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INVESTIGATION OF THE CYTOGENETICS OF MARINE AND TERRESTRIAL GASTROPODS

by

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ABSTRACT

Investigation of the cytogenetics of marine and terrestrial gastropods.

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The investigation of the chromosomal variation in populations of the land snail Cepaea nemoralis (L.) and the marine snail Nucella lapillus (L.) is presented.

The first study (Part 1) concerns the investigation of the karyotype of C. nemoralis in populations from a region of the Berkshire Downs (U.K.)in which there are marked area effects for both the visible and allozymic characters.

The present investigation has shown that there are inter-populational differences in chromosome structure. The differences fall within the range found previously in several widespread populations in the British Isles, Northern Europe and America.

There are no immediately obvious variations in chromosome structure associated with observable environmental variables. There are, however, marked non-random associations of karyomorphs within some of the "area effect populations".

The implications of the distribution of the karyotypic variations between the populations are discussed.

The second study (Part 11) concerns the identification of the chromosome pairs involved in the numerical (Robertsonian) and structural (inversion) polymorphisms of Nucella lapillus and the investigation of the two types of polymorphism in populations of low chromosome number.

A new classification of the karyotype into five main groups A to E has been made. The chromosome pairs thought to contribute to the numerical polymorphism occur in groups A, B and C and the two inversion polymorphisms occur in groups A and C.

The distribution of the two types of chromosomal polymorphism at Rottingdean, Sussex (U.K.) suggest that the inversion polymorphism from group C, and the numerical polymorphism, also from group C, occur independently of each other.

The differences in the distribution of the two polymorphisms in the Rottingdean area and the differences in the distribution of the chromosome pairs involved in the numerical polymorphism in different populations are discussed.

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INTRODUCTION

Many snail species show a high degree of variation in their shell shape and colour and accordingly have been subject to extensive investigations as to the possible agent or agents responsible for inter colony variations in morph frequency (for reviews see Clarke *et al.* 1978, Jones *et al.* 1977). In spite of the many ecological investigations of the two snail species in this particular study; *Cepaea nemoralis* (L.) and *Nucella lapillus* (L.) few have concerned chromosomal variation.

The role of chromosome change in the evolution of genetic variation in natural populations has long been subject to debate (White 1968, Key 1968, Bush 1981). It has been suggested, for example, that because of the lack of association of chromosomal variation with readily observable variations in morphology, chromosomes are adaptively neutral. (Ohno 1974, Dobzhansky 1961). Although this may be true for some arrangements (Thoday 1975), the widespread distribution and maintenance of both fixed and polymorphic chromosomal differences suggests they are adaptive in some way (John 1981). It is generally believed that populations may show some degree of co-adaption and interaction of genes within the genotype (Dobzhansky *et al.* 1948) and this may confound any underlying association between chromosomal variation and morphology.

Changes within the genotype can occur by gene mutation, numerical variation in chromosome number or structural rearrangements of the chromosomes. The latter includes inversions, translocations interchanges and meiotic crossing over (John 1976). Such rearrangements can alter the spatial relationships of the genes and thus change epistatic interactions between them.

Recent advances in cytogenetic techniques have demonstrated that many animal and several plant species show both intra- and inter-specific variation in chromosome number and structure. There has, however, been a marked lack of research in the field of molluscan cytogenetics. This must in part be attributed to difficulties in preparation techniques and the nature of the chromosomes themselves

which are often small and usually numerous. Consequently research emphasis has usually been on chromosome number rather than detailed chromosome morphology. (For reviews see Patterson 1968, Patterson and Burch 1978). The recent rapid progress in cytological techniques in invertebrate cytogenetics has facilitated several molluscan studies. Information on chromosome size and centromere position have been given for marine bivalves (Thiriot Quivreaux et al. 1982, Moynihan et al. 1979, Raghunathan 1976, Goldman et al. 1980). In a few studies differential staining techniques on pretreated chromosomes to give C and G bands have been used success fully to identify specific chromosome pairs (Brabrakzai et al. 1975, Rodriquez Romero et al. 1979) but for the most part, banding techniques have failed to provide consistent results. (eg. Page 1980).

There are several consequences of chromosomal variation within a species:-

In the majority of cytogenetic investigations the chromosomal rearrangements show little or no association with changes in the visible phenotype. For example in the grass hopper Podisma pedestris (Hewitt 1975, Barton 1980), the rodent Ellobius talipinus (Pall.) (Lyapunova 1980) and the common shrew (Sorex araneus (L.) (Ford and Hamerton 1970, Frykman et al. 1983), there is no obvious morphological or allozymic variation associated with the different chromosomal types, nor is their distribution correlated with particular environmental variables.

In other studies however, there are indications of an adaptive relationship between the observed structural rearrangements and environmental variables. e.g. in Drosophila pseudoobscura there are temporal fluctuations in the frequency of specific paracentric inversions (Dobzhansky 1971) and in Peromyscus maniculatus (Wagner) in which the frequency of both pericentric inversions and the number of heterochromatic chromosome arms vary with altitude. (Dixon et al. 1980). In both these examples there are no concomitant variations in morphology. In some cases, however morphological differences are observed. For example the multivariate analysis of the shape components of the mandible and scapula in populations of Mus have

revealed clear morphometric differences between populations of different chromosome constitution (Thorpe et al.1982).

The association of chromosomal rearrangements with the phenotypic and environmental variables is rare but has been reported in the Australian gekko Phylodactylus marmaratus (Gray) in which three distinct chromosome races are morphologically distinguishable and have a degree of habitat specialization which defines their distribution (King et al. 1976).

There are no known variations in chromosome number between populations of Cepaea nemoralis. Recently, however, Page (1978, 1980) has established widespread interpopulation differences in chromosome structure likely to be due to pericentric inversions in several chromosome pairs. Relationships between the chromosomal variation and the morphological or genetic variables in the population studies have not been established.

Both numerical (Robertsonian) (Staiger 1950, 1954, Hoxmark 1970, Bantock et al. 1975) and structural (Bantock and Page 1976) variations have been reported in several populations of Nucella lapillus. In some instances variation in chromosome number can be associated with the degree of exposure to wave action of the foreshore but in others chromosome number remains constant irrespective of any obvious environmental variation. There is no apparent relationship between the numerical polymorphism and variations in the shape or size of the shell. The distribution of the structural,(inversion),polymorphism, is not known nor is its relationship with the numerical variation, environmental variables, or shell morphology.

In view of the paucity of the data concerning the nature and distribution of chromosomal variations in both C. nemoralis and N. lapillus the main purposes of the present study are as follows:-

1. To examine, in detail, the karyotypes of both species.
2. Where possible, to investigate the variation in chromosome structure and number with respect to phenotypic and environmental variables.

The work has been divided into two parts, the first concerning Cepaea nemoralis and the second Nucella lapillus. A synopsis of the previous ecological and cytogenetic research relating to each species and details of the present investigations are given at the beginning of each part.

PART 1

The investigation of the chromosomal variation in populations of Cepaea nemoralis from the Western Berkshire Downs.

1. INTRODUCTION

Cepaea nemoralis and Cepaea hortensis are pulmonate molluscs belonging to a genus of which members have different geographical distributions and show varying degrees of shell polymorphism. The two species are distributed throughout Britain, Western Europe, and parts of North America (Jones et al,1977) and share a complex polymorphism involving several loci many of which are linked to form a supergene. The phenotypes and inheritance of the shell morphs are given by Cain and Sheppard (1954, 1957), Cain et al (1960) and are summarized by Cain et al (1968). The four main loci concerned are (i) The ground shell colour in order of dominance: Brown C^B, Pink C^P and Yellow C^Y. (ii) Shell banding: B^B bands present, recessive to B^O bands absent. (iii) Spread bands: S^S spread bands dominant to S^O normal bands. C, B and S are linked. (iv) A single central, mid band U^3 is dominant to U^O more than one band. This gene loci is unlinked to C, B or S.

Cepaea vindobonensis occurs in Western Russia and Cepaea sylvatica is found only in the Western Alps. Both species are far less variable than either C. nemoralis or C. hortensis; the polymorphism is restricted to variation in band number and pigmentation.

Ecogenetic studies on variation in morph frequencies, particularly in C. nemoralis, have shown that predation and climate may affect morph frequencies (for reviews see Clarke et al.1978 and Jones et al 1977) and although a few of these claim to demonstrate a relatively straight forward relationship between a particular environmental factor and the frequency of a particular morph, it seems impossible to predict morph frequencies at all accurately. (eg. Jones 1973, Cain 1968).

In some populations morph frequencies over large (larger than the panmictic unit) ecologically diverse areas are relatively constant with only slight intercolony variations. These area effects (Cain and Currey 1963a) may be separated by steep clines where morph frequency can change over short distances in apparently uniform areas.

