
·135 ·038	·10 ·022	·007 ·0023	·0101 ·0040	·016 ·0048	·014 ·0038	·076 ·020	·31 ·071
·111 ·020	·19 ·058	·009 ·0025	·0113 ·0025	·011 ·0029	·016 ·0028	·064 ·022	·42 ·083
·070 ·020	·13 ·036	·018 ·0049	·0066 ·0031	·019 ·0051	·014 ·0046	.141 ·080	·29 ·083
·084 ·020	·15 ·041	·007 ·0013	·0084 ·0025	·013 ·0031	·012 ·0040	·113 ·041	·46 ·162
·070 ·020	·08 ·069	·012 ·0044	·0062 ·0017	·009 ·0023	·010 ·0028	·027 ·007	·27 ·059
·123 ·030	·12 ·041	·010 ·0063	·0137 ·0085	·016 ·0038	·014 ·0056	·116 ·144	·10 ·324
·098 ·029	·14 ·051	·016 ·0074	·0087 ·0027	·013 ·0044	·016 ·0046	·040 ·016	·34 ·098

in table 11*. All further comparisons and any conclusions drawn from them have used these adjusted values and not the original unadjusted means of table 9.

The means and variances of the adjusted characters were now found for all populations, and are given with their standard errors in tables 12*a*, *b*. The standard errors for the means were found from the usual formula—the standard deviation divided by the square root of the number of observations. The standard errors of the variances were found from the following formula, which as far as we know is unpublished in this form. It is easily used on a computer, and has the advantage that it is valid whether or not the distribution is Gaussian, unlike Bartlett's homogeneity test, which presupposes a Gaussian distribution.

> Let $X_1, X_2, \ldots, X_n$ be a set of measurements of a single character in a random sample of n individuals. Let their mean be $\bar{X}=\Sigma X_r/n$, and their variance $V=\Sigma(X_r-\bar{X})^2/(n-1)$. Then the standard error of V is given by
>
> $$\text{S.E.}(V)=\sqrt{\frac{\Sigma(X_r-\bar{X})^4-V^2(n-3/n)}{(n-2)\ (n-3)}}$$

While performing these calculations the computer was asked to identify and print out all individual measurements that differed by more than three standard deviations from their expected values on the basis of the regression on the humerus. There were 98 such values, and the measurements were all repeated on the original skeletons. It was found that 14 of the values were in error. These were corrected and all calculations were performed a second time (except for table 10, where the slight gain in accuracy that would have resulted again did not seem to justify the labour and computer time required). Thirteen out of the 84 outlying values that were confirmed were derived from a single rat (from Kundara West, a control population), which was clearly suffering from an unidentified systemic disease of the skeleton and for that reason the data on this animal were eliminated from all calculations. While there may be errors in the remaining data, it seems unlikely that they are numerous, and any large ones would have been detected by this check.

These means and variances were now tested for heterogeneity: that is to say, we asked whether the variation between populations within the strip is larger than might be expected if they were in effect parts of a single homogeneous population, and similarly for the control populations. The method of doing this was based on the following general theorem, applicable to samples of at least moderate size. Suppose that $z_1, z_2, \ldots, z_k$ are estimates of some parameter θ derived from samples $S_1, S_2, \ldots, S_k$. Let $s_1, s_2, \ldots, s_k$ be the standard errors of $z_1, z_2, \ldots, z_k$ respectively; then

$$\Sigma(z_r^2/s_r^2)-\Sigma(z_r/s_r^2)/\Sigma(1/s_r^2)=\chi^2$$

can be referred to a chi-squared table with (k–1) degrees of freedom. In our case we get for each character 8 different chi-squareds with 7 degrees of freedom each, namely by all combinations of the following dichotomies:

---

* In all calculations the two sexes were kept separate. Although the adjustments in table 11 were based on the control populations only, they were applied equally to control animals and to those exposed to radiation. It was felt that any very small gain in accuracy that might have been obtained by taking into account the regression coefficients of the animals from the strip would not justify the extra labour and computer time required. The adjusted values were subsequently analysed as if they were directly observed values. Strictly speaking, some allowance should have been made in the analysis for the fact that the formulae for adjustment were derived from the data themselves; but again the difference this would have made will be very small, and it did not seem worth the trouble.

PLATE I

Aerial view of the southern end of t
Ashtamudi Lake

Transferring a rat from the trap into a

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djusted means of table 9.
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ors in tables 12*a*, *b*. The
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bservations. The standard
g formula, which as far as
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ution is Gaussian, unlike
ussian distribution.

of a single character in a
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was asked to identify and
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s_k be the standard errors of

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es. Strictly speaking, some allow-
the formulae for adjustment were
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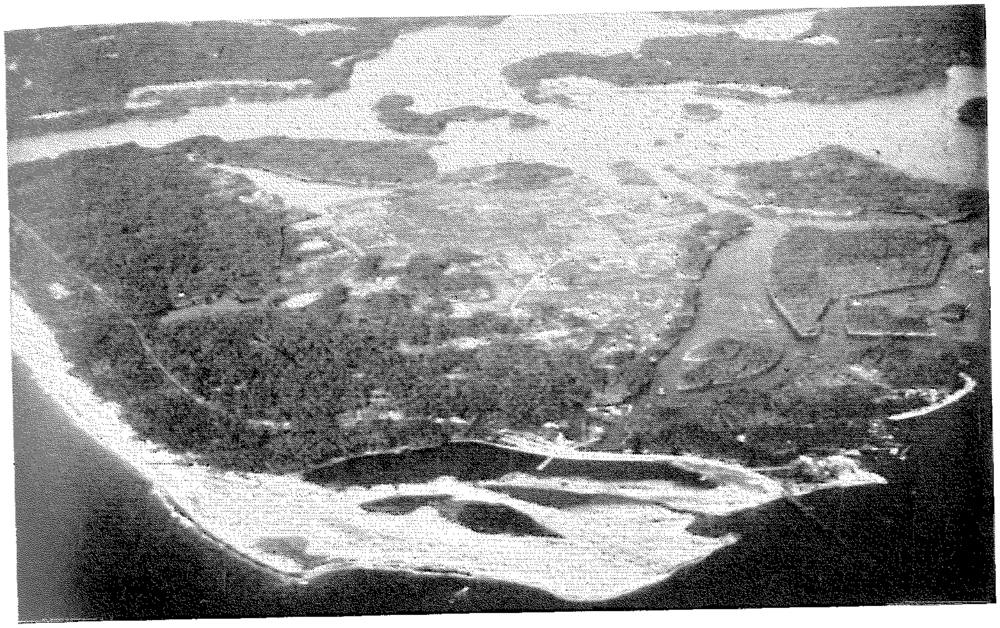
PLATE I

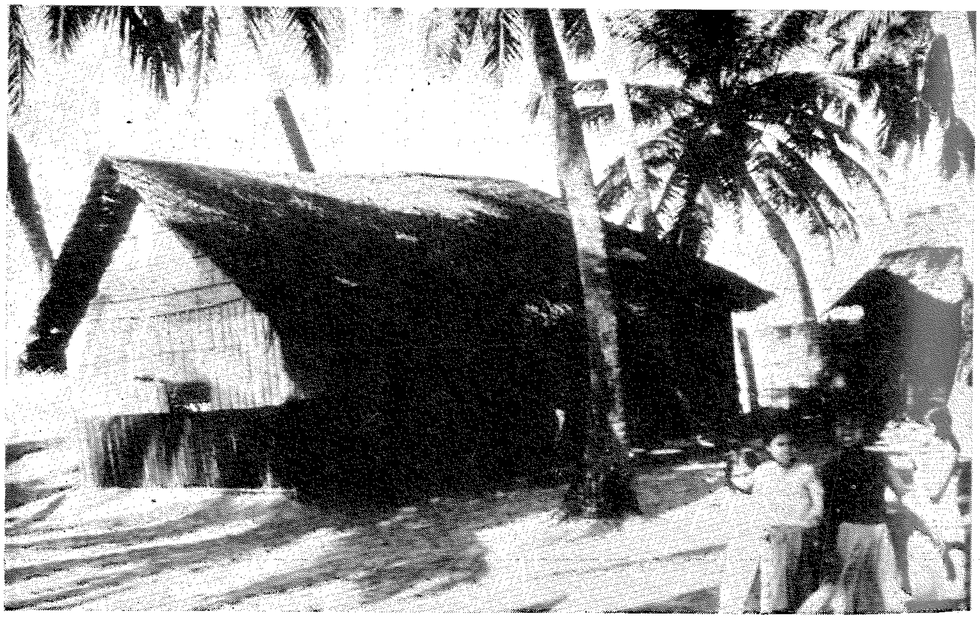


Aerial view of the southern end of the strip with Neendakara Bridge and the entrance to Ashtamudi Lake