It is probable that area effects are maintained by environmental selection on morphs either directly on the visible shell characters or on pleiotropic or closely linked characters (Cain and Currey 1963 a,b). In the absence of any obvious environmental correlates with certain morphological area effects in Cepaea, Clarke (1966, 1968) has suggested that they could be explained using a gene interaction model whereby each area is characterized by a co-adapted gene complex differentiated from an originally uniform series of populations. Epistatic interactions within each complex would, therefore, be different, so that a particular selective agent may not have the same outcome in different populations. It seems reasonable to assume that co-adaptation of the genotype should include genes other than those involved in phenotypic variation. Johnson (1976) has found several enzyme loci associated with an area effect in Cepaea nemoralis from the Berkshire Downs. In other colonies, however, no such relationship could be found (Jones et al 1980, Ochman et al 1983)

It is possible that chromosomal rearrangements, such as paracentric inversions, can preserve blocks of co-adapted loci by prevention of crossing over in the inverted region of the chromosome. (Dobzhansky 1971). It seems entirely possible, therefore, that in some instances area effects detected on the basis of morphological and allozymic variation may also be correlated with chromosomal rearrangements.

An alternative view has recently been proposed by White (1980). In this particular model of stasipatric speciation, known as 'area effect' speciation, a chromosomal rearrangement originates within an already established co-adapted area effect. The rearrangement spreads until it is concordant with the limits of the area effect where its only adaptive value is that of protection of the co-adapted population from intro gression from neighbouring populations.

In either event, the outcome will be similar in that the morphological, biochemical and chromosomal variations will show some strong degree of correlation.

The chromosome number of Cepaea nemoralis (2n=44) was reported by Perrot and Perrot (1938), confirmed by Rainer(1967)

and by Bantock (1972). In addition several studies have shown intercolony variation in chiasma frequency. (Price 1974, 1975, 1981). The cytological data described by these authors are from meiotic metaphases which are unsuitable for detailed karyotype analysis. Page (1978), however, has developed a technique for obtaining mitotic metaphases and from detailed chromosome analysis of several widespread populations has shown interpopulation differences in chromosome structure. This variation is probably due to pericentric inversions in one or more of the small chromsomes in group C. (Page 1980). In this study the large chromosomes of the complement in groups A and B were not investigated nor was any possible relationship between the chromosomal variation and either shell morphology or environmental variations.

The purposes of the present study is to investigate the karyotype of Cepaea nemoralis (including chromosome groups A, B and C) in populations exhibiting marked area effects in order to determine the extent of any chromosomal variations in relation to the visible and allozymic variation.

2. MATERIALS AND METHODS.

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  - (ii) The differences in distribution of the R values and relative lengths between populations.

2. 1. THE STUDY AREA

A marked 'area effect' for shell morphs in populations of Cepaea nemoralis from the Lambourne district of the Berkshire Downs was first reported by Cain and Curry (1963). A detailed study of the distribution of morph frequency was presented by Carter (1968) and this study was extended by Johnson (1976) by an investigation of polymorphic enzyme loci.

The region can be divided into 5 contiguous districts running for approximately 40km. east to west along the high chalk plateau of the Berkshire Downs. The delineation of the districts is to some extent arbitary as there are no physical barriers but each can be distinguished by characteristic morph frequencies. The areas are as follows:-

A. The five-banded area (Liddington district).
There is an area effect for five-banded morphs which are at very high frequencies in all habitats.

B. The western transition area (Uffington district).
There is an area effect for brown shell colour which shows no consistent variation with habitat. Five-banded morphs are at high frequencies in the west and are replaced in the east with the midbanded morph.
This area forms a transition zone between areas A and C.

C. The western midbanded area (West Lambourne district).
There is a considerable area effect for the midbanded morph in both the high plateau to the north as well as in the valleys to the south. There is also an excess of the yellow spread-banded morph.

D. The eastern midbanded area and transition zone. (East Lambourne district).
This area forms a transition zone between areas C and E. The midbanded gene increases to the west Lambourne area effect and decreases to the east where it joins area E.

E. The eastern non-midbanded area (Wantage district). In this area the open habitats have a higher proportion of yellows than the woods. The frequency of effectively banded morphs varies in both woods and open habitats but tends to be low in both types. Samples from the east show morph variation with habitat. Yellows are at high frequency throughout the entire region.

Geographic variation of six polymorphic enzyme loci (Est-f, Lap-2, Mdh-1, 6 pgd, Pgi and To-2) and four shell morph loci

show significant pairwise associations in all combinations of the midbanded, spread banded, Est-f and 6 pgd loci. At each of these loci an allele which is rare outside the midbanded area reaches a high frequency within the area indicating a direct association of the allelic frequencies with the midbanded area effect.

2. 2. THE POPULATIONS USED IN THE STUDY.

Ten populations were sampled from the Western Berkshire Downs where there is an extensive area effect for the midbanded gene. Two samples from each of the five areas A to E described by Johnson (1976) were selected as follows (see also Fig. 1)

Area A: Five-banded area

Population	A1	Grid reference:	225 795
		Altitude :	200 m.
		Habitat :	Beech wood, nettles and short grass.
Population	A2	Grid reference:	265 791
		Altitude :	230 m.
		Habitat :	Beechwood and nettles

Area B: Western transition area

Population	B^1	Grid reference:	282 813
		Altitude :	165 m.
		Habitat :	Nettles and hawthorn.
Population	B^2	Grid reference:	284 840
		Altitude :	200 m.
		Habitat :	Nettles and long grass

Area C: Western midbanded area

Population	C^1	Grid reference:	302 871
		Altitude :	150 m.
		Habitat :	Short grass and hawthorn.
Population	C^2	Grid reference:	301 845
		Altitude :	240 m.
		Habitat :	Long grass and nettles.

A second sample 50 metres from the above population was collected to compare karyotypic differences, if any, over a short distance.

Population	C^3	Grid reference:	301 845
		Altitude :	240 m.
		Habitat :	Long grass and nettles.

Area D: Eastern midbanded area and transition zone

Population D^1 Grid reference: 338 828
Altitude : 200 m.
Habitat : Beechwood forest.

Population D^2 Grid reference: 354 855
Altitude : 180 m.
Habitat : Hawthorn and nettles.

Area E: Eastern non-midbanded area

Population E^1 Grid reference: 395 852
Altitude : 150 m.
Habitat : Beechwood, brambles and nettles.

Population E^2 Grid reference: 388 875
Altitude : 110 m.
Habitat : Nettles and long grass.

The number of snails collected and allelic frequencies for each population are presented in section 3.

2. 3. SAMPLING AND CULTURE METHODS

(a) Snail collection

Adult C. nemoralis were collected from each population in the Spring of 1980. Sampling areas were within the panmitic unit, that is not greater than 40 metres linear (Lamotte 1951). The snails were put in cloth bags without food or water and transported to the laboratory as soon as possible, usually within two to three days from the time they were removed from the field.

(b) Snail maintenance

The snails were brought into the laboratory and kept in plastic boxes containing natural chalk and damp filter paper. They were fed on carrot, fresh nettles and porridge oats. At the beginning of the usual egg laying season (May to July) small plastic pots containing damp soil were placed in the boxes. The pots were inspected daily for egg clutches. Pots containing clutches were labelled and transferred to a separate box containing damp filter paper and left undisturbed until required for chromosome preparation.

2. 4. CYTOLOGICAL METHOD

Chromosome preparations were made according to the method

described in detail by Page (1980). A summary of the technique is presented below.

(i) Daily inspection of newly laid egg clutches was made to assess the stage of development of the embryos.

(ii) Removal of 10 to 20 eggs from the clutch was made when stage 3 (Fig.2) of development was reached. The eggs were then washed in molluscan saline.

(iii) Five eggs were transferred to a watch glass containing molluscan saline, each egg capsule was split open and the embryo transferred to another watch glass containing molluscan saline.

(iv) The albumin sac, rudimentary gut, shell and shell gland were removed and the remaining tissue was teased out and transferred to a watch glass. This procedure was repeated until all the embryos had been dissected.

(v) The watch glass containing the dissected embryos was filled with 0.01% aqueous colchicine (at Room Temperature) and left for 15 minutes.

(vi) The colchicine/tissue solution was transferred to a $5cm^3$ glass centrifuge tube and spun at 1000 r.p.m. for 2 minutes. The supernatant was removed.

(vii) The remaining tissue pellet was resuspended in a 3:1 methanol/glacial acetic acid fixative.

(viii) The fixative was changed three times.

(ix) The tissue/fixative solution was then left to stand at room temperature for 30 minutes, spun down and the tissue pellet resuspended in 50% acetic acid.

(x) Heat-dried slides were prepared on a hot plate ($40^{o}C$).

(xi) The slides were allowed to cool and then stored at room temperature in slide boxes.

Staining techniques

Routine (non-differentiated) staining was carried out using a 2% solution of giemsa (G.T. Gurr.) in Sorrensens phosphate buffer pH 6.8 for 2 minutes. The slides were then rinsed in buffer, dried, soaked in michrome essence and mounted in michrome.

2. 5. PHOTOGRAPHY

All slides were scanned under low power (x 16) using a Zeiss

photomicroscope with x 10 eye pieces. The location of well spread metaphase plates, with few or no overlapping chromosomes were noted and on completion of the scan each metaphase was examined under high power phase contrast (oil immersion x 100) and photographed on Ilford high contrast film HS23. Photographic prints were made on Ilfobrom photographic paper grades 2 and 5.

2. 6. ANALYTICAL METHOD

a. Introduction

In the author's previous study of Cepaea nemoralis (Page 1980) the six largest pairs of chromosomes in each karyotype were omitted from the analysis as they were easily identified and appeared to show no variation either within or between populations.