Transferring a rat from the trap into a sack

PLATE II

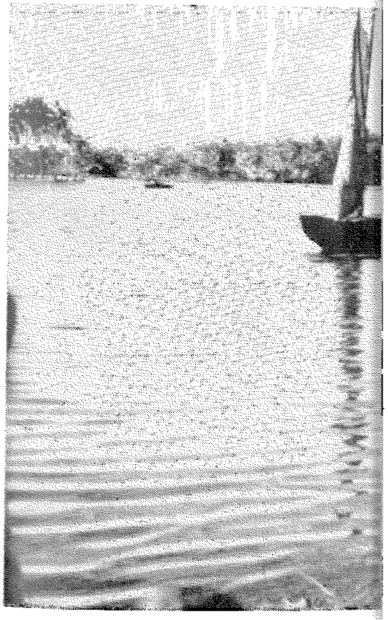
Beach at Cheriazhiekal



Hut at Cheriazhiekal

PLATE III

Backwaters at Cheriazhiekal



Backwaters at Shraikadu

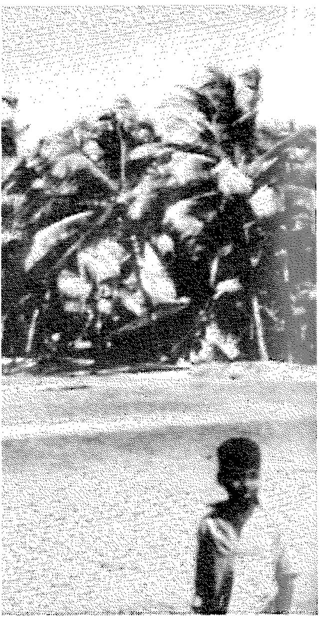
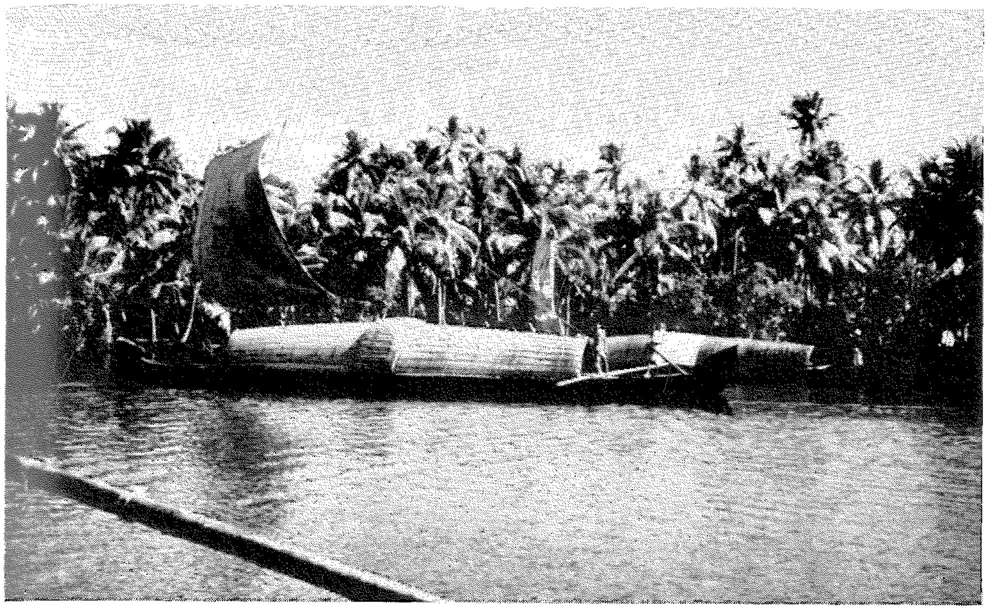
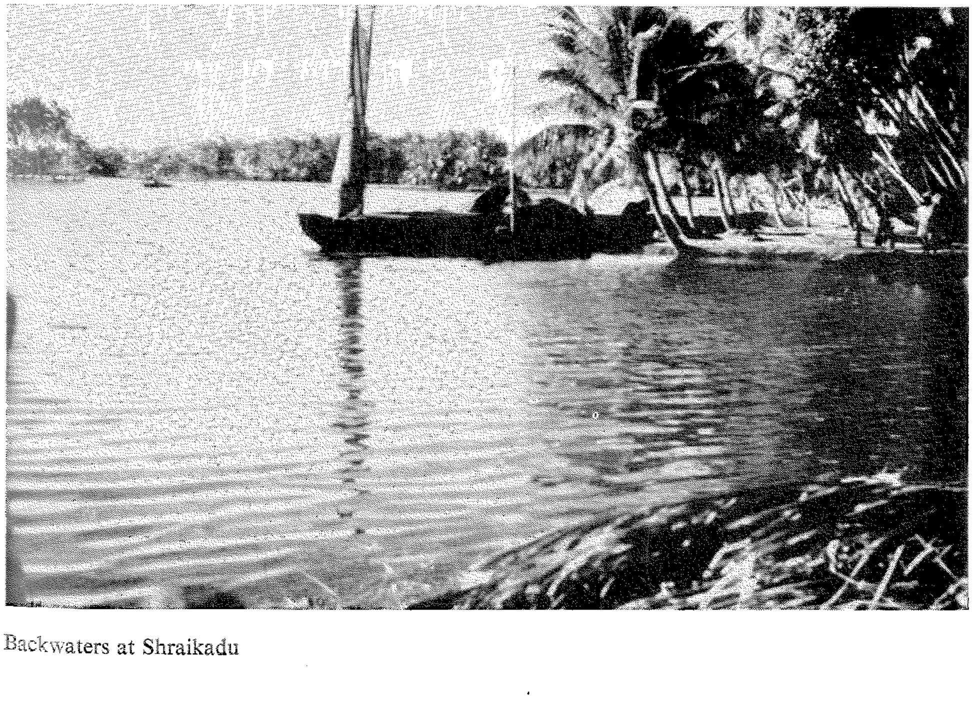


PLATE III



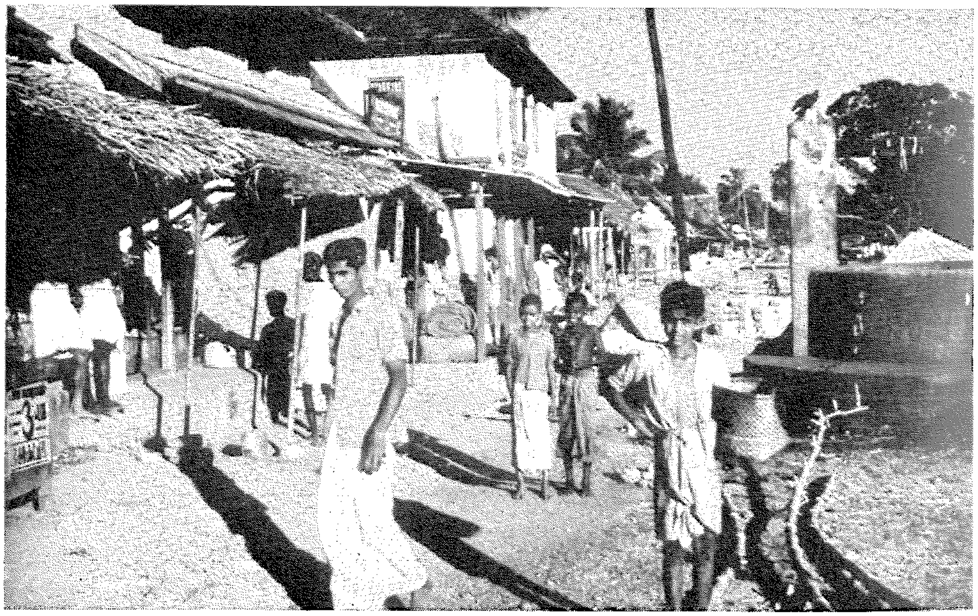
Backwaters at Cheriazhiekal



Backwaters at Shraikadu

PLATE IV

Kilikollur



Kottiyam

TABLE 13 Values of heterogeneity χ^2 for testing the variability of means and variances between one population and another within the coastal strip and within the control region

D.f. of each χ^2	Character no. 2	3	4	5	6	7	8	9	10	11	12	13	14	15
For comparisons of means														

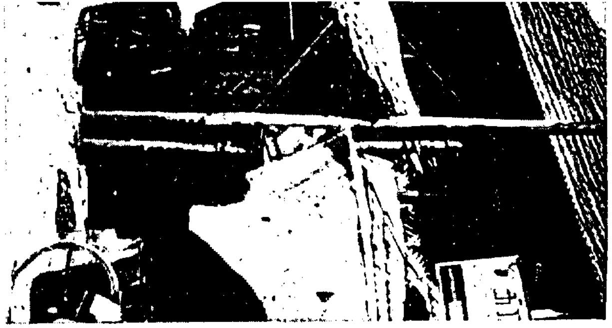


TABLE 13 Values of heterogeneity χ^2 for testing the variability of means and variances between one population and another within the coastal strip and within the control region

	D.f. of each χ^2	Character no. 2	3	4	5	6	7	8	9	10	11	12	13	14	15
For comparisons of means															
Strip: female	7	19·6	14·1	18·7	20·4	13·2	14·4	13·6	12·8	3·1	43·1	12·8	10·1	10·4	24·3
Strip: male	7	16·5	5·3	22·1	21·9	12·4	10·8	8·8	4·4	10·5	10·0	13·4	18·1	7·8	13·3
Controls: female	7	12·5	12·1	8·8	16·2	17·5	13·1	6·1	23·6	11·3	29·7	11·9	16·4	8·3	15·0
Controls: male	7	23·3	11·3	19·0	12·9	24·2	15·2	34·0	9·0	14·2	16·2	35·4	14·1	5·8	19·8
Total	28	71·9	42·8	68·7	71·4	67·3	53·5	62·5	49·8	39·1	99·0	73·5	58·7	32·3	72·4
For comparison of variances															
Strip: female	7	12·2	10·2	19·2	10·8	3·5	4·7	6·6	7·9	4·5	5·0	10·1	2·0	5·3	6·5
Strip: male	7	10·8	9·9	3·4	11·0	12·7	8·8	1·6	14·1	5·2	7·4	21·5	7·6	5·2	16·5
Controls: female	7	7·2	9·8	10·3	26·2	19·2	8·2	12·1	2·8	9·2	9·5	8·3	11·9	14·8	2·0
Controls: male	7	9·6	12·8	10·1	9·8	10·3	9·0	6·8	8·3	8·8	6·0	10·5	3·6	18·1	9·4
Total	28	39·8	42·7	43·0	57·8	45·7	30·7	27·1	33·1	27·7	27·9	50·4	25·1	43·4	34·4

(i) for z_r=*mean* of sample S_r or for z_r=*variance* of sample S_r;
(ii) in *females* or in *males;*
(iii) in the *strip* or in *controls.*

These homogeneity chi-squareds are given in table 13. The four χ^2 corresponding to the last two dichotomies have been added together to give a total χ^2 with 28 d.f. to test the general homogeneity of the data. Since the 1 per cent significance point for χ^2 with 28 d.f. is 48·3, and the 0·1 per cent point is 56·9, it will be seen that many of the χ^2 relating to heterogeneity of means are very highly significant, showing quite clearly the presence of heterogeneity. Since high values of χ^2 arise in both females and males, and in both strip populations and controls, it is evident that the heterogeneity is general, and not confined to either sex or either region. The χ^2 for heterogeneity of variance are rather lower, but one of them is significant at the 0·1 per cent level and one at the 1 per cent level, and there is a general tendency for their values to be raised in comparison with the number of degrees of freedom. Hence it seems clear that there is also heterogeneity of variance.

An inspection of table 12 suggests that the heterogeneity consists of a rather haphazard variation from population to population rather than, say, a steady rise or fall from one end of the strip to the other, or from one end of the control area to the other. For example, there is a tendency for many measurements of animals from the strip to have high values in populations nos. 1 and 6, and low values in population 8, but there are irregular fluctuations in between.

In view of this heterogeneity the comparison between the strip and the control populations was done by a simple Student's *t* for each character and sex. In effect this answers the question: is the average difference between the two values more than might be expected in view of the natural variation from population to population? The values of *t* are given in table 14. (A positive value indicates that the strip populations give a higher average than the controls in the comparison in question, and a negative value indicates the reverse.)

TABLE 14 Values of Student's *t* with 14 d.f. for comparisons between strip and control populations

Character no.	Comparison between means		variances	
	Females	Males	Females	Males
2	−2·1	− ·9	−2·9	− ·1
3	·5	1·6	−1·8	·4
4	−1·2	−1·0	−1·2	−1·0
5	− ·9	− ·4	− ·6	− ·9
6	− ·3	·5	− ·5	·7
7	−1·6	−3·1	·1	1·9
8	− ·5	− ·1	−1·8	·7
9	−2·5	−2·5	−1·0	− ·6
10	1·2	1·3	4·0	·8
11	1·7	·6	3·4	−2·5
12	−1·4	−1·8	1·2	1·3
13	− ·5	·8	− ·8	− ·0
14	−1·2	− ·3	− ·2	− ·9
15	− ·6	1·0	−1·5	−1·3

It is at once clear that mo
contrast to the values of th
exceptions occur in the comp
10 and 11 respectively. Howev
variance than have the strip
radiation would be to increase
is confined to the females, and
opposite directions. There are a
for means. However, there is
values of *t*, or among the other
The strip and control animals
about ten miles, and their envi
would not be surprising if th
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or genetic isolation, quite apa
differences observed that reach
due to such causes, and some
In view of the absence of any st
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masked by the variation alread
population. It is only possible t
it could plausibly be due to
influences could also play a par

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Since the 1 per cent significance
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populations nos. 1 and 6, and
ar fluctuations in between.
etween the strip and the control
for each character and sex. In
ifference between the two values
tural variation from population
e 14. (A positive value indicates
e than the controls in the com-
tes the reverse.)

. for comparisons between strip

	parison between variances	
s	Females	Males
9	−2·9	− ·1
6	−1·8	·4
0	−1·2	−1·0
4	− ·6	− ·9
5	− ·5	·7
·1	·1	1·9
·1	−1·8	·7
·5	−1·0	− ·6
·3	4·0	·8
·6	3·4	−2·5
·8	1·2	1·3
·8	− ·8	− ·0
·3	− ·2	− ·9
·0	−1·5	−1·3

It is at once clear that most of these values are non-significant, in striking contrast to the values of the heterogeneity chi-squareds. The three notable exceptions occur in the comparisons of variance in females, for characters 2, 10 and 11 respectively. However, in character 2 the controls have higher average variance than have the strip animals, whereas it is assumed that the effect of radiation would be to increase the variance. In characters 2 and 10 the deviation is confined to the females, and in character 11 the males and females deviate in opposite directions. There are also a few significant differences in the comparisons for means. However, there is no discernible consistent pattern among these values of t, or among the others, which fail to reach the 0·05 level of significance. The strip and control animals are separated geographically from each other by about ten miles, and their environments are to some degree different. Hence it would not be surprising if they had developed some difference between the distributions of the measured characters as a result of environmental differences or genetic isolation, quite apart from the effects of radiation. Some of the differences observed that reach a formal level of statistical significance may be due to such causes, and some may be merely the result of chance fluctuation. In view of the absence of any strong and consistent pattern of difference the only possible conclusion seems to be that if there is any effect of radiation it is masked by the variation already existing within both areas from population to population. It is only possible to speculate about the cause of this variability; it could plausibly be due to genetic drift, but environmental and selective influences could also play a part.

Non-metrical skeletal variations

Methods

In addition to the metrical characters treated in the two preceding sections, there exist numerous minor skeletal variations. These were first systematically studied in the mouse (for a recent review see Grüneberg, 1963). They are largely under genetic control, but unlike most discontinuous variations—such as albinism—they have a multifactorial basis, at least in the mouse, where they have been studied in crosses. Similar variants have been found in the black rat (Grüneberg, 1961) and in all rodent species that have been studied (Berry and Searle, 1963). They also occur in man and are a general feature of mammalian, if not vertebrate, organization. It may safely be assumed that, as a group, they have a multifactorial basis similar to that found in the mouse. In the mouse considerable differences in the incidences of these characters are found between wild populations (Weber, 1950; Deol, 1958; Berry, 1963), and the same applies to *Rattus rattus* (Grüneberg, 1961).

The designation of this group of variants as non-metrical is not strictly correct since many if not all of them are in fact graded characters. They are, however, difficult to measure, and for that reason it is more convenient to treat them as all-or-none affairs—that is, to substitute counting for measurement. This involves, in many instances, arbitrary conventions as to where to draw the line between 'normals' and 'abnormals' (if these terms are appropriate for slight deviations, most of which are well within the limits of normality). In some cases, the distinction between two phenotypes is completely objective: whether or not there is fusion between vertebrae is an example of a distinction in this category. The number of presacral vertebrae is almost as objective if a convention is made about the classification of asymmetrical attachments of the pelvis; however, an arbitrary decision has to be made occasionally when a transverse process of a vertebra is intermediate between a lumbar and a sacral. In other instances the arbitrary element in classification is greater, and though an experienced observer will be reasonably consistent, two different observers may differ about where to draw the line. For these reasons, it is essential that all classifications are made by the same observer, and that reasonable precautions are taken against gradual and unnoticed changes in the conventions of classification. In the present investigation all classifications were made by R.J.B.; the rats from the strip and from the control area were placed in alternate trays for classification: in both cases the village of origin determined the order of classification, the sequence being for the strip from south to north and for the control area round the triangle clockwise, starting with Kilikollur. The rats in one of the trays were classified twice, both at the beginning and at the end, with no significant difference in scoring. There is no evidence of progressive divergence of populations from Neendakara to Azhiekal, or from Kilikollur to Pallimukku, which might indicate a progressive chang
realized that, whereas abse
may be taken at its face v
establish a difference in ch
classified without any ambi

It is formally possible to e
of the underlying continuo
method is rather indirect a
refrained from any attempt
the simple data of incide
differences between popula

TABLE 15 Non-metrical

	Variant
1.	Maxillary foramen doubl
2.	Foramen palatinum maju
3.	For. sphenoidale medium
4.	Processus pterygoideus pr
5.	Accessory processus petro
6.	Foramen ovale double
7.	Foramen pterygoideum do
8.	Preoptic sutures present
9.	Metoptic roots abnormal
10.	Foramen hypoglossi doub
11.	Accessory mental foramen
12.	Accessory scapular foram
13.	Fossa olecrani perforata
14.	Processus spinosus of C3
15.	Arch foramen of C3 doub
16.	Arch foramina in C4
17.	Arch foramina in C5
18.	For. transversaria imperfe
19.	Tuberculum anterius of C
20.	Dystopia cranialis tub. ant
21.	Dystopia caudalis tub. ant
22.	Cervical ribs on C7
23.	Fusions between cervical v
24.	Dyssymphysis of thoracic
25.	Sacral fusions
26.	26 presacral vertebrae

* 90/874 stands for '90 out of a total of
given refer to sides of animals rather t
vertebral spaces which can undergo os
† Italicized values differ significantly fro

Results

The incidence of the 26 non-
The data for the eight strip
have been pooled. The test o
It will be seen that in only
significantly between the tw
accessory mental foramen,
scarcely be regarded as sign

Now if the pooled values
other, this may mean one o

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berg, 1963). They are largely
inuous variations—such as
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: been found in the black rat
ave been studied (Berry and
neral feature of mammalian,
sumed that, as a group, they
in the mouse. In the mouse
:haracters are found between
, 1963), and the same applies

metrical is not strictly correct
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ing for measurement. This
as to where to draw the line
ns are appropriate for slight
of normality). In some cases,
ely objective: whether or not
a distinction in this category.
ective if a convention is made
ents of the pelvis; however,
when a transverse process of
sacral. In other instances the
ough an experienced observer
:rs may differ about where to
ıll classifications are made by
ns are taken against gradual
lassification. In the present
I.B.; the rats from the strip
rays for classification: in both
f classification, the sequence
ontrol area round the triangle
ie of the trays were classified
h no significant difference in
ergence of populations from
Pallimukku, which might in-

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dicate a progressive change in criteria for scoring. Nevertheless it should be realized that, whereas absence of a significant difference between two samples may be taken at its face value, rather more stringent criteria are required to establish a difference in characters of this kind than in characters which can be classified without any ambiguity.

It is formally possible to extract from lateral variants an estimate of the variance of the underlying continuous distributions (Green, 1951, 1954, 1962), but the method is rather indirect and requires certain simplifying assumptions. We have refrained from any attempt to calculate the variance, and will discuss here only the simple data of incidence. These are sufficient for the discovery of any differences between populations that might exist.

TABLE 15 Non-metrical skeletal variants

Variant	Strip		Control	
	No.	%†	No.	%†
1. Maxillary foramen double	90/874*	10·3	84/912	9·2
2. Foramen palatinum majus double	267/876	30·5	255/910	28·0
3. For. sphenoidale medium present	25/437	5·7	29/456	6·5
4. Processus pterygoideus present	50/876	5·7	46/912	5·0
5. Accessory processus petrosus	133/876	15·2	148/912	16·2
6. Foramen ovale double	11/876	1·3	12/912	1·3
7. Foramen pterygoideum double	21/876	2·4	34/912	3·7
8. Preoptic sutures present	7/876	·8	13/910	1·4
9. Metoptic roots abnormal	61/876	7·0	73/910	8·0
10. Foramen hypoglossi double	47/868	*5·4*	102/902	*11·3*
11. Accessory mental foramen	9/874	1·0	22/912	2·4
12. Accessory scapular foramen	433/872	49·7	416/910	45·7
13. Fossa olecrani perforata	187/876	*21·3*	315/912	*34·5*
14. Processus spinosus of C3 present	324/437	74·1	328/455	72·1
15. Arch foramen of C3 double	171/876	19·5	161/910	17·7
16. Arch foramina in C4	149/874	17·0	136/912	14·9
17. Arch foramina in C5	74/876	8·4	79/912	8·7
18. For. transversaria imperfecta in C6	1/876	·1	4/912	·4
19. Tuberculum anterius of C6 absent	2/876	·2	1/912	·1
20. Dystopia cranialis tub. ant. of C6	1/876	·1	4/912	·4
21. Dystopia caudalis tub. ant. of C6	4/876	·3	9/912	1·0
22. Cervical ribs on C7	7/874	·8	5/912	·5
23. Fusions between cervical vertebrae	3/438	·7	10/456	2·2
24. Dyssymphysis of thoracic vertebrae	7/438	1·6	10/456	2·2
25. Sacral fusions	173/1314	13·2	215/1368	15·7
26. 26 presacral vertebrae	410/438	93·6	429/456	94·1

* 90/874 stands for '90 out of a total of 874' etc. The majority of variants are bilateral characters, and the figures given refer to sides of animals rather than to animals. In the case of sacral fusions (no. 25), there are three intervertebral spaces which can undergo ossification; hence the total is three times the number of the animals.

† Italicized values differ significantly from each other at the 5 per cent level.

Results

The incidence of the 26 non-metrical variants that we scored is set out in table 15. The data for the eight strip populations and for the eight control populations have been pooled. The test of significance used here is a χ^2 test for a 2×2 table. It will be seen that in only 2 out of the 26 characters does the incidence differ significantly between the two groups of populations (in the case of no. 11, *accessory mental foramen*, $\chi^2 = 4{\cdot}224$ with Yates's correction, and this can scarcely be regarded as significant for a character of this kind).

Now if the pooled values for a variant do not differ significantly from each other, this may mean one of two things. Either the two population groups are homogeneous as regards the variant in question; or they are heterogeneous, but the differences between the individual populations have cancelled out in the process of summation (as with *maxillary foramen double* and *metoptic roots abnormal*—see table 16). In either case, it is clear that there are no systematic differences between strip and control populations. Hence, for the purposes of the present discussion, the question of whether these 24 variants are homogeneously distributed over the respective populations is irrelevant and may be disregarded.

TABLE 16 Incidence of four non-metrical variants by populations

N=normal; A=abnormal; n=total; χ^2_7=homogeneity χ^2; χ^2_1=χ^2 testing divergence between the strip and control totals

Population no.	13. Fossa olecrani perforata			10. Foramen hypoglossi double			1. Maxillary foramen double			9. Metoptic roots abnormal		
	N	A	n	N	A	n	N	A	n	N	A	n
1.	97	15	112	104	8	112	99	13	112	100	12	112
2	88	14	102	97	5	102	99	3	102	99	3	102
3.	79	27	106	101	5	106	93	13	106	102	4	106
4.	82	30	112	100	10	110	105	7	112	104	8	112
5.	85	17	102	91	7	98	97	5	102	94	8	102
6.	97	21	118	111	5	116	99	19	118	107	11	118
7.	77	23	100	98	2	100	80	18	98	98	2	100
8.	84	40	124	119	5	124	112	12	124	111	13	124
Total 1–8	689	187	876	821	47	868	784	90	874	815	61	876
χ^2_7	23·041			8·238			23·701			13·635		
P	$\simeq$0·002			$\simeq$0·32			$\simeq$0·0015			$\simeq$0·06		
9.	85	29	114	97	17	114	93	21	14	111	13	114
10.	73	35	108	100	8	108	95	13	108	96	12	108
11.	123	11	134	108	22	130	116	18	134	130	4	134
12.	72	44	116	103	9	112	113	3	116	112	4	116
13.	53	61	114	108	6	114	110	4	114	113	1	114
14.	52	48	100	87	13	100	94	6	100	90	8	98
15.	76	42	118	107	11	118	115	3	118	88	30	118
16.	63	45	108	90	16	106	92	16	108	97	11	108
Total 9–16	597	315	912	800	102	902	828	84	912	837	73	910
χ^2_7	76·016			15·045			37·980			74·558		
P	$<10^{-10}$			$\simeq$0·035			$\simeq 3\times10^{-6}$			$<10^{-10}$		
χ^2_1	38·494			19·926			0·600			0·721		
P	$\simeq 10^{-9}$			$\simeq 10^{-5}$			$\simeq$0·44			$\simeq$0·40		

The two variants whose incidence, in the totals, is significantly different in strip and control populations are *fossa olecrani perforata* and *foramen hypoglossi double*. Both of these variants are known to be under genetic control in the mouse (Stein, 1957; Deol, 1955), and it may be assumed that the same is true for the rat. The data for these two variants are set out in more detail in table 16. In both cases the variant is more frequent in the control than in the strip

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TABLE 17 Measures of d
(negative values implying zer