In this study, however, it was decided to analyse the twelve larger chromosomes as well as the thirty two smaller ones. This could provide useful information on possible differences in centromere position, in the larger pairs, that might not be immediately obvious from visual identification.

b. Preparation of karyotypes.

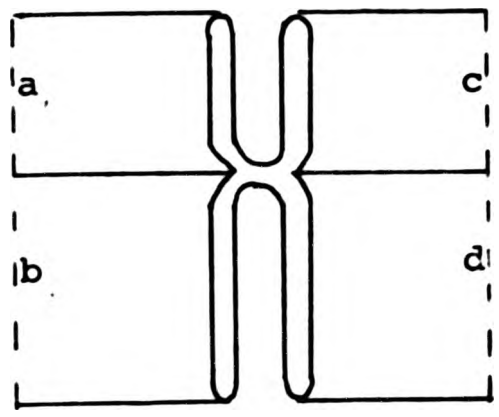
Photographic prints from well spread and clearly defined metaphases were chosen from each population. The prints were coded according to the population origin and measured at random so that karyotypes from the same population were measured on different occasions.

The twelve largest chromosomes from each print were numbered in pairs from 1 to 6 and the remaining 32 smaller chromosomes numbered from 13 to 44. The chromosomes were not cut out from the print as in previous investigations (Page 1980, 1978) but were left intact. This method has the advantages of both saving time in preparation of the karyotype and also in avoiding any unintentional judgements made as to the size and centromere position of the smaller chromosomes.

c. Chromosome measurement.

The chromatids of the long and short arms of each chromosome were measured using a Jocal digital caliper.

The absolute length of each arm was calculated as the average of the two chromatid measurements.



Length of short arm

$$= \frac{a+c}{2}$$

Length of long arm

$$= \frac{b+d}{2}$$

In cases where the chromatids were bent or twisted (usually in the larger chromosomes) sequential measurements were made along the chromatid and summed to give the total arm length.

d. Calculation of centromere position.
The location of the centromere may be calculated in several ways (e.g. Levan et al. 1964), Adhikary 1974). In the present investigation the centromere position was determined by dividing the length of the short arm by that of the long arm to give an arm ratio R. This value was used to classify the chromosomes using the nomenclature presented in Table 1.

e. Calculation of relative length.
It is usual in this type of study to use both length and centromere position to distinguish chromosome pairs. In previous studies of the 32 smaller and similar sized chromosomes of Cepaea nemoralis (Page loc. cit.), the analysis of length was considered inappropriate as it provided no additional information for use in chromosome identification. The present study, however, includes the analysis of the whole karyotype and therefore the calculation of the lengths of the twelve larger chromosomes can aid in their specific identification.
The absolute chromosome measurements are subject to variation due to differences in chromosome condensation and magnification during print production. This makes the comparison of lengths between and within karyotypes difficult. The lengths, however, can be standardized by expressing the length of individual

chromosomes as a percentage of the total length of the karyotype.

2. 7. STATISTICAL METHOD

a. Introduction

The statistical analysis of karyotype data presents two main problems. The first is concerned with the arrangement of the chromosomes within the karyotype and the second with the nature of the data for centromere position and relative length.

In the absence of banding techniques allowing the precise identification of chromosome pairs, length, centromere position and occasionally the presence of a secondary constriction, are the only criteria available for chromosome identification.

It is usual to arrange the chromosomes of each karyotype in order of decreasing size and to match pairs by similarities in size and centromere position. In some cases the karyotype is divided into groups containing pairs of similar centromere position also arranged in order of decreasing size.

Direct comparison between karyotypes are often made at this stage with no further analysis (Capanna et al. 1973 , Badr and Asker 1980, Shaw and Wilkinson 1980 and Thiriot Quievreaux et al. 1982). It is more usual however to calculate the mean length and centromere position of the chromosomes from several karyotypes (eg. Lucca 1975, Diaz de la Guardia et. al. 1979) and to present standard deviations or standard errors of these means (Winking 1976, King and Rofe 1976, Benazzi 1974). In some investigations confidence limits of the means are given (Nakamura 1982, Koref 1980) or comparisons are made using idiograms constructed from the mean values for each chromosome pair (Bogart 1970, 74 and 76, Chandravadana 1976, De Boer 1975). Reig et al. (1980) working on the chromosomes of the spiny rat (Proechimys species) used the student t-test to compare idiograms from populations with similar karyomorphs. They also made direct comparisons and pairwise tests of significance of mean values of whole chromosomes or chromosome

segments, again using the students t-test.
Direct statistical comparisons of this type, however, are rarely possible in karyotypic analysis.
The paucity of data of this kind must, in part, be due to the difficulties in in identification of truely homologous pairs of chromosomes both within and between karyotypes. Chromosomes that are obviously different from those in the rest of the karyotype present little problem as their identification is unambiguous. If, however, the chromosomes are of similar size or form a group with only small gradations in size it is by no means certain that two chromosomes classified as a pair are in fact homologous. In consequence calculations of mean length and centromere position and subsequent comparisons between them are likely to be inaccurate. This fact was noted by Borzan and Papes (1978) in their study of the black pine; Pinus nigra (Arn). Eight of the twelve chromosomes in this species are of similar size and the risk of interchanging one chromosome for another within the group is high. The high risk of this reversal also results in an unusually low co-efficient of variation compared with that of the four remaining chromosomes which are easily identified.
Chromosome reversal has also been reported by Matern and Simak (1968, 69) in Larix decidua (Mill) and by Chetty et al (1970) in Pinus roxburghii (Sarg), but for the most part has been overlooked in the majority of karyotypic studies.
In Cepaea nemoralis it was appreciated early on that the 32 smaller chromosomes (Group C) of the karyotype could not be paired accurately (Page 1978, 1980) and that the risk of 'reversal' in this group was high. Comparisons between and within populations could only be those which made no assumptions about the equivalence of particular chromosomes with each other.
Preliminary analysis of the relative lengths of the karyotypes in this study have revealed that although chromosome pairs one to six (Groups A and B) are easily distinguished by sight, pairs three, four and six are indistinguishable by length alone. Furthermore 20 per

cent of the karyotypes measured had at least one chromosome in the C group equal to or greater than the length of one of these pairs. It is possible, therefore, in these circumstances, to confuse a chromosome from groups A or B with one from Group C or visa versa. Unambiguous identification of these pairs is, therefore not possible and in view of this it was decided for the purposes of this study to include pairs three, four and six in the analysis of the thirty two group C chromosomes.

In practice this has the effect of increasing the number of both metacentric and submetacentric chromosomes within the group. These increases are common to all the karyotypes and, therefore, the relationships between different populations remain similar to those presented in the authors previous investigations.

The second problem associated with karyotypic analysis concerns the nature of the data for centromere position and relative length. These measurements are both derived variables and as such may have unusual non-normal distributions. Many statistical tests used in karyotype analysis such as standard deviations, standard error, confidence limits and t-tests require normally distributed data. It was decided, therefore to test the variables, where appropriate, for normality using the Kolmogorov-Smirnov test the details of which are given in Section 2.

In some cases it is possible to transform the variables so that they meet the assumptions for analysis (Sokal and Rohlf 1969). In the present study no suitable transformation technique could be found, accordingly it was decided to use non-parametric statistical tests in the event of non-normal distribution of the variables.

The analysis of the karyotype can be divided into two sections.

b. The analysis of the three largest chromosome pairs.

c. The analysis of the remaining 38 chromosomes.

b. (i) The normality of both relative length and R values was tested using the Kolmogorov-Smirnov test which is based on the absolute differences between observed and expected frequency distributions. These differences are expressed as differences between relative cumulative frequencies. The maximum difference; D max. can be compared with tabled critical values to test significance. In this investigation the cumulative frequency of the data on both relative length and R value were compared with that for a normal distribution.
On the basis of the results of these tests(see Results section 3) it was concluded that these particular measurements are distributed normally and therefore the usual parametric tests can be used in the analysis.

(ii) The mean ($\bar{Y}$) and standard deviation (s) were calculated for both length and R value of each chromosome pair within a population. The 95 per cent and 99 per cent confidence limits for each were calculated as follows;

95%confidence limits

$$L\ 95 = \bar{Y} \pm t0.05(n-1) \frac{S}{\sqrt{n}}$$

99% confidence limits

$$L\ 99 = \bar{Y} \pm t0.01^{(n-1)} \frac{S}{\sqrt{n}}$$

where

t = students t distribution

n = number of chromosomes measured.

(iii) The analysis of variation in length and R value for each pair within and between populations was tested using a single classification analysis of variance (Sokal and Rohlf 1968). In order to compare the variability of the standard deviations of different chromosomes which differ appreciably in their means the co-efficient of variation was used. It is defined as the standard deviation expressed as a percentage of the mean.

$$CV\% = \frac{S \times 100}{\bar{Y}}$$

This can also be used to compare the variability of the data from this study with that from other karyotypic analysis.

(iv) Variation of the length and R value between populations was tested using the Kruskal-Wallis one way analysis of variance of ranks details of which are presented in section 2 c (i).

c. The analysis of variation in length and centromere position in the remaining 38 chromosomes.