Population no.	1	2
1	—	0·0167
2	—	—
3	—	—
4	—	—
5	—	—
6	—	—
7	—	—
8	—	—

TABLE 18 Measures of div

Population no.	9	10
9	—	0·0031
10	—	—
11	—	—
12	—	—
13	—	—
14	—	—
15	—	—
16	—	—

or they are heterogeneous,
itions have cancelled out in
ramen *double* and *metoptic*
is clear that there are no
populations. Hence, for the
of whether these 24 variants
populations is irrelevant and

its by populations
$\chi_1^2=\chi^2$ testing divergence between

	Maxillary foramen double A	n	9. Metoptic roots abnormal N	A	n
	13	112	100	12	112
	3	102	99	3	102
3	13	106	102	4	106
5	7	112	104	8	112
7	5	102	94	8	102
	19	118	107	11	118
	18	98	98	2	100
2	12	124	111	13	124
4	90	874	815	61	876
	23·701		13·635		
	$\simeq 0{\cdot}0015$		$\simeq 0{\cdot}06$		
3	21	14	111	13	114
5	13	108	96	12	108
6	18	134	130	4	134
3	3	116	112	4	116
0	4	114	113	1	114
4	6	100	90	8	98
5	3	118	88	30	118
2	16	108	97	11	108
8	84	·912	837	73	910
	37·980		74·558		
	$\simeq 3\times10^{-6}$		$<10^{-10}$		
	0·600		0·721		
	$\simeq 0{\cdot}44$		$\simeq 0{\cdot}40$		

ls, is significantly different in
rforata and *foramen hypoglossi*
under genetic control in the
assumed that the same is true
out in more detail in table 16.
the control than in the strip

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populations. An apparently significant difference, as judged by χ^2, could possibly arise as a result of heterogeneity between different populations, as well as because of a real difference between strip and control areas. The use of a t-test will give a result less sensitive to the effect of heterogeneity. In both cases, the two groups of populations still differ significantly from each other ($t=2{\cdot}870$; $n=14$; $P\simeq 0{\cdot}013$; and $t=3{\cdot}457$; $n=14$; $0{\cdot}01>P>0{\cdot}001$ respectively), but the level of significance is much reduced. Even if we were dealing with characters that can be classified without ambiguity, the presence of these two values in a sample of 26 variants would scarcely be regarded as sufficient evidence for a systematic difference between the two groups of populations. Since, however, these characters have to be classified according to somewhat arbitrary criteria, we must conclude that, like the dental and skeletal measurements, the data on non-metrical variants do not indicate any systematic difference between the rat populations on the strip and in the control areas. Like the data on dental and skeletal measurements, the present figures clearly show that, both on the strip and in the control area, rat populations are genetically heterogeneous like those in Delhi (Grüneberg, 1961).

We have so far discussed the incidence in the two areas of individual variants taken one at a time. It is possible to calculate the degree of divergence between any two populations, or groups of populations, with regard to the whole array of variants taken together. Such a measure of divergence has been devised by C.A.B.S.; for a description of the method see Berry (1963). In the absence of a real difference the average measure of divergence becomes zero. In the

TABLE 17 Measures of divergence between pairs of strip populations (negative values implying zero divergence)

Population no.	1	2	3	4	5	6	7	8
1	—	0·0167	0·0206	−0·0041	0·0010	0·0326	0·0148	0·0017
2	—	—	0·0259	0·0170	0·0290	0·0856	0·0599	0·0382
3	—	—	—	−0·0027	0·0232	0·0406	0·0108	0·0216
4	—	—	—	—	0·0047	0·0255	0·0044	−0·0019
5	—	—	—	—	—	0·0209	0·0253	−0·0025
6	—	—	—	—	—	—	0·0868	0·0228
7	—	—	—	—	—	—	—	0·0397
8	—	—	—	—	—	—	—	—

TABLE 18 Measures of divergence between pairs of control populations

Population no.	9	10	11	12	13	14	15	16
9	—	0·0031	0·0403	0·0180	0·0372	0·0356	0·0517	0·0238
10	—	—	0·0441	0·0114	0·0192	0·0395	0·0507	0·0216
11	—	—	—	0·0567	0·1044	0·1140	0·0726	0·0506
12	—	—	—	—	0·0093	0·0380	0·0360	0·0263
13	—	—	—	—	—	0·0125	0·0606	0·0315
14	—	—	—	—	—	—	0·0473	0·0155
15	—	—	—	—	—	—	—	0·0194
16	—	—	—	—	—	—	—	—

calculations, the rare *variants of the tuberculum anterius of C6* (nos. 19–21 of table 15) have been pooled and variant no. 25 has been omitted because of its correlation with age (it had been scored in the first instance as giving some idea of the age structures of the different populations). The analysis is thus based on 23 variants in all. The results for the strip populations are given in table 17 and those for the control populations in table 18. In each case there are 28 paired comparisons between populations. None of the measures of divergence are large although a number of them are formally significant at the 5 per cent level (cf. Grüneberg, 1961). There is more heterogeneity between the control populations than between the strip ones but this is not a very marked difference. The reason for it is probably to be sought in the greater geographical and ecological separation between control populations. There is no sign of a trend corresponding with the gradient of radioactivity along the strip.

Perhaps the most meaningful way of interpreting tables 17 and 18 is to compare the values given there with the measure of divergence between the strip and control populations treated as two single populations (as in table 15). The mean divergence between the pooled strip and control populations is 0·0046—much smaller than most of the values differentiating pairs of either strip or of control populations from each other. Grewal (1962b) found that sublines of an inbred strain of mice diverged at the rate of 0·003 per character per generation. Although it would be incorrect to base too much on a comparison of these two figures, it does tend to confirm that there is only a trivial difference between strip and control populations as a whole. This clearly confirms our previous conclusions.

Fertility and p

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Fertility and prenatal mortality

The relevant data are set out in table 19. The proportion of pregnant females varied considerably from population to population both on the strip and in the control areas. The reasons for this variation are not known. However, the overall mean pregnancy rates for the strip and the controls are very similar (18·64 and 18·07 per cent respectively). The mean number of implantations per litter was slightly (but not significantly) larger on the strip than in the controls (4·88 as compared with 4·42). Embryonic loss following implantation, as represented by deciduomata and dead embryos, was almost the same for both groups (6·5 and 7·0 per cent respectively). For part of the material, counts of corpora lutea made on the fresh ovaries by means of a hand lens are also available. The accuracy of such counts is not very great, and we are not inclined to attach much importance to them; but in no case did the number of implantations in a uterine horn exceed the number of corpora lutea in the corresponding ovary. In 14 pregnant rats from the strip, there were 72 corpora lutea and 63 implantations (preimplantation loss 12·5 per cent). In 42 pregnant rats from the control area, there were 235 corpora lutea and 190 implantations (preimplantation loss 19·1 per cent). On the basis of these data the number of ova per ovulation is 5·14 for the strip and 5·60 for the controls, the difference again not being significant. With the exception of these last values, the slight differences are all in favour of the strip populations; there is thus no indication in these data, so far as they go, that the strip populations are inferior to the controls as regards either fertility or survival of zygotes in uterine life. No data are available on the survival of young after birth.

TABLE 19 Number of pregnancies, litter size and embryonic mortality

Locality	♀♀	Pregnancies No.	Pregnancies %	Implantations No.	Implantations Mean	Living embryos	Deciduomata, dead embryos	Postimplantational loss %	Preimplantational loss	Preimplantational loss %
1 Neendakara	26	6	22·2	31	5·2	29	2	6	—	—
2 Puthenthura	18	5	27·8	22	4·4	22	0	0	—	—
3 Kovilthottam	30	3	10·0	12	4·0	12	0	0	1/13 (3)*	8
4 Ponmana	33	4	12·1	25	6·3	24	1	4	4/9 (1)	44
5 Cheriazhickal	26	9	34·6	46	5·1	42	4	9	1/5 (1)	20
6 Allapad	30	9	30·0	38	4·2	37	1	3	2/18 (4)	11
7 Shraikadu	22	2	9·1	12	6·0	11	1	8	1/13 (2)	8
8 Azhickal	35	3	8·6	14	4·7	10	4	29	0/14 (3)	0
Total 1–8	220	41	18·64	200	4·88	187	13	6·5	9/72 (14)	12·5
9 Kilikollur	28	7	25·0	30	4·3	30	0	0	5/35 (6)	14
10 Karikode	28	4	14·3	17	4·3	17	0	0	0/13 (3)	0
11 Chandanathoppu	39	2	5·1	10	5·0	10	0	0	0/5 (1)	0
12 Kundara West	32	8	25·0	34	4·3	31	3	9	15/49 (8)	31
13 Kundara East	29	6	20·7	27	4·5	19	8	30	5/32 (6)	16
14 Kottiyam	27	9	33·3	39	4·3	37	2	5	13/52 (9)	25
15 Oomainalur	33	1	3·3	5	5·0	5	0	0	1/6 (1)	17
16 Pallimukku	33	8	24·2	37	4·6	36	1	3	6/43 (8)	14
Total 9–16	249	45	18·07	199	4·42	185	14	7·0	45/235 (42)	19·1

* 1/13 (3) = 1 corpus luteum out of 13 (from 3 pregnancies) not represented by an implantation.

Mean implantation litter size on the strip = 72/14 = 5·14
Mean implantation litter size of controls = 235/42 = 5·60

Discussion

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14 Kottiyam	27	9	33·3	39	4·3	37	2	5	13/52 (9)	25
15 Oomainalur	33	1	3·3	5	5·0	5	0	0	1/6 (1)	17
16 Pallimukku	33	8	24·2	37	4·6	36	1	3	6/43 (8)	14
Total 9–16	249	45	18·07	199	4·42	185	14	7·0	45/235 (42)	19·1

* 1/13 (3)=1 corpus luteum out of 13 (from 3 pregnancies) not represented by an implantation.

Mean implantation litter size on the strip=72/14=5·14
Mean implantation litter size of controls=235/42=5·60

Discussion

The result of the four lines of investigation is a failure to discover, within our experimental limits, any genetic effects of exposure to high natural radioactivity on the rats inhabiting the Neendakara–Kayankulam strip. It could be argued that the differences in ecology between the strip and control areas might produce systematic differences in the rats from these areas. We found no such differences. There is the logical possibility that the strip rats were changed in such a way by the radiation that this expected difference is masked. This would be a far-fetched argument and is, in any case, contradicted by the fact that there are much greater differences between individual populations, both on the strip and in the control areas, than between strip and control, each considered as a single population. It is necessary therefore to discuss other ways in which our negative results can be interpreted.

The pioneer work of Muller and many others established the fact that with medium and high doses there is a linear relation between X-ray dose and the rate of induced mutations. Later, it was shown that in *Drosophila melanogaster* this linear relation extends down to 25 r units (Spencer and Stern, 1948), and recent work has made it probable that it holds for as small a dose as 5 r (Glass and Ritterhoff, 1961); the demonstration of the genetic effect of so small a dose involved the scoring of well over one million flies. The overall radiation on the strip is about 1·6 r/y (see appendix I). The reproductive biology of the black rat is not known at all accurately, but under tropical conditions the animals breed all the year round (Buxton, 1936); it is probably reasonable to assume that the mean reproductive life of the wild rat is between 6 months and one year and probably much nearer the former. If so, the radiation dose to which our Kerala rats are exposed is of the order of 1 r—even less than the 5 r dose in the (acute) irradiation experiments of Glass and Ritterhoff (1961). Nonetheless, it seems reasonable to assume that the linear relation between dose of radiation and mutation rate extends down to the level of 1 r—that is, there are no grounds to invoke a threshold effect such that, whereas a dose of 5 r has a genetic effect proportional to its size, a dose of 1 r has none.

Whereas the dose of radiation to which an individual rat is exposed is thus comparatively modest, the cumulative dose to which, say, 500 consecutive rat generations, in perhaps 300 years, have been exposed is of the order of 500 r, compared with 67 r accumulated during the same interval by the control animals.

Earlier experiments based on the irradiation of mature spermatozoa of *Drosophila* led to the conclusion that mutation rate is a function of total dose alone, and that it makes no difference whether that dose is administered acutely in a short time or whether it is spread thinly over a long period. More recently, Russell (1963) and his collaborators have discovered the important fact that this is not true for the irradiation of spermatogonia and oocytes in the mouse, i.e., for those cell types which in man are of the greatest medical importance. They found that a given dose produces between three and four times as many mutations when administered to spermatogonia at the rate of 90 r/min as when administered at the rate of 0·009 r/min. On the other hand, there is no further lowering of the mutation rate if the same dose is administered at the rate of 0·001 r/min, the lowest dose rate so far studied. (Dose rate effects have also been reported in other organisms, but they are irrelevant here). It is pertinent to point out that the dose rate on the strip is far lower than 0·001 r/min. As discussed in detail in appendix I, it amounts to about 0·18 mr/h or 0·003 mr/min and is thus over 300 times lower than the lowest dose rate studied experimentally. Whereas down to a dose rate of 1 mr/min there is no evidence for the existence of a threshold, it is not inconceivable that there is a threshold somewhere above the extremely low dose rate encountered on the strip.