Since it is not currently possible to classify individual chromosomes within the C group only comparisons between and within populations which make no assumption about the equivalence of particular chromosomes with each other are possible. Nonparametric statistical tests are particularly suited to this kind of analysis because their null hypotheses are not concerned with specific parameters (such as the mean) but only with relative distribution of the variates.

Two different methods were used to test.

(i) The differences in distribution of the R values and relative lengths within the karyotypes from each population.

(ii) The differences in distribution of the R values and relative lengths between populations. In the former (i) The Kruskal-Wallis one way analysis of variance by ranks was used. The technique tests the null hypothesis that the samples come from the same or identical populations with respect to averages.

$$H = \frac{12}{\left(\sum^{a} n_i\right)\left(\sum^{a} n_i + 1\right)} \sum^{a} \frac{\left(\sum^{n_i} R\right)}{n_i} - 3\left(\sum^{a} n + 1\right)$$

a = groups

n_i = number of items in group i

12,3 are constants

R = rank.

The statistic H as shown above is appropriate for data without ties, but is divided by a correction factor D when ties are present.

$$D = 1 - \frac{\sum^{m} T_j}{\left(\sum^{a}_{i} n - 1\right)\sum^{a}_{i} n \left(\sum^{a}_{i} n + 1\right)}$$

Where T_j is a function of the tjs the number of variates tied in the j^{th} group of the ties.

$$T_j = t^3_j - t_j$$

In the latter (ii) the data for both relative length and R value from each population were rearranged into ten arbitary, equal and continuous classes as follows:-

Relative length: Ten classes each of 0.2 per cent within the range one to three per cent of the total diploid chromosome length.

R value: Ten classes each of 0. 10 R value units within the range 0 (telocentric) to 1 (metacentric).

The frequency distribution of the values in each class were then compared between populations using the log likelihood ratio test (G test) (Sokal and Rohlf 1968). G is distributed in the same way as χ^2 especially in cases where the sample size is large. G can therefore be compared with the critical value of with a distribution of (a-1) (b-1) where a = the number of columns and b = the number of rows. The G statistic is estimated as follows.

$$G = 2\left[\sum^{a}\sum^{b} f \ln - f_{ij} - \sum^{a}\left(\sum^{b} f_{ij} \ln\right)\left(\sum^{a}_{i} f_{ij} - \sum^{b}\right)\left(\sum^{b}_{ij} f \ln\right)\left(\sum^{b}_{ij} f_{ij} + n \ln n\right)\right]$$

$$G = 2\left[\left(\sum f \ln f \text{ for the cell frequencies}\right) - \left(\sum f \ln f \text{ for the row and column totals}\right) + r \ln r.\right]$$

The quantity fij refers to the observed frequency of row i and column j.

In the event of a significant difference between populations it is possible to subject the data to an S. T. P. (simultaneous test proceedure) analysis which tests the independence of selected subsets of data. (Sokal and Rohlf loc. cit.) If populations from the same area (see section 2.2.) are included in a non-significant subset their data can be combined and used for comparison with other combined populations. Details of R value partitioning and combination of population data within areas are given in the results section 3.

3. RESULTS

3.1. Population data.

3.2. Clutch and slide preparation data.

3.3. Chromosome measurement.

3.4. The variation in centromere position and relative length of three largest chromosome pairs.

a. Normality of the data.
b. The variation in length and R value within and between populations.

3.5. The variation in centromere position and relative length of the remaining 38 chromosomes (Group C).

a. Variation within populations.
b. Variation between populations.
   (i) Relative length.
   (ii) R value.

3. RESULTS

3.1. POPULATION DATA

The morph frequencies of the snails collected from each population are presented in Table 2. The number of snails collected from each population, although small compared with those collected by Carter (1968) and Johnson (1976) reflect a similar pattern of colour and banding morph frequency distribution. Yellow shells are at high frequency throughout the area. Samples from areas C and D (see Fig.1) have high midbanded frequencies (U^3)decreasing in the west in areas A and B. No midbanded snails were found in the most easterly area E.

3.2. CLUTCH AND SLIDE PREPARATION DATA

The details of clutch and slide preparation are given in Table 3. The amount of material wasted in the preparation for karyotype analysis is high. A single clutch may provide up to 12 slides, but, mitoses suitable for analysis are not always present. At least 50 per cent of the slides produced were discarded. The karyotype analysis for each population was based on metaphases from two or more clutches with the exception of populations A^2 and C^1 where only one clutch in each case provided suitable material.

The slide preparation technique used in this study assumes that the metaphases originate from several embryos in the clutch. There is a slight risk, however, that karyotypes from a single clutch could represent cells from a single individual. The likelihood of this occurring is considered to be low. Firstly the number of dividing cells present on all slides is usually high, far larger than would be expected from one embryo. Secondly the karyotypes from one individual would be expected to be less variable than those from several embryos. The results of the Kruskal Wallis test (Table 5) and co-efficients of variation (Table 7) show that the variation between karyotypes within all populations, regardless of their origin *ie*. from one or more clutches, is very similar. Comparisons between and within populations can therefore, be considered to be those concerned with several individuals the exact number of which is not known.

The slides produced from population E^2 did not produce metaphases suitable for chromosome analysis. The population was therefore dropped from the study.

3.3. CHROMOSOME MEASUREMENT.

The relative lengths and R values for each chromosome measured are given in appendix A.

3.4. VARIATION IN CENTROMERE POSITION AND RELATIVE LENGTH OF THE THREE LARGEST CHROMOSOME PAIRS.

a. Normality of the data

The results of the Kolmogorov-Smirnov test are given in Table 4. Only three of the sixty tests computed show a significant deviation of the variables from normality, a value that would be expected by chance alone. In view of this it was decided that, for the purposes of the present investigation, parametric statistics could be used to analyse the data (see also section 2.5.)

b. Variation in length and R value within and between populations.

The results of the Kruskal-Wallis one way analysis of variance are presented in Table 5. There are no significant differences in either length or R value for any of the chromosome pairs between the karyotypes within each area.

The mean, standard deviation, and 95 per cent and 99 per cent confidence limits are given in Table 6. The results of one way analysis of variance for length and R value for each pair in the ten populations are given in Table 6A.

It can be seen that although small differences occur between the mean R values and relative lengths both within and between populations none are significant.

The co-efficients of variation (CV%) are given in Table 7. The similarities in variation between populations for the same chromosome pair reflect the result of the analysis of variance and also suggest that the measurement technique used in the present investigation is consistent from karyotype to karyotype. The largest variation in all populations

occurs in chromosome pair three. This is probably due to the presence of a secondary constriction in the long arm. Variations in length and centromere position can be brought about by increases or decreases in the length of the secondary constriction. Preliminary analysis of this region in pair three suggests this is true for the karyotypes of Cepaea nemoralis. Secondary constrictions are generally represented as a distinct gap in the chromatid during mitosis. If, however, the chromosomes are very condensed the length of the gap is often shortened and in some cases it is not visible at all. Various techniques both physical and chemical (Sharma and Sharma 1972) can be used to exaggerate the gap by causing de-spiralization of the secondary constriction region and condensation of the chromosome arms. This indicates that the constriction region can also be sensitive to variations in preparation techniques.

Variation in the length of secondary constrictions also occurs in the human karyotype. The constrictions are present in pairs 13,14,15,16 and 21. (Paris Conference 1972). Calculation of the co-efficients of variation from the measurement data provided in this study (see Appendix A) indicate that variability within these pairs is generally larger than that in the remaining autosomes. Similar differences are seen in several, but not all, of the chromosomes having secondary constrictions in the karyotypes of Xenopus species (Tymowska 1977).

The amount of variation observed in pair three of the C. nemoralis karyotype is therefore considered to be comparable with that expected in chromosomes possessing a secondary constriction and does not represent any real difference in chromosome structure.

3.5. THE VARIATION IN CENTROMERE POSITION AND RELATIVE LENGTH OF THE REMAINING 38 CHROMOSOMES (GROUP C).

a. Variation within populations.

The results of the Kruskal-Wallis one way analysis of variance are presented in Table 5A. The analysis gives consistently non-significant results and suggests

that there are therefore no large scale differences in length or R value. There is some indication, however, that R values between some karyotypes with in populations, show quite substantial variations. These differences will be swamped in the overall statistical analysis but may represent intra population variation for the chromosomal re-arrangements in some chromosome pairs.

b. Variation between populations.

(i) Relative length. (RL)(Table 9)

No RL values were recorded in the first two of the ten classes. The overall G test was therefore computed on the eight by ten contingency table. The overall G test $G_{(63)} = 75.04$ $(0.5 > P > 0.1)$ is not significant suggesting, as expected, that there are no appreciable differences in the length of the C group chromosomes. No further statistical analysis was applied to the data.

(ii) R value.