Our negative findings could thus be explained by postulating that gamma rays have no genetic effect at the very low dose rate to which the Kerala rats are exposed. However, in view of what is known about the mutagenic mechanism of ionizing radiations, this is not a probable assumption.

If, then, we assume that there is no such threshold, and if we accept our negative findings at their face value, we may conclude that the production of mutations by radiation has been accurately counterbalanced by selection so that the level of genetic variance (as inferred from the phenotypic variance) has remained constant. The fate of radiation-induced mutations depends of course on their effect on fitness, in the Darwinian sense, both in the homozygous and in the heterozygous condition. In a purely formal way, the fate of any given gene with known effect or effects on fitness can be predicted by making the arbitrary assumption that its effect on fitness is independent of the genetic background—that is, that a gene will raise or lower the fitness by a constant amount regardless of the residual genotype. It is, of course, well known that this is a fiction. Still less is it possible, at present, to make a legitimate forecast about the whole array of genes affecting metrical characters and their interactions. The degree to which newly arising mutations of this kind will be eliminated by natural selection, or incorporated into the gene pool of the population, is thus completely unknown. It appears improbable that natural selection should not rapidly eliminate some at least of the newly arising variance; and insofar as this happens, the negative result obtained in this investigation may be explained on the basis of selection. Though our data on fertility and embryonic mortality do not, in themselves, suggest the operation of selective processes, they certainly do not exclude the low level of selection required to achieve equilibrium.

Alternatively, we may assume that the genetic variance has, in fact, increased on account of the radiation, but that this increase has been accurately counterbalanced by a decrease of the non-genetic variance, the total (phenotypic) variance remaining constant. Every geneticist who has worked with inbred strains of animals and crosses between them is familiar with the fact that the phenotypic variance is not simply the sum of the genetic and the environmental variances (for a general discussion see Falconer, 1960). Whether, in a genetically mixed population like that of the rats on the strip, it is possible for there to be an accurate replacement of environmental by genetic variance such that the phenotypic variance remains constant is a question which is easier asked than answered: we are inclined to doubt it. If *Rattus rattus* were amenable to experi-

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observed heterogeneity bet
parison with the averages of
characters are considered
correlations with other cha

TABLE 20 Approximate
control rats which would
1 per cent level

Character no.	Average d bet
	Females
2	·26
3	·19
4	·24
5	·36
6	·18
7	·05
8	·04
9	·17
10	·03
11	·07
12	·06
13	·04
14	·08
15	·26

nia and oocytes in the mouse,
e greatest medical importance.
three and four times as many
t the rate of 90 r/min as when
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genetic and the environmental
960). Whether, in a genetically
p, it is possible for there to be
enetic variance such that the
ion which is easier asked than
attus were amenable to experi-

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mentation, the level of genetic variance of strip and control rats could be assessed by their response to selection in the laboratory. This being impracticable, it may be doubted whether with the means at our disposal a decision between these two hypotheses can be obtained. They are, in any case, not mutually exclusive.

It might be thought that it makes little difference whether the strip rats show no detectable effects of radiation because the radiation is genetically ineffective at very low dose rates, or because its effects are completely counterbalanced by those of natural selection, or because an increase in genetic variance is completely absorbed by a corresponding decrease of environmental variance. So far as the metrical and non-metrical entities themselves are concerned, this is certainly so. But we have used these entities to probe a wider problem. If it were true that radiation-induced genetic variance has been added cryptically to the phenotypic variance, the same presumably would have happened with genes with major pathological effects, which could not have been detected by our method—if only because individuals carrying them tend not to survive into adult life. Whereas our findings thus give no positive indication of genetic damage to the rats living on the strip, they do not rule out the possibility of there being induced mutations lurking beyond the reach of our method.

Our data, so far as they go, show no consistent differences between the rat populations on the strip and the controls as regards the characters that we have investigated, which may be regarded as representative of the whole genotype of the rat. This, of course, does not prove that no such differences exist. We may ask how big a difference between irradiated and control populations could have escaped detection as the result of accidents of sampling. In other words, how large an average difference in means and variances between the strip and the control animals would there have to be to reach significance at about the 1 per cent level? The average differences required, calculated on the basis of the observed heterogeneity between populations, are given in table 20. A comparison with the averages of the figures given in table 9 shows that if the different characters are considered individually without taking into account possible correlations with other characters, a change in the means for the strip popu-

TABLE 20 Approximate value of the average difference between strip and control rats which would be required to give a significant difference at the 1 per cent level

Character no.	Average difference required between means		Average difference required between variances	
	Females	Males	Females	Males
2	·26	·26	·16	·12
3	·19	·15	·11	·10
4	·24	·18	·15	·18
5	·36	·25	·19	·25
6	·18	·18	·07	·06
7	·05	·06	·010	·008
8	·04	·18	·045	·033
9	·17	·11	·15	·15
10	·03	·04	·006	·005
11	·07	·04	·005	·004
12	·06	·07	·008	·010
13	·04	·05	·006	·005
14	·08	·08	·066	·052
15	·26	·29	·13	·36

lations amounting to something between 1 and 3 per cent would be required. Table 10 shows that a much larger proportional increase in variance for the animals from the strip would be needed to show significance, amounting mostly to something between 10 and 50 per cent of the variance of the controls.

The results given in the preceding chapters may be summarized as follows:

Type of measurement	*No. of comparisons*	*No. significant at 1% level*
Dental (means)	12	0
Dental (variances)	12	0
Skeletal (means)	28	1
Skeletal (variances)	28	2
Non-metrical	26	2
Fertility	4	0
All	110	5

(We have chosen a 1 per cent significance as a critical level to distinguish a real effect. This is an arbitrary choice. If we take the more usual 5 per cent level, the details of the following argument will be changed, but the general conclusions will not be greatly altered. The significance levels given take into account the heterogeneity between populations.) Taken at its face value, the finding of 5 significant values in 110 comparisons would suggest a real difference; but as we have shown above in some detail, some of these go in the wrong direction, and others follow no consistent pattern, and so these apparent significances may be discounted: there is no detectable effect of radiation.

We may, however, still ask how great an effect of radiation might be present on the assumption that it is masked by random fluctuations. It is difficult to give any precise answer to this question, partly because it is to some extent a subjective matter to decide when the differences between the control and the strip series follow a clear and consistent pattern, and partly because we do not know whether the different measured characters differ appreciably in their sensitivity to radiation. However, let us consider the metrical skeletal characters as an example, and for the sake of argument assume that the effect of radiation is to add the same percentage to all means (and the same percentage to all variances). Suppose, for example, that all means were increased by 0·3 per cent. Now the standard errors for the observed differences between means vary between about 0·3 and 1·0 per cent of the means themselves. If the standard error were 0·3 (per cent), a radiation effect represented by an increase of 0·3 per cent would raise the chance of getting a significant difference (at the 1 per cent level) to something like 0·05, while if the standard error were 1·0, this chance would scarcely be affected, although the few significances which were then obtained would be more often in the 'right' than in the 'wrong' direction. In all, out of the 28 comparisons between means we might have an increased expectation of about 0·5 of a significant result, instead of 0·25. Thus an increase of 0·3 per cent in all the means would hardly produce a detectable effect. On the other hand, if the radiation raised each mean by 1 per cent, then for those characters for which the standard error was about 0·3 per cent this would be as likely as not to give a significant result in the 'right' direction; and several such consistent significant results would give a clear *prima facie* case for the existence of a radiation effect, or at any rate of some kind of consistent difference between

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control area and strip. This a
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control area and strip. This accordingly suggests that an effect up to something like 0·3 per cent in the means could possibly be concealed in our data, but not much more. We do not wish to insist at all strongly on the precision of the value of 0·3 per cent suggested here, since there are a number of uncertainties about the effect that radiation could have on multifactorial characters, but it seems a reasonable estimate of the order of magnitude. Similar arguments suggest that radiation could increase the variances of the characters by about 3 per cent without being detected, but not by very much more.

Our knowledge of mutation rates, spontaneous and induced, is almost completely based on work with 'major' genes, which can be individually identified. The genetic basis of the metrical and non-metrical characters used in this investigation is multifactorial or 'polygenic': that is, it depends on the additive action of many genes with individually small effects. Mutations in such genes are generally discovered statistically by an increase in the genetic variance of a chosen parameter in a given population. The increase in the genetic variance is detected either by an increase in the phenotypic variance or by an increased response to selection. In view of technical difficulties, knowledge of mutations in such genes is still very rudimentary. Most of the work has been done on *Drosophila melanogaster*. For a variety of reasons, the results of these investigations have no very close bearing on our findings. In the first instance, *Drosophila* is much less sensitive to radiation than is the mouse, the only mammal for which comparable data for major genes are available. Secondly, all the *Drosophila* experiments have been carried out with massive doses of radiation running into hundreds or thousands of r units per generation, which cannot be compared with the low-level exposure of the Kerala rats. Thirdly, for technical reasons almost all the work on *Drosophila* has been carried out either on isogenic stocks or on stocks that had reached a plateau as the result of selection; by contrast, our rats are genetically heterogeneous populations. As recently shown by Mukai and Yoshikawa (1964), the phenotypic effect of mutations of this general kind may vary depending on whether they have been induced in genetically homogeneous or in heterogeneous populations.

In view of these limitations a detailed review of the literature on *Drosophila* may be dispensed with. We mention here merely two basic facts and a number of the more recent papers, from which the earlier literature can be traced. In the first instance, there is ample evidence for the occurrence of spontaneous mutations of polygenes, and recent work suggests that the mutation rate, for genes affecting viability at any rate, is surprisingly high (Mukai, 1964; for the mouse see also Grewal, 1962b). Secondly, mutation of polygenes occurs as the result of irradiation and can be discovered through an increase in the phenotypic variance or by the response to selection (Scossiroli, 1954; Clayton and Robertson, 1955; Wallace, 1956, 1963; Yamada and Kitigawa, 1961; Sankaranarayanan, 1964). On the other hand, little is known yet about the relation of their mutation rate to dose or dose rate. Nor is anything known about the relation of genotypic to phenotypic variance in genetically heterogeneous irradiated populations.

Equilibrium between mutation and natural selection takes so many generations to establish that irradiation experiments with mammals cannot proceed, in practice, very far along that course. Preliminary data on mice for the first few generations only are so far available (Lüning, 1960, 1963, 1964; Spalding, Strang and LeStourgeon, 1961; Muramatsu, Sugahara and Okazawa, 1963; Searle, 1963, 1964). Also, as the measurement of the effects of small doses of radiation presents almost insuperable difficulties, all the above authors have used much greater doses of radiation than those to which our Kerala rats were exposed. Little is therefore to be gained from discussing here the results of these investigations.

Finally, we have to discuss some studies purporting to relate the incidence of human congenital malformations to the intensity of background radiation. In none of these papers is it made clear whether the relationship postulated is of the somatic type (damage to the developing embryo by radiation) or whether it is a genetic effect caused by a change of gene frequencies on account of induced mutations. Gentry, Parkhurst and Bulin (1959), on the basis of birth and death certificates from New York State (excluding New York City), tried to establish a relation between the incidence of congenital malformations in various counties and the geological distribution of rock formations and minerals with a high radioactivity. Differences in the intensity of background radiation, in most instances, are inferred rather than measured and, in any case, are rather small. Indeed, as discussed in some detail by Neel (1963), there are so many sources of error that the hypothesis of Gentry *et al.* can hardly be regarded as established. A preliminary report by Kratchman and Grahn (1959) covering the whole area of the United States tries to relate the incidence of deaths due to congenital malformations (as published in the vital statistics of the United States) to the distribution of radioactive minerals (uranium etc.), the uranium content of the drinking water and the helium content of the air (as an index of the presence of minerals undergoing radioactive decay). This suggestion, however, was not borne out by more detailed studies (Grahn and Kratchman, 1963). Finally, Wesley (1960) tried to show that most human congenital malformations can be ascribed to 'background' radiation, of which the cosmic-ray energy flux is taken as a measure; the author thus seeks to explain an alleged variation of incidence of malformation with geomagnetic latitude. The paper has been severely criticized by Spiers, Burch and Reed (1960) and need not be considered further.