The R values were scored in seven of the ten classes in the range of 0.31 to 1.00. The frequency distributions are given in Table 10. The overall G test was computed on a seven by ten contingency table. The overall G test $G_{(54)} = 97.816 (P < 0.005)$ is highly significant indicating that there are differences in the proportions. Prior to the S.T.P. analysis the populations were arranged in order of increasing metacentricity of the group C chromosomes. This gives some indication of the order in which the populations should be tested. The metacentricity was assessed for each population by summing the number of R values falling into the submetacentric (SM) and metacentric (M) classes for the karyotypes in each population and dividing this by the number of karyotypes measured. The average value, adjusted to the nearest whole number, for each population are presented below:

Population	Average M	Average SM
A1	26	12
A2	28	10
B1	30	8

Population	Average M	Average SM
B2	30	8
C1	29	9
C2	30	8
C3	29	9
D1	31	7
D2	29	9
E	28	10

The results of the S.T.P. analysis are shown in a diagrammatic form in Fig.3. Individual G tests for the subsets of data for all S.T.Ps. are given in Appendix A. In the S.T.P. test any pair of populations enclosed by a range of any one line are not significantly different, so that, although populations within the same area may show differences in their average metacentricity, i.e. populations D1 $_{(31M)}$ and $D2_{(29M)}$ and populations $A1_{(26M)}$ and $A2_{(28M)}$, the differences between them are not significant. On this basis the data from populations within the same area can be combined and used to compare differences in distribution of R values between areas. The frequency distributions for the combined data are given in Table 10. The result of the G test; $G_{(24)} = 55.696$ ($P < 0.005$) again shows highly significant differences between the distributions. The results of the S.T.P. analysis are given in Fig. 4. The average combined metacentricity of the populations were calculated as described previously and are given below.

Area	Average M	Average SM
A	27	11
B	30	8
C	29	9
D	29	9
E	28	10

In both S.T.P. tests the R value data falls into two non-significant subsets of data each of which represents a group of populations or areas containing similar proportions of metacentric and submetacentric chromosomes.

The first S.T.P. analysis (see Fig.3) probably gives

the most accurate representation of the differences between the populations as it assumes no a priori differences in the proportions of metacentric and submetacentric chromosomes within a population. Nor does it combine the populations on the basis of their geographical position within the visible 'area effects'.

The populations fall into three main groups:- those having a high number of metacentrics B^1 B^2 C^2 and D^1, those with an intermediate number of metacentrics D^2, C^3 and C^1, and those with a low number of metacentrics A^1, and A^2 and E. The lack of significant differences between either the high or low metacentric groups and those in the intermediate group, suggests that the intermediate populations may represent an intermediate situation between the two other groups.

The geographic distributions indicate that this may be true for populations in the east but to the west between A^1, A^2 and B^1, B^2 no such intermediate populations are found. The small sample of populations used in the present study, however, does not exclude the possibility that colonies intermediate for the number of chromosomal re-arrangements exist between the two areas.

It seems unlikely that populations of intermediate chromosomestructure represent a hybrid zone firstly, because the area covered by the populations is greater than the panmitic unit and secondly, because there is some evidence that in many populations the chromosomal rearrangements are maintained in a polymorphic state.

The second S.T.P. analysis (see Fig.4) examines the relationship between populations between areas A to E which are based on the visible 'area effects' for C. nemoralis on the Berkshire Downs. In this analysis the areas fall into two groups as follows; areas A,C,D and E and areas B,C,D and E. The only significant difference in the proportions of metacentric and submetacentric chromosomes in group C occurs between areas A and B. There are no

significant differences between the two major area effect regions A and C as might have been expected if each area was defined by a particular chromosomal arrangement. The non random arrangement of the distribution of similar populations within an area, however, suggests that regional differentiation of some kind may be present. The implications of these results are discussed in section 4.

Variations in R value between karyotypes from the same population for specific chromosome pairs can be estimated by the use of confidence limits (see Table 6). The average expected variation for 99% confidence limits is $\bar{Y} \pm 0.047$ (calculated from chromosome pairs 1 and 2 from ten populations). It is probable that intrapopulation variation found in these chromosomes is similar to that of the remaining autosomes. In view of this it is possible that, for the C group chromosomes, differences in the proportions of R values falling into contiguous classes do not reflect true differences in centromere position but represent normal variation between chromosomes of a pair. This is particularly appropriate to R values falling in the class range 0.51 to 0.60 and 0.61 to 0.70, where the expected variation of $Y \pm 0.047$ could place a chromosome in either the M or SM category. Analysis of these two classes (Table 11) $G_{(9)} = 9.294$ $(0.5 > P > 0.5)$ is not significant suggesting that there is no inter population differences in the R values in these classes. Analysis of the remaining five classes, however, (Table 12) $G_{(36)} = 71.494$ $(P < 0.005)$ is highly significant indicating that differences that occur between populations are those involving metacentric and submetacentric chromosomes differing by at least 0.20 R value units. This difference is far greater than that expected between homologous chromosomes from different karyotypes. Misplacement of chromosomes between classes must occur to some extent, but, it remains certain that large differences in the proportions of the metacentric chromosomes in classes 0.71 to 1.00 and submetacentric

classes 0.31 to 0.50 are responsible for the major differences found between the populations.

Representative karyotypes for each population are presented in Plates 1 to 10.

Fig.1.The map of the Western Berkshire Downs showing the sampling localities of C.nemoralis .The dashed lines separate the five sampling areas discussed in the text; A,The western fivebanded area;B,The western transition area;C,The western midbanded area;D,The eastern midbanded and transition zone; E,The eastern non-midbanded area.

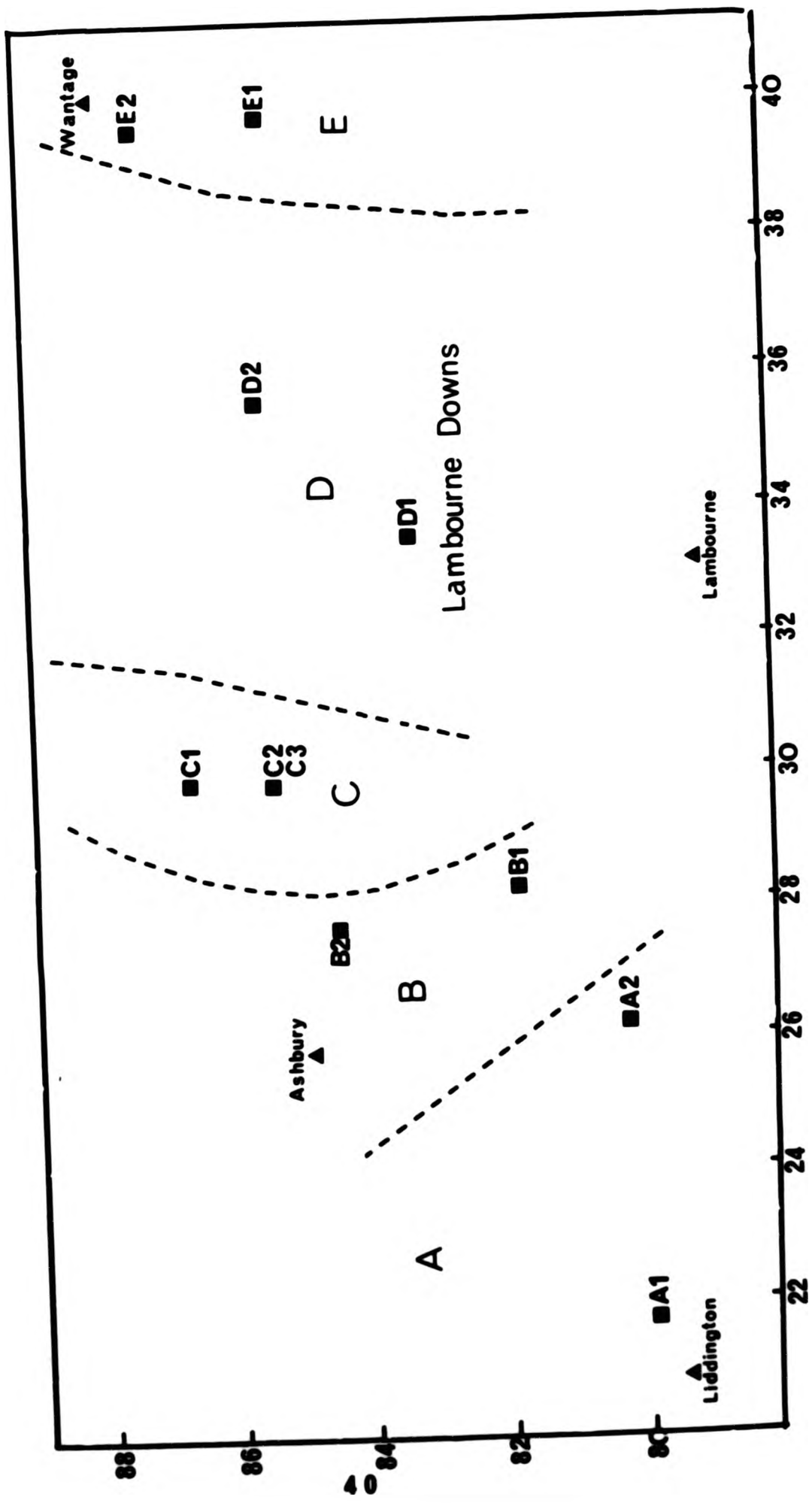
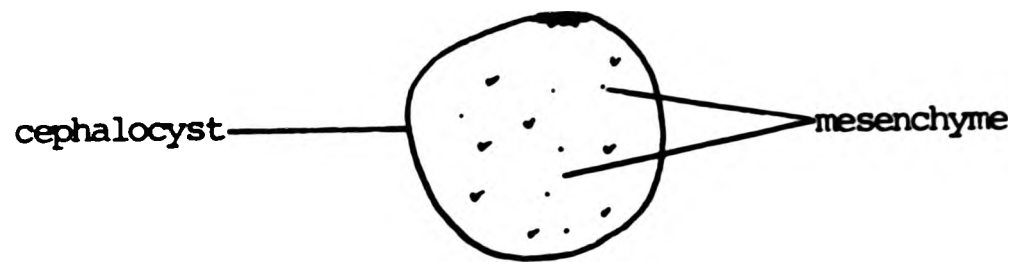


Fig.2.The stages in developement of the embryo of Cepaea nemoralis.