The genetic consequences of the atomic bombs on Hiroshima and Nagasaki (Neel, 1963, and earlier papers) are outside the scope of this investigation as the populations in question were exposed to a single acute dose of irradiation.

In conclusion, we consider that our negative result would not be influenced by the addition of further similar data. Furthermore, we are not aware of any other area in which more critical information could be obtained on this point.

Summary

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2. A search for genetic d
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Summary

1. The coastal area between Neendakara and Kayankulam, north of Quilon in Kerala, South India, (which is effectively an island) has high natural radioactivity owing to the presence of monazite sand, which contains thorium. The mean gamma radiation on the strip is about seven-and-a-half times that of the control areas inland. The strip has been inhabited and geographically isolated for a very long period.

2. A search for genetic damage has been made in rats (*Rattus rattus* L.) inhabiting this area. The material available includes the macerated skeletons and teeth of 438 rats from eight localities on the strip and of 458 rats from eight control localities inland. In addition, data were collected from these animals on fertility and embryonic mortality.

3 Six dental and fifteen skeletal measurements were made. Whereas the dental measurements are virtually unaffected by the age of the animals, the skeletal measurements had to be adjusted to eliminate the effects of general size differences. In addition, a classification was made in terms of 26 non-metrical skeletal variants.

4. Significant heterogeneity as regards the means of the metrical variants was found both between populations on the strip and between the control populations. The degree of genetic differentiation was about the same in both groups of populations. However, there was no systematic difference between the group of irradiated populations on the one hand and the control group on the other. Essentially the same situation was encountered for the non-metrical skeletal characters. Similarly, though individual populations differed from each other, there was no sign of a systematic difference in fertility or embryonic mortality between irradiated and control populations.

5. There is no evidence in our data that variance is greater in the irradiated than in the control populations.

6. If all the different lines of investigation are taken together, there is no evidence for significant differences between irradiated and control populations for the characters investigated.

7. There are at least four possible ways of explaining these negative findings. Firstly, it is conceivable that gamma rays, at the extremely low dose rate to which the Kerala rats are exposed (some 300 times lower than the lowest dose rate for which a genetic effect has been demonstrated), do not induce mutations. Secondly, if there is no such threshold, it may be postulated that the mutations induced by the radiation are almost exactly counterbalanced by natural selection so that the genetic variance (as gauged by the phenotypic variance) remains constant. Thirdly, it may be that an increase in the genetic variance has in fact taken place, but that this has been masked by a reduction in the environmental variance such that the total (phenotypic) variance has remained unchanged.

The latter two hypotheses are not mutually exclusive. If a cryptic increase of the genetic variance should have taken place, the irradiated populations might also carry an increased load, in the heterozygous condition, of genes with major pathological effects whose presence could not have been detected in the present investigation. Fourthly, accidents of sampling may obscure a real effect. It is possible to put an upper limit to the magnitude of differences between irradiated and control populations for which this is likely to happen at any assigned level of probability.

APPENDIX I

Dosimetry of th

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APPENDIX I

Dosimetry of the strip

The radioactivity of the Kerala coast is due to the presence of thorium, which is a constituent of monazite. Thorium (^{232}Th) is widely distributed in the earth's crust, but usually it occurs in very low concentrations. It is the parent element of a radioactive series, decaying in several steps with the emission of alpha, beta and gamma rays to ^{208}Pb, a stable isotope of lead. It has a half-life of $1{\cdot}39 \times 10^{10}$ years. Besides thorium itself, mesothorium 1 (^{228}Ra), with a half-life of 6·7 years, and radiothorium (^{228}Th), with a half-life of 1·9 years, are the only daughters with long enough half-lives to warrant biological consideration (World Health Organization, 1959). The presence of uranium in traces does not contribute significantly to the total radioactivity.

Geology

Monazite is a monoclinic phosphate of cerium and other rare-earth metals, including lanthanum, praseodymium, neodymium and samarium; it includes in its lattice variable proportions of ThO_2 (thoria). Uranium is occasionally present, and also traces of radium and mesothorium.

The monazite deposits of the Kerala coast contain from 8 to 10·5% thoria (Brown and Dey, 1955). These deposits are probably derived originally from the pegmatites that occur as intrusions in the Archaean gneisses of the southern hills of the Western Ghats. In the coastal deposits the monazite occurs in the form of small, rounded, translucent amber-coloured grains; but its appearance is masked by ilmenite, a titanate of iron ($FeTiO_3$), a fine black sand with which it is associated. Other minerals present in these deposits include zircon, rutile and garnet. The biggest deposits of these sands are at Manavalakurichi, near Cape Comorin, and at the south end of the Neendakara–Kayankulam strip where the rats were collected. Lesser deposits are widely spread along the Malabar coast and on the west coast of Ceylon. Large amounts of monazite also occur in Bihar State and in Brazil.

The formation of localized concentrations of monazite along the Malabar coast is not entirely understood. Possible mechanisms have been discussed by Tipper (1914), who came to the conclusion that the present-day conditions on the sea beach are a continuation of older conditions—in other words, that the monazite has been in the same places for some considerable period of time. This assessment of the situation is consistent with the fact that people living on the Neendakara–Kayankulam strip say that it used to be wider and that the sea has eroded the dunes that it once formed. While we were there, a stone sea wall was being built at Cheriazhiekal to arrest the encroachment; actually, there is evidence that an outlet once existed at the same place (see appendix II). Whereas the size and distribution of the deposits is thus probably liable to seasonal and longer-term changes, it may safely be assumed that the radioactive material has been on the strip long enough to allow the local rat population to reach genetic equilibrium.

Estimation of the mean dose

For assessment of the radiation dose received by the rats, the overall mean level of radioactivity of the strip is the most useful parameter. Rats move from hut to hut, and in a few minutes can migrate from high-radiation areas along the sea beach to places by the backwater with very low levels. In our study of the genetic effects of radiation over many generations the rats have been considered as a single population exposed to the mean level of radioactivity of the strip.

Dosimetric surveys of the monazite deposits along the Malabar coast have been undertaken by the Indian Atomic Energy Commission (Gopal-Ayengar, 1957; Bharatwal and Vaze, 1958; Vaze, 1961). None of these data were sufficiently detailed to allow the calculation of an overall value of radioactivity for the strip. At our request, a very complete survey of the strip was carried out in April 1962 by members of the Indian Atomic Energy Establishment (Rao, 1962), and at the same time the areas where control rats were obtained were also monitored. The following calculations are based entirely on this survey.

Observations were taken along 131 west–east transects across the strip; from north to south these are labelled A_1, B_1, C_1, . . ., Z_1; A_2, B_2, . . .,Z_2 and so on to A_6. From A_1 to O_4 the intervals between transects are approximately 170 yards, and successive points along each transect (A_1–N_4) are approximately 33 yards apart. From O_4 to A_6 intervals between transects are approximately 160 yards, and successive points along each transect approximately 52 yards apart. Thus there is a grid of observations from which an overall mean value may be obtained and which allows an examination of the general and localized distribution of the radioactivity.

TABLE 21 Gamma radiation (mr/h) 3 ft above ground level as determined are by Geiger–Müller survey meters calibrated against radium

Sample transects are arranged in the north–south sequence; a, b, c, . . . are points along the transects from the Arabian Sea in the west to the backwater in the east.

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
O_1	·1	·06	·1	·07	·03	·04	·03	—	—	—	—	—	—	—	—
P_1	·1	·12	·08	·06	·04	·05	·03	—	—	—	—	—	—	—	—
J_2	·2	·11	·06	·08	·06	·04	·04	·03	—	—	—	—	—	—	—
K_2	·1	·1	·1	·09	·04	·04	·04	·03	·03	·03	—	—	—	—	—
L_2	·14	·14	·12	·03	·06	·04	·04	·03	—	—	—	—	—	—	—
V_4	·5	·3	—	—	—	·1	—	—	—	—	—	—	—	—	—
W_4	·4	·4	·2	·2	·2	—	—	—	—	—	—	—	—	—	—
X_4	·3	·2	·15	·3	·2	—	—	—	—	—	—	—	—	—	—
S_5	1·1	1·3	·9	·3	·4	·6	·15	·15	—	·07	·1	·08	·03	·04	·08
T_5	·9	·8	1·0	·9	1·1	·4	·2	·2	·2	·2	·1	·06	—	—	—
U_5	1·0	1·0	·8	·8	·8	·4	·3	·2	·2	·2	·2	·1	—	—	—

Observations for some typical transects are shown in table 21. Apart from local variations, there are two major gradients in radiation intensity. Generally there is a marked fall in intensity from the sea coast to the backwater (figure 5), where it is often not much in excess of the control areas. In the northernmost 5 miles of the strip (A_1–Z_2), where it is about 200 yards wide, there is a steady

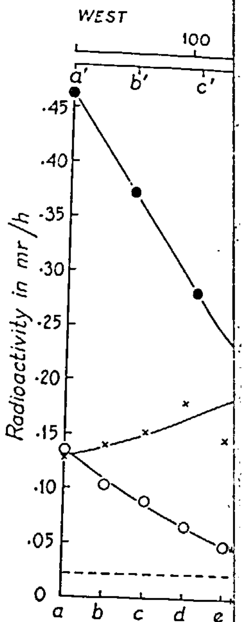

FIGURE 5
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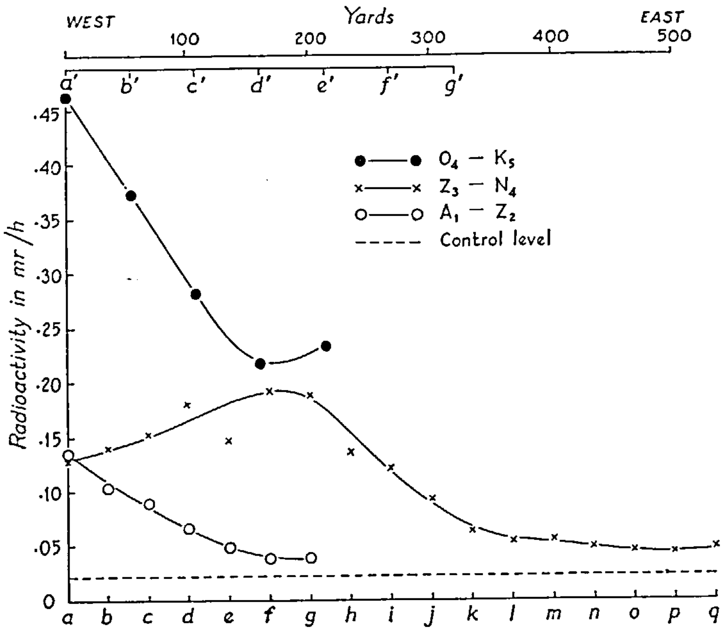

FIGURE 5
West–east radioactivity gradients from three different regions of the strip, O_4–K_5, Z_3–N_4 and A_1–Z_2. Each point represents the mean value of equivalent points (*a*, *b*, *c*, . . . from west to east) for the three regions; the *a'* . . . *g'* scale at the top refers to the O_4–K_5 region.

fall from over five times the control value to only a little above it. A similar type of curve (though on a much higher level) is found in the region O_4–K_5, in which lie three of the four mineral factories on the strip. The region Z_3–N_4 (near Ponmana), where the strip is up to 800 yards wide, shows first a slight and somewhat irregular increase, which is followed by a decline down to about twice the control value. Thus in this wide region segment *g*–*m* shows the same profile as the entire strip in the narrower regions.

The second major gradient (figure 6) is in the north–south direction. There is a gradual increase of radioactivity from the Kayankulam Bar towards a plateau in the Ponmana region; south of Ponmana radioactivity increases steeply and almost linearly. There is a discontinuity in the curve at 9°N, which is the boundary region between Ponmana and Chavara (R_4–T_4). It is also the only considerable discontinuity of habitat along the whole strip; in this region of about a quarter of a mile, it consists of bare sand dunes from the sea to the backwater and is void of vegetation or huts and it is unlikely that rats cross this barrier frequently.

For the estimation of the mean dose, the strip has been divided into two areas owing to the change in spacing of the monitored points and transects, which necessitated independent computation of the radioactivity of the two areas. The division occurs at transect O_4, which happens to correspond approximately with the change in radioactivity gradient and the discontinuity of habitat. The mean values for the separate areas may therefore be useful.

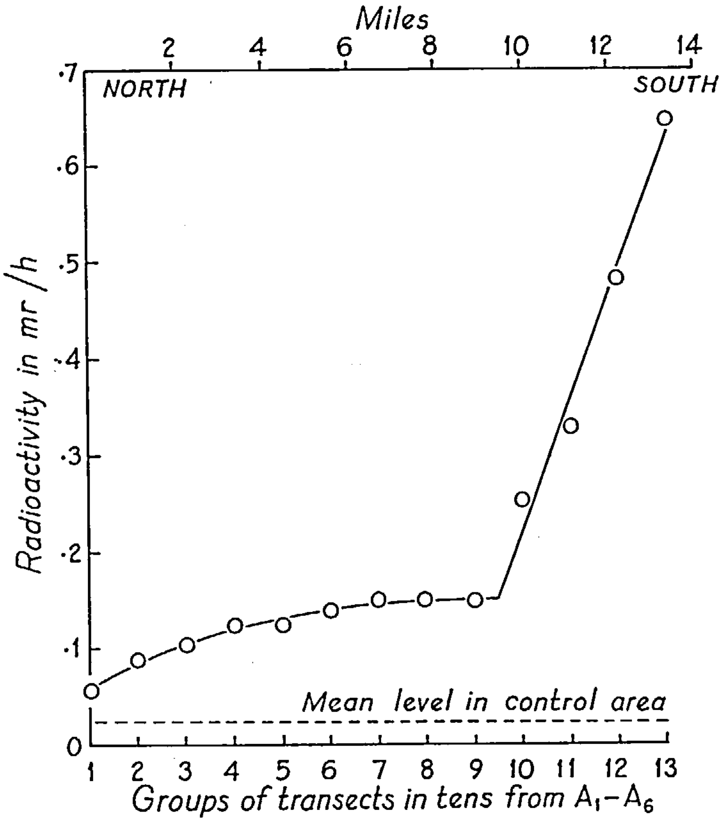

FIGURE 6
Radioactivity gradient along the strip. Each point represents the mean radiation level of a group of 10 transects (=approx. 1 mile) for the coastal area of the strip (approx. 100 yards wide).

In order to estimate the overall mean for the whole strip, the frequency of observations in area 2 (O_4–A_6) has been weighted to correspond to the frequency in area 1 (A_1–N_4), as set out in table 22. If the intervals between transects and points in area 2 were the same as in area 1, the number of observations in area 2 would be

$$\frac{213\times 160\times 52}{170\times 33}=316.$$

The adjusted sum of observations for area 2 is thus 316×0·3273 mr/h=103·43 mr/h, and the overall mean for areas 1+2 is

$$\frac{103{\cdot}43+80{\cdot}56}{316+690}=0{\cdot}1830 \text{ mr/h or } 1602 \text{ mr/y}.$$

This value is in need of some further adjustment, as several points on the grid were not monitored owing to barriers that prevented easy access, such as small

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TABLE 22 Radioactivity

Area	Intervals between rows	Interva betwe point
1	170 yd	33 y
2	160 yd	52 y

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Discussion

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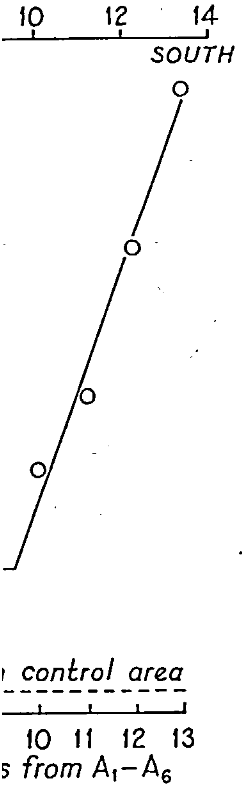

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TABLE 22 Radioactivity in two areas of the strip

Area	Intervals between rows	Intervals between points	Sum of observations	No. of points	Mean level of radiation
1	170 yd	33 yd	80·56 mr/h	690	0·1168 mr/h
2	160 yd	52 yd	69·71 mr/h	213	0·3273 mr/h

creeks of the backwater, paddy fields and coir pools. The levels at these points may reasonably be interpolated from neighbouring values; if these interpolated values are taken into account, the final estimate of the mean radioactivity level for the entire strip is

0·1797 mr/h or 1574 mr/y.

Radiation measurements for the control areas were also made in April 1962. They were generally taken in front of shops along the main road, except in Chandanathoppu (a cashew nut factory area). The overall mean for the control areas is

0·0238 mr/h or 208 mr/y.

The ratio strip/control is thus 1574/208=7·56. For area 1 of the strip separately the ratio would be 4·91, and for area 2 it would be 13·70.

Surveys carried out in 1956 and in 1962 to measure, over certain areas, the combined doses of beta and gamma radiation, simultaneously with surveys of the gamma contribution alone, show that the beta contribution represents approximately 16 per cent of the total radiation at ground level (Bharatwal and Vaze, 1958; Rao, 1962). The biological effect of this beta radiation may not be negligible because two decay products of thorium (mesothorium 2 and thorium C) are high-energy beta emitters (World Health Organization, 1959).

Discussion

We can state with confidence that the radiation exposure dose on the strip is 7–8 times greater than the control value, but there is some doubt as to the accuracy of the absolute values.

Surveys on the monazite sands were carried out in July 1956 (Gopal-Ayengar, 1957), May 1957 (Bharatwal and Vaze, 1958), and in April 1962 (Rao, 1962). The 1956 survey included two areas on the strip, one at Pandura and the other at Neendakara. An area in Sakthikulangara, just south of the Neendakara bridge, was also monitored during this survey. According to Bharatwal and Vaze (1958) measurements were made using a milliroentgen meter with a Geiger–Müller probe, calibrated for dose rate in millirads per year using a ^{60}Co source. However, Gopal-Ayengar (1957), referring to the same measurements, states that a thin-walled ionization chamber was used for calibration. His tables for the three areas mentioned give the gamma radiation three feet above ground level, recorded in counts per second with a calibration of 100 counts (per second?), as equivalent to 2·86 r/y. No record of radiation outside the monazite area is given. Vaze (1961) gives the same tables, but with a modified calibration of 1 gamma count=73·7 mrad/y, and he also gives a value of 1 count/s for background radiation outside the monazite area.

In the 1962 survey, observations were recorded directly in milliroentgens from G.M. survey meters calibrated against radium. Where the areas monitored overlap (Pandura, Neendakara and the region outside the monazite area), the 1962 survey gave values 2–3 times higher than the 1956 survey as calibrated by Vaze's constant. Such a difference is unlikely to be due to changes in the quantity of radioactive deposits, especially as the control areas show a similar discrepancy. Thus there is difficulty in ascertaining the absolute radiation level, probably owing to the use of different monitoring instruments and different systems of calibration.

The calibration with radium used in the 1962 survey is probably the most accurate, though this means that the radioactivity in the control areas is more than twice that of the average world background level (given as 70 mrad/y, excluding highly radioactive areas—United Nations, 1958). On the other hand, Vaze's (1961) figure of 73·7 mrad/y for background radiation outside the monazite area corresponds closely with the world figure of the United Nations report, and his calibrations may be preferred.

Whereas the absolute radiation level, both on the strip and in the contro areas, must thus remain uncertain, there is no doubt that the mean radiation exposure dose is about 7·5 times higher on the strip than in the control areas, and that this situation has probably been maintained for a very long time.

APPENDIX II

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APPENDIX II

Historical geography of the strip

The validity of the conclusions drawn from this investigation rests on the assumption that the strip has been occupied and isolated from the mainland long enough for the rat population to have approached or reached genetic equilibrium, and in any case long enough for the accumulation of an appreciable dose of radiation. As the rat lives in or near human habitations, it may safely be assumed that the historical geography of the strip will give evidence on the question of occupation that applies equally to man and to the rat. In view of its basic importance, a considerable body of information from many sources has been brought together (by R.A.W.). It is far too extensive to be published in full, and we have to confine ourselves to presenting enough evidence to prove the main points.

The Malabar coast has been a place of trade since ancient times. Phoenicians, Jews and Arabs were trading with Kerala before the Greeks and Romans, and the ancestors of the 'Black Jews' of Malabar probably settled there in Solomon's era. The Elder Pliny (who wrote about A.D.75) and, about ten years later, the anonymous author of *Periplus Maris Rubri* (probably a Greek merchant living in Egypt who had travelled to India himself; McCrindle, 1879) refer to the pepper trade with the Malabar coast, the south-west monsoon (called *hippalos* after the Greek pilot who first observed it) and the backwater system, which made safe navigation along the coast possible even during the monsoon season. Unfortunately, the identification of some of the places mentioned in these accounts presents difficulties, and it must remain conjectural to what extent they refer to the particular part of the coastline with which we are here concerned.

During the next 1300 years Quilon (in Malayalam *Kollam*, from *kulam*, a tank) was the chief city and port of the Malabar coast, not only doing considerable trade in goods produced locally and from Ceylon and the east coast of India, but also serving as a centre of trade between the Arabs and the Chinese. In the early centuries of the Christian era Quilon was known to the Arabs as *Mali*, and to the Chinese as *Mahlai*—probably from the indigenous word *malai*, meaning 'mountain' (from the Sanskrit *malaya*), which was specifically applied to the southern end of the Western Ghats. The Arabs did not know the meaning of the word but they called the place, or island as they imagined it, *Mali or Kulam-Mali.* Later the Persian suffix *-bar* was added, so the Arabs were the first to use the name Malabar—Land of Mali—afterwards adopted by the Portuguese and then by the British (Nainar, 1942).

The accounts of Arab and Chinese writers are not informative on the geography of the region until the 14th century. In 1343, the great Moroccan traveller, Abū Abdullah Muḥammad, commonly known as Ibn Baṭṭūta, journeyed by backwater down the Malabar coast. He was at that time in the service of the Sultan of Delhi (Muḥammad bin Tughluq), who had sent him as his ambassador to China when his *kakam* (small junk), after other ships had been wrecked in a storm, left Calecut without him:

> 'I was told that the kakam must call and anchor at the port of Kawlam [Quilon]. Hence I resolved to travel up to Kawlam—a distance of ten days journey from Calecut whether one travels by land or by river. I travelled by river and hired a Muslim porter to carry my carpet.
>
> 'When Indians travel by this river they disembark in the evening and pass the night in the villages lying along the bank; then they return to the ship on he morrow. We used to do the same. On the ship there was no Muslim except the one I had hired. He used to drink with the infidels after we had landed and used to quarrel with me and this augmented my unhappiness. On the fifth day of our journey we came to Kanjarkara [probably Vanji, i.e. Tiruvanjikulam, or Cranganore]. It lies high on a hill and is inhabited by the Jews who have their own chief and pay taxes to the Sultan of Quilon.
>
> 'All the trees which are to be found along by this river are Canella or Brazil-wood [*Caesalpina* spp.] trees, which are used as fuel. We used to light fires of that wood to cook our meals in the course of that journey.
>
> On the tenth day we came to the city of Kawlam. It is one of the most beautiful places in the country of Malabar with magnificent bazaars ... Of the whole country of Malabar this city of Kawlam lies nearest to China, and to it travel the Chinese for the most part. Here Muslims are respected.'
>
> *From Hussain* (1953) *and Lee* (1829)

Ibn Baṭṭūta later remarks that Quilon was the greatest port he knew, save for Zaiton (Ts'üen-chow), and Marco Polo (who visited Quilon in 1294) thought likewise. In the account quoted above, we have definite evidence of the backwater system between Calecut and Quilon with 'villages lying along the bank'. The last stretch of his journey must have been past the strip, for there is no possible water-way further inland connecting the Ashtamudi Lake to the backwaters further north.