Stage 1



0.2mm.

Stage 2

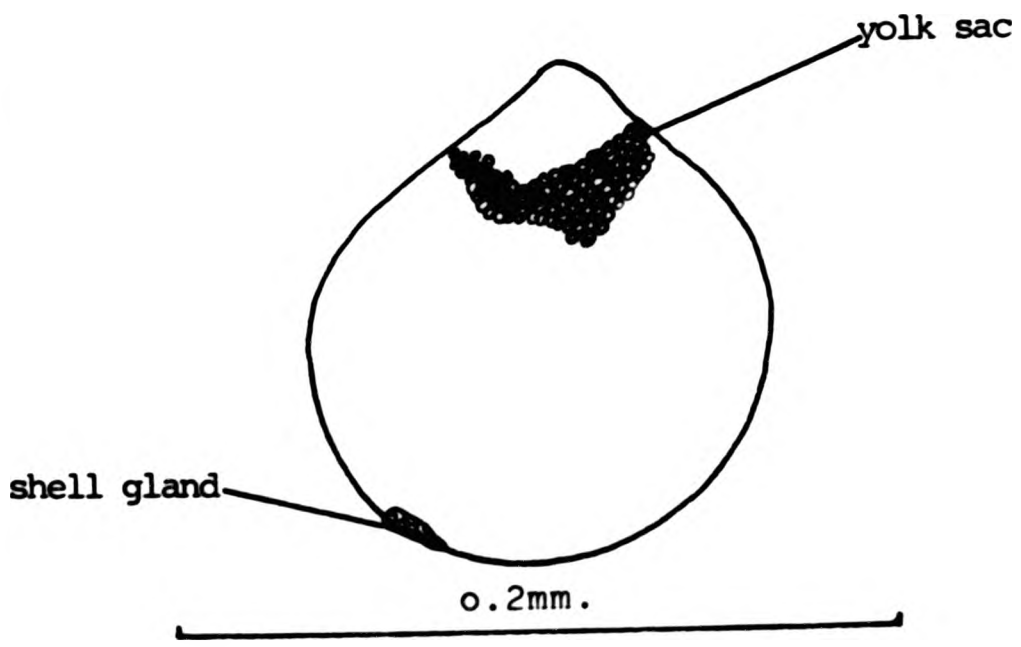
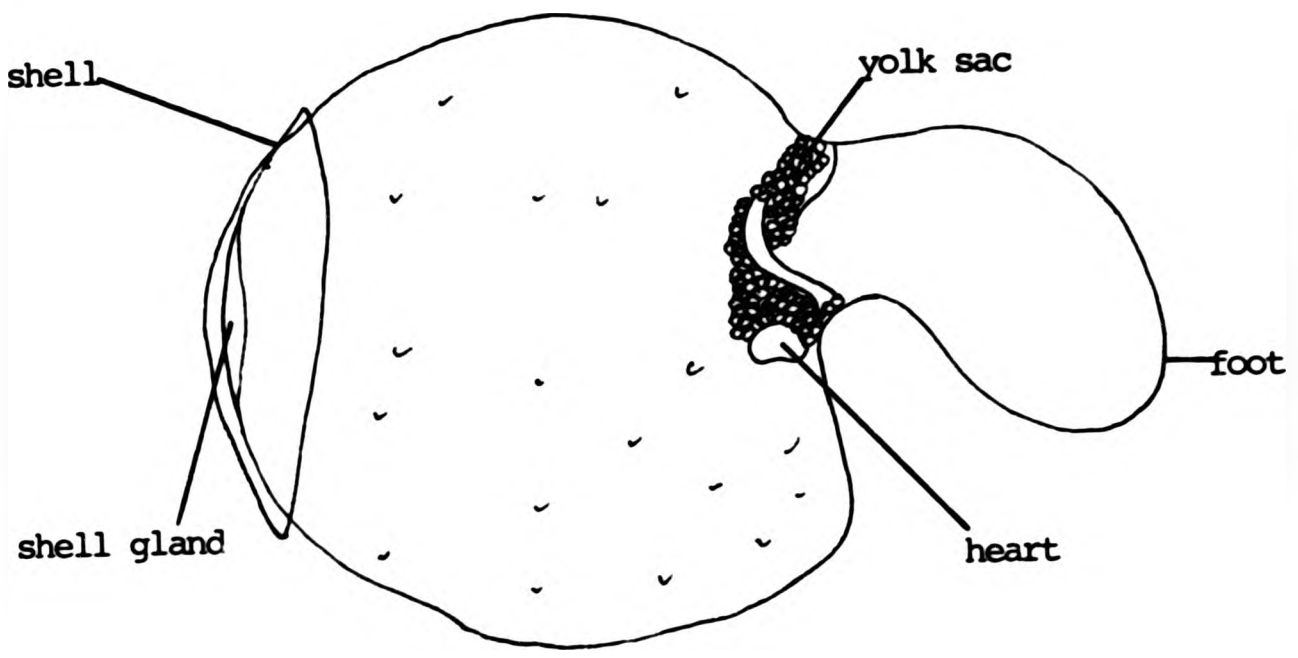


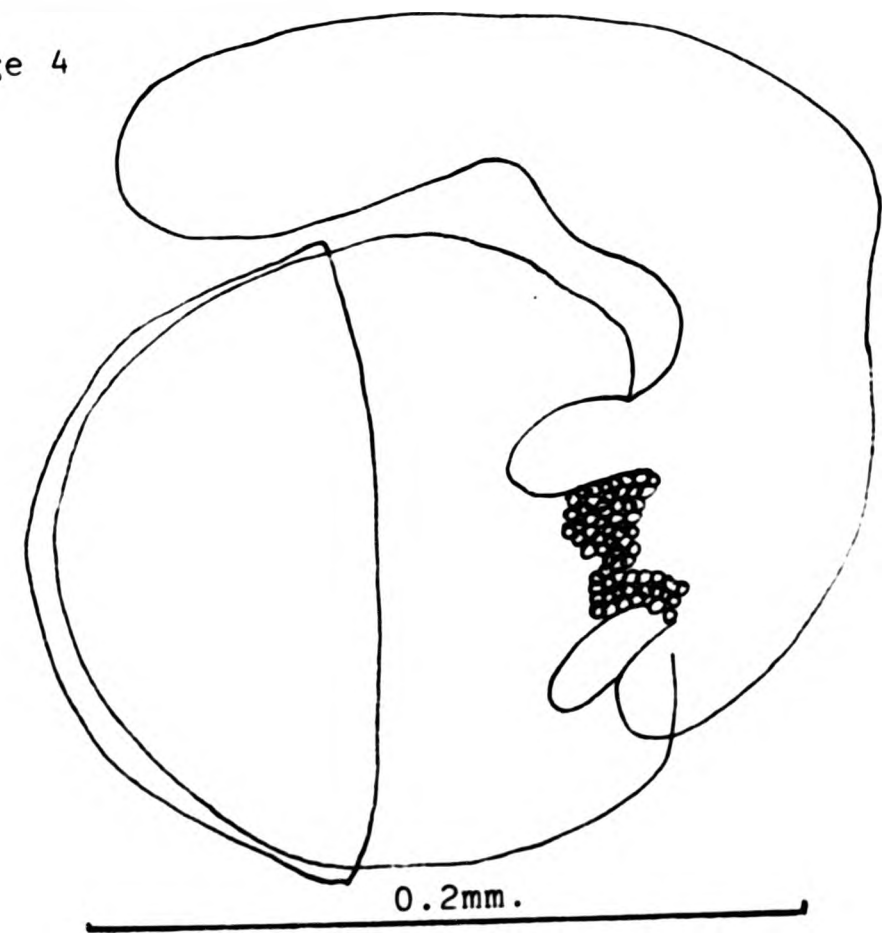
Fig.2.The stages in developement of the embryo of Cepaea nemoralis.

Stage 3



0.2mm.

Stage 4



0.2mm.