Ibn Baṭṭūta does not mention Kayankulam or any of the outlets to the sea. This may be due to the admitted and necessary abridgment of Ibn Baṭṭūta's account by his 'ghost-writer' and editor, Ibn Juzayy, who was appointed to the task by Sultan Abū 'Inan Marini of Morocco in 1354 (Hussain, 1953). Only two years before Ibn Baṭṭūta's visit to Malabar (i.e. in 1341) a severe flood had caused a breach in the sand spit enclosing the Periyar lagoon, where the Cochin outlet now lies (Achyuta Menon, 1911; Yule, 1913–16). This breach became permanent, creating Vaipeen Island between it and the older outlet at Cranganore. The new bar gradually scoured itself to become the major outlet of the lagoon while that at Cranganore began to silt up, so that many merchants of that ancient city—Muslims, Jews and Hindus—settled at the new outlet, founding Cochin and Ernakulam. Cochin is first mentioned in 1409 by Ma-Huan (Phillips, 1896) and at about the same time by Nicolo Conti, who travelled there from Quilon (Major, 1858). Evidently the position of bars and spits cannot be regarded as permanent throughout historical times. In 1875 there was another breach in the island of Vaipeen, three miles north of Cochin at Cruz Milagre (Achyuta Menon, 1911). Similar changes in the continuity of the coast may have occurred at other sites, and evidence will be presented below

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that the Neendakara–Kayankulam strip itself was once divided into two parts by a bar at Cheriazhiekal.

Neither Ibn Baṭṭūta nor any previous Arab travellers mention coconut plantations along the Malabar coast. Ibn Baṭṭūta gives a detailed and accurate description of the life-history and exploitation of the coconut in the Maldives, but in the account of his travels along the backwaters he says that all the trees were canella. However, both Friar Jordanus and Friar Oderic, who visited Quilon about ten years before Ibn Baṭṭūta, describe the coconut palm, and Friar Jordanus (Yule, 1863) mentions the use of coir: 'From the rind of that fruit is made the twine with which they stitch their boats together in those parts'—as they do still today. So it is possible that the coconut, though grown there, was not yet the dominant vegetation along the coast in the 14th century. Malabar folklore suggests that the coconut was introduced in 'recent' times from Ceylon by the Izhava caste. Coconut cultivation and toddy drawing are still the hereditary occupations of the Izhavas, who are traditionally believed to have come from Ceylon (Achyuta Menon, 1911; Nagam Aiya, 1906), and some authorities have suggested a similar origin for the fisherman castes, the Mukkuvans and Marakkans (Achyuta Menon, 1911). A majority of the people living on the strip today belong to one of these castes, or are descended from them; so it is possible that these people, with their thatched palm huts and coconut trees, which form the habitat of the rats, have settled there only during the Christian era, perhaps during the last thousand years. The Mukkuvans are first referred to by the Portuguese at the beginning of the 16th century.

The breaking of the Arab–Mediterranean monopoly of the spice trade following Vasco da Gama's famous journey in 1498 to Malabar via the Cape of Good Hope led, among other things, to a more detailed documentation of the Malabar coast. The strength of the Arabs in Calecut forced the Portuguese to establish their stations further south, in Cochin, Quilon and Kayankulam. On his second journey, in 1502, Vasco visited Quilon at the request of its queen, who did not wish all the trade to go through Cochin. Gaspar Corrêa, Vasco's chronicler, writes:

> 'She had in her kingdom pepper enough to fill twenty ships each year . . . for the greater quantity of pepper which went to Cochym, the merchants bought it in this kingdom of Coulão [Quilon], and carried it in boats to Cochym by rivers which flow inside the country.'

And, after the agreement was signed,

> 'There went on board with them the Queen's minister, who took the ships to a river called Calle Coulão [Kayankulam] which was five leagues from the Port.'
>
> *From Stanley* (1869)

The first passage quoted shows that the backwater was in use at that time, and the second that the Kayankulam bar was open. So the strip was fully isolated from the mainland.

Two travellers not long afterwards visited the region; in 1505 Ludovico di Varthema travelled from Calecut by river—'the most beautiful river I have ever seen'—and arrived at 'Cacolon' (Kayankulam). After leaving Kayankulam he came to 'Colon' (Quilon), a distance of twenty leagues (Badger, 1863). Nine years later Duarte Barbosa travelled by the same route:

> '. . . Having passed this place [Porca] the kingdom of Coulam commences, and the first town is called Cayncolam in which dwell many gentiles [Hindus], Moors,

> and Indian Christians of the doctrine of St Thomas. There is much pepper in this place of which there is much exportation . . . Further along the same course towards the south is a great city and good seaport which is named Coulam . . .'
>
> *From Stanley* (1865)

The most accurate account of Malabar of that time is contained in the *Suma Oriental* of Tomé Pires, written in Malacca between 1512 and 1515. Pires describes many of the castes, including the Mukkuvan and Izhava castes:

> 'The whole country is thickly populated . . . In one part of this land of Malabar there are large rivers, deep in some places and shallow in others, which make it strong, and where they fish, where they can go in "tones", to wit, from Panane [Ponnani] to Coulam [Quilon]. The other part of Malabar is dry and easy to travel over by land, but in this part [you have to go] in "tones catures".
>
> There are countless palm trees and arecas along the coast of Malabar; but they do not extend for more than a league and a half inland, or two leagues at the most'.

Pires also lists Caya-Coulam and Coulam amongst the 'inhabited seaports where there are ships' and briefly describes their respective kingdoms (Cortesão, 1944).

The Portuguese accounts show that in the early 16th century the Malabar coast was much as it is today. The Neendakara–Kayankulam strip had its present boundaries, though it may not itself have been a continuous spit at that time. However, there is not as yet any direct information concerning places on the strip.

These begin to be mentioned with the establishment of European settlements, notably in some Dutch sources of the 17th century (e.g. Captain John Nieuhoff; see Churchill and Churchill, 1704). Prominent among those mentioned early is Kovilthottam (in Tamil meaning 'church' or 'temple garden'), where an elegant Portuguese church dedicated to St Andrew is still in existence; it can be traced back to 1581. The village of Neendakara certainly existed in the early 18th century, and presumably very much earlier. Owing to limitations of space, no detailed discussion can be given here of the history of these places.

It was mentioned above that the strip may not always have been a single entity from Neendakara to Kayankulam. The reason for this surmise is mainly linguistic. It will be seen by reference to figure 1 that there are two places on the strip where rat populations were collected: Azhiekal, near the Kayankulam bar, and Cheriazhiekal some miles further south. *Azhiekal* means in Malayalam 'by the outlet', and *cheria* means 'small'. Hence it may be suspected that a small outlet at one time existed in or near Cheriazhiekal, a supposition also supported by some other evidence. If so, a population of rats on the northern, less radioactive, section may have merged with the rats of the southern section in comparatively recent times. But the total population has been isolated from the mainland for many centuries, probably since it was first established.

APPENDIX III

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APPENDIX III

Notes on the localities in which rats were trapped

Unless otherwise stated, the rats from the villages of the strip (1–8) were caught in the houses of fishermen.

1. *Neendakara* This population was trapped mainly in the huts around and to the south of the area of the Indo-Norwegian Project, about a mile to the north of Neendakara bridge. Few rats were caught actually in the Norwegian village area, which is not very densely populated. The trapping area extended over about half a mile on both sides of the main road and took in some shops (which were not very productive of animals).
2. *Puthenthura* Rats were trapped in the neighbourhood of the southernmost, and most active, of the sand factories (Travancore Minerals Factory 2). About two-thirds of the animals were caught in the shops around the entrance to the factory in traps distributed by the storeman of the factory. The rest were collected mainly from shops, and also from houses along the main road to the south of the factory. Puthenthura is not a village in its own right but is a part of the village of Neendakara.
3. *Kovilthottam* The only bridge across the backwaters north of Chavara (a decrepit iron footbridge) is at Kovilthottam; in this region the backwater canal is at its narrowest (about 20 yards), and immediately opposite the end of the footbridge is a large Roman Catholic church. This village is isolated fairly completely both to the north and to the south by sand factories. Most of the inhabited area (about $\frac{1}{2}$ mile) was covered by our trapping.
4. *Ponmana* Separated from Kovilthottam by a sand factory is the village of Ponmana. The density of the rat population was low, and trapping was carried out over a large area (about $\frac{3}{4}$ mile along the strip). To the north of Ponmana is the small village of Vellathuruthu followed by the larger village of Pandarathuruthu, neither of which was sampled.
5. *Cheriazhiekal* This is a large, densely populated village, in which trapping was easy. It was undertaken between the northern limit of the village and its centre.
6. *Allapad* The Allapad rat population is virtually continuous with the Cheriazhiekal one. The two villages are separated by only about 100 yards of cultivated ground, and trapping was carried out from the southern boundary of the village for about $\frac{1}{2}$ mile in the northerly direction. The next village (Kuzhithura) was not sampled.
7. *Shraikadu* This is a rather odd village with a fairly low density of houses

have a correspondingly low density in relation to the houses and some difficulty was experienced in catching 50 rats here. Trapping extended over about a mile and many small channels separating parts of the village. The rats seemed to of the strip. Between Shraikadu and Azhiekal there is about ½ mile of sand with little vegetation.

8. *Azhiekal* There are fewer small canals here than at Shraikadu, and the density of rats was higher. The huts are fairly close together. Trapping was carried out for about ½ mile to the south of the main ferry crossing at Ayiramthengu ('A Thousand Coconut Trees'). The backwater is 200–300 yards wide here, and soon opens into Kayankulam lake, with the outlet to the sea completing the 'island' of the strip. To the north of Azhiekal the strip is narrow and thinly populated and entirely devoid of vegetation for about 500 yards.

9. *Kilikollur* Most rats came from roadside shops scattered over about 1–2 miles east of Quilon, and about 14 came from a cashew nut factory.

10. *Karikode* Most of the rats came from shops to the east of the railway crossing near Kilikollur station and a few came from a copra factory.

11. *Chandanathoppu* This was a unique population in that 40–45 rats came from a large cashew nut factory to the east of the village. The factory was not actually working at the time of trapping (in the period between the processing of local nuts and the importation of East African nuts). Some difficulty was experienced in catching animals from the shops in this rather small village.

12. *Kundara West* All except about 6 rats (which came from a soap factory) were caught in roadside shops, 15–20 animals coming from shops in a small market area.

13. *Kundara East* About 3 rats came from a cashew nut factory and 7 or 8 more from a soap factory; the rest were from roadside shops over a distance of about ½ mile from the Trivandrum junction of the road to Kallada.

[*Kananalur* In this Muslim village half way along the 'opposite' side of the triangle only seven rats were caught. It was then discovered that the shopkeepers were killing and throwing away the rats they caught because we were not paying tail money; hence trapping was discontinued.]

14. *Kottiyam* This village lies mainly on the Quilon–Trivandrum road. About 10 rats came from two cashew nut factories on the edges of the village; all the other animals were caught (fairly easily) in roadside shops.

15. *Oomainalur* Under ten rats from this village came from a cashew nut factory. Otherwise it was found difficult to catch animals. Trapping extended over almost two miles along the road towards Quilon, and about 10 animals were caught in houses set back from the road.

16. *Pallimukku* This population centres on a road junction to Eravipuram, where there is a footbridge over the canal and a certain amount of black sand on the coast. All the rats came from roadside shops around a road junction and market place.

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ew nut factory and 7 or 8
de shops over a distance of
oad to Kallada.
the 'opposite' side of the
ɪvered that the shopkeepers
ıght because we were not
l.]
ı–Trivandrum road. About
:dges of the village; all the
shops.
came from a cashew nut
ıimals. Trapping extended
lon, and about 10 animals

l junction to Eravipuram,
tain amount of black sand
ɔs around a road junction

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