Fig 3. A diagramatic representation of the S.T.P. analysis of the R values of the group C chromosomes from populations of C.nemoralis from the western Berkshire Downs.a.The populations enclosed within one line are not significantly different.b.Populations of low mean chromosome number ▨ Populations of intermediate chromosome number ▩ Populations of high mean chromosome number ▨

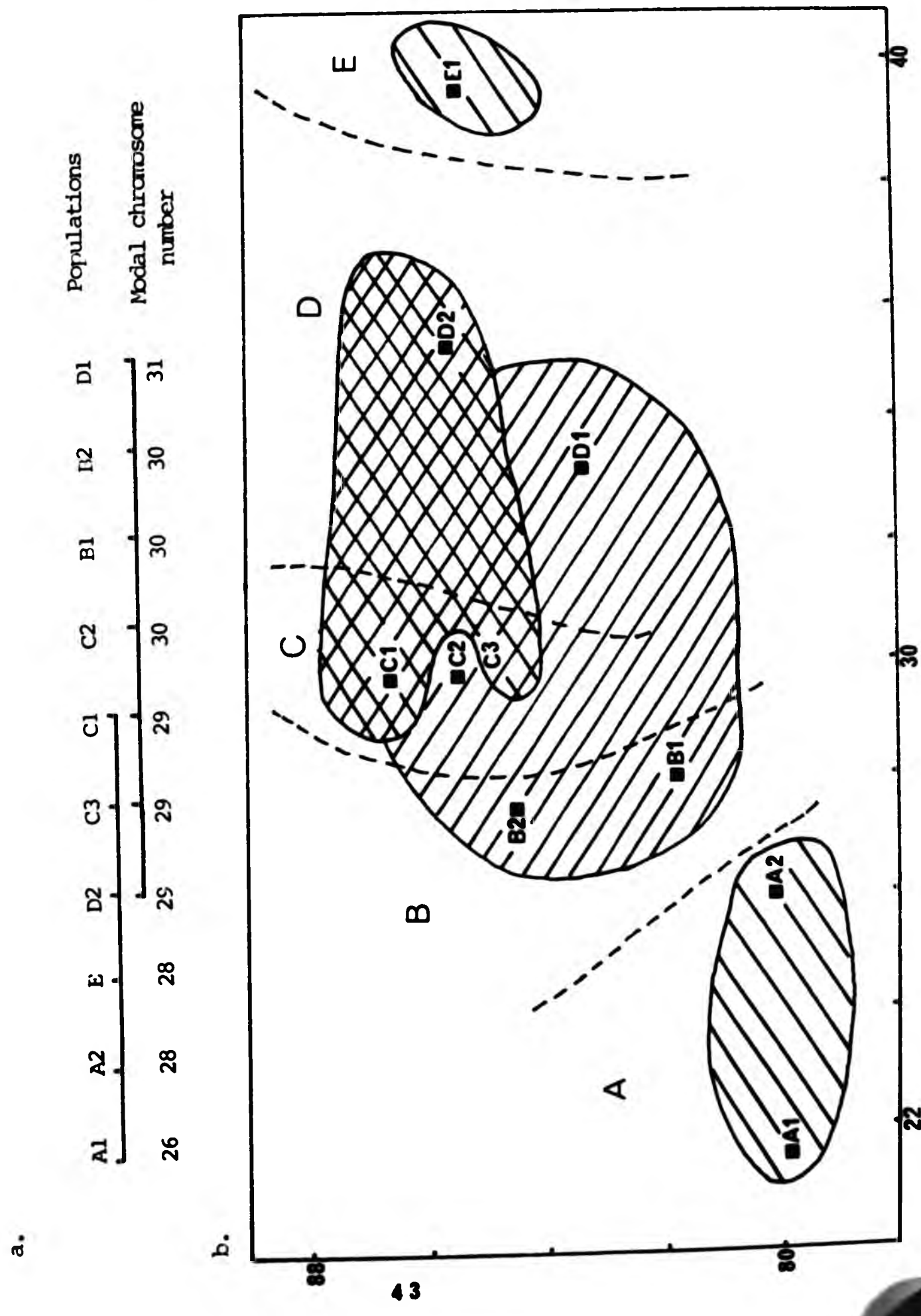


Fig. 4.A diagramatic representation of the S.T.P. analysis of the R values of the group C chromosomes of populations combined within each area from the western Berkshire Downs.a.Areas enclosed within one line are not significantly different.b.Areas of low chromosomal number Areas of intermediate modal chromosome number Areas of high modal chromosome number

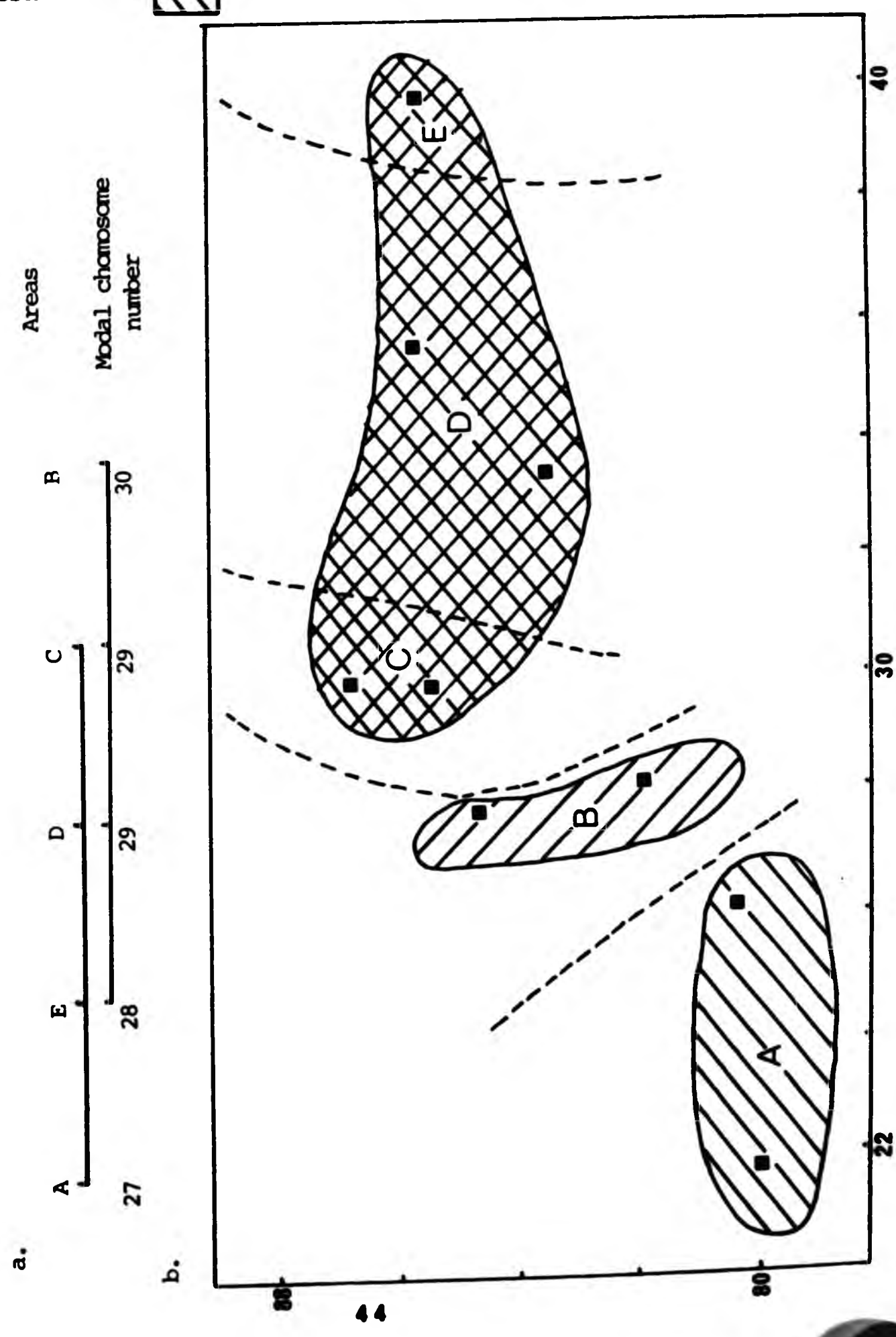


Table 1. Nomenclature for centromere position (R value) used in the present study.

CHROMOSOME TYPE	ABBREVIATION	R VALUE
Metacentric	M	0.61 to 1.00
Submetacentric	SM	0.33 to 0.60
Acrocentric	A	0.10 to 0.32
Telocentric	T	0

Table **2.**The allelic frequencies at the loci affecting colour and banding of the shell in C.nemoralis from the western Berkshire Downs.

Area	Pop	N	Cy	Cp	Cb	Bb	Ss	U3
A	1	10	0.70	0.30	-	1.00	0.10	0.20
A	2	9	0.78	0.11	0.11	0.78	-	0.25
B	1	8	1.00	-	-	1.00	-	0.25
B	2	9	0.67	0.11	0.22	0.67	-	0.17
C	1	9	0.67	0.33	-	1.00	0.11	0.44
C	2	17	0.59	0.29	0.12	0.88	0.13	0.67
C	3	18	0.72	0.28	-	1.00	-	0.67
D	1	14	0.79	0.21	-	1.00	0.07	0.79
D	2	12	1.00	-	-	0.92	-	0.91
E	1	4	0.75	-	0.25	0.75	-	-
E	2	1	-	-	1.00	-	-	-

The frequencies of Bo,So and Uo are one minus the frequency of thier respective alternative alleles.

The loci are as follows:-

C	Shell colour	Yellow	Cy
		Pink	Cp
		Brown	Cb
B	Bandedness	Bands present	Bb
		Bands absent	Bo
U	Midbandedness	Single central band	U3
		More than one band	U0

Table 3. Clutch and slide data for populations of C. nemoralis from the western Berkshire Downs.

Population	Clutch laid.	Clutch prep.	Slide no.	K
A1	1.7.80	10.7.80	5	*
	6.7.80	11.7.80	3	*
	8.7.80.	15.7.80	5	
	21.7.80	28.7.80	2	
	26.7.80	1.8.80	8	
A2	2.7.80	10.7.80.	5	*
	2.7.80	11.7.80	5	*
	15.7.80	22.7.80	3	
	18.7.80	25.7.80	5	
B1	6.7.80	11.7.80	5	*
	8.7.80	13.7.80	5	*
	10.7.80	15.7.80	5	
B2	20.6.80	29.6.80	5	*
	21.6.80	29.6.80	5	
	5.7.80	12.7.80	5	*
	10.7.80	15.7.80	3	
	12.7.80	19.7.80	3	
C1	16.7.80	22.7.80	10	*
	20.7.80	22.7.80	8	*
	20.7.80	27.7.80	5	*
	21.7.80	29.7.80	3	
C2	20.6.80	26.7.80	5	
	25.7.80	30.7.80	2	*
	25.7.80	1.8.80	6	
	26.7.80	2.8.80	5	*
C3	20.7.80	27.7.80	5	*
	1.8.80	10.8.80	5	
	17.8.80	22.8.80	5	
	17.8.80	22.8.80	6	*
D1	12.7.80	21.7.80	3	
	13.7.80	23.7.80	5	*
	22.7.80	31.7.80	4	*
D2	20.6.80	26.6.80	3	
	20.6.80	29.6.80	5	*
	21.6.80	29.6.80	5	
	26.6.80	2.7.80	6	*
	29.6.80	5.7.80	5	
	10.7.80	13.7.80	5	*
	11.7.80	21.7.80	3	
E1	14.7.80	20.7.80	6	
	16.7.80	23.7.80	5	*
	19.7.80	24.7.80	3	*
E2	26.8.80	2.8.80	5	

K: Karyotypes used in the analysis

Table 4. The results of the Kolmogarov-Smirnov test for chromosome pairs 1 to 3.

Chromosome length

POP	PAIR 1	P	PAIR 2	P	PAIR 3	P
A1	0.20	0.2>P>0.1	0.16	P>o.2	0.18	P>0.2
A2	0.18	P>0.2	0.10	P>0.2	0.16	P>0.2
B1	0.18	0.2>P>0.1	0.11	P>0.2	0.14	P>0.2
B2	0.23	0.1>P>0.05	0.14	P>0.2	0.17	P>0.2
C1	0.07	P>0.2	0.14	P>0.2	0.13	P>0.2
C2	0.09	P>0.2	0.14	P>0.2	0.14	P>0.2
C3	0.12	P>0;2	0.19	P>0.2	0.15	P>0.2
D1	0.21	P>0.2	0.17	P>0.2	0.14	P>0.2
D2	0.12	P>0.2	0.18	0.05>P>0.02*	0.11	P>0.2
E	0.15	P>0.2	0.08	P 0.2	0.14	P>0.2

Centromere position(R).

POP	PAIR 1	P	PAIR 2	P	PAIR 3	P
A1	0.11	P>0.2	0.15	P>0.2	0.09	P>0.2
A2	0.18	P>0.2	0.23	0.2>P>0.1	0.14	P>0.2
B1	0.10	P>0.2	0.13	P>0.2	0.18	0.2>P>0.1
B2	0.17	P>0.2	0.17	P>0.2	0.11	P>0.2
C1	0.25	0.05>P>0.02*	0.20	0.2>P>0.1	0.09	P>0.2
C2	0.15	P>0.2	0.13	P>0.2	0.31	=0.05 *
C3	0.20	P>0.2	0.16	P>0.2	0.22	P>0.2
D1	0.18	P>0.2	0.12	P>0.2	0.12	P>0.2
D2	0.17	0.1>P>0.05	0.16	0.1>P>0.05	0.16	0.1>P>0.05
E	0.14	P>0.2	0.25	0.2>P>0.1	0.13	P>0.2

* P≤0.05
POP Population
P Probability

Table 5. The results of the Kruskal-Wallis one way analysis of variance for chromosome pairs 1 to 3.

		LENGTH			CENTROMERE POSITION			
POP	PAIR	H	P		H	P		N
A1	1	24.692	0.1>P>0.05	ns	20.757	0.5>P>0.1	ns	17
	2	15.042	0.9>P>0.5	ns	22.510	0.5>P>0.1	ns	17
	3	20.016	0.5>P>0.1	ns	18.536	0.5>P>0.1	ns	17
A2	1	8.974	0.9>P>0.5	ns	15.052	0.5>P>0.1	ns	13
	2	13.359	0.5>P>0.1	ns	8.430	0.9>P>0.5	ns	13
	3	19.122	0.1>P>0.05	ns	9.345	0.9>P>0.5	ns	13
B1	1	18.823	0.5>P>0.1	ns	18.157	0.5>P>0.1	ns	17
	2	23.800	0.1>P>0.05	ns	19.969	0.5>P>0.1	ns	17
	3	22.047	0.5>P>0.1	ns	16.693	0.5>P>0.1	ns	17
B2	1	19.711	0.5>P>0.1	ns	9.517	0.9>P>0.5	ns	15
	2	19.532	0.5>P>0.1	ns	13.703	0.5>P>0.1	ns	15
	3	14.884	0.5>P>0.1	ns	23.356	0.1>P>0.05	ns	15
C1	1	18.074	0.5>P>0.1	ns	12.451	0.9>P>0.5	ns	16
	2	14.283	0.9>P>0.5	ns	21.236	0.5>P>0.1	ns	16
	3	12.976	0.9>P>0.5	ns	18.487	0.5>P>0.1	ns	16
C2	1	9.439	0.5>P>0.1	ns	7.439	0.5>P>0.1	ns	9
	2	12.987	0.8>P>0.1	ns	5.925	0.9>P>0.5	ns	9
	3	9.334	0.5>P>0.1	ns	9.067	0.5>P>0.1	ns	9
C3	1	7.714	0.5>P>0.1	ns	6.284	0.5>P>0.1	ns	7
	2	7.316	0.5>P>0.1	ns	1.639	0.975>P>0.9	ns	7
	3	5.825	0.5>P>0.1	ns	9.494	0.5>P>0.1	ns	7
D1	1	2.528	0.9>P>0.5	ns	1.85	0.975>P>0.9	ns	6
	2	5.172	0.5>P>0.1	ns	1.385	0.975>P>0.9	ns	6
	3	5.423	0.5>P>0.1	ns	8.170	0.5>P>0.1	ns	
D2	1	36.923	0.5>P>0.1	ns	39.062	0.1>P>0.05	ns	29
	2	32.980	0.5>P>0.1	ns	40.198	0.1>P>0.05	ns	29
	3	28.161	0.5>P>0.1	ns	35.833	0 .5>P>0.1	ns	29
E	1	10.844	0.5>P>0.1	ns	10.274	0.5>P>0.1	ns	10
	2	11.845	0.5>P>0.1	ns	11.718	0.5>P>0.1	ns	10
	3	9.736	0.5>P>0.1	ns	12.256	0.5>P>0.1	ns	10

ns no significant difference
n number of karyotypes measured
H Kruskal-Wallis statistic

Table 5A. The results of the Kruskal-Wallis one way analysis of variance for the chromosomes in group C in populations from the western Berkshire Downs.

POP	LENGTH			CENTROMERE POSITION			
	H	P		H	P		N
A1	1.544	0.975	ns	1.939	0.995	ns	17
A2	10.331	0.9>P>0.5	ns	10.072	0.9>P>0.5	ns	13
B1	7.031	0.975	ns	8.980	0.975>P>0.9	ns	17
B2	6.048	0.975>P>0.9	ns	21.768	0.1>P>0.05	ns	15
C1	14.373	0.9>P>0.5	ns	20.159	0.5>P>0.01	ns	16
C2	8.234	0.5>P>0.1	ns	11.820	0.5>P>0.1	ns	9
C3	5.464	0.5>P>0.1	ns	4.837	0.9>P>0.5	ns	7
D1	1.832	0.9>P>0.5	ns	3.961	0.9>P>0.5	ns	6
D2	20.620	0.9>P>0.5	ns	16.560	0.9>P>0.5	ns	29
E	4.841	0.9>P>0.5	ns	12.599	0.5>P>0.1	ns	10

Table 6. The mean(Y), standard deviation(SD) and confidence limits (CL) for chromosome pairs 1 to 3 .

Chromosme pair 1.

	RELATIVE LENGTH					CENTROMERE POSITION			
POP	Y	SD	CL95	CL99	N	Y	SD	CL95	CL99
A1	8.300	0.555	0.201	0.261	34	0.87	0.075	0.026	0.035
A2	8.320	0.639	0.257	0.348	26	0.86	0.066	0.027	0.036
B1	8.230	0.521	0.182	0.244	34	0.86	0.074	0.026	0.035
B2	8.180	0.489	0.183	0.246	30	0.85	0.060	0.022	0.030
C1	8.178	0.761	0.273	0.367	32	0.86	0.060	0.022	0.029
C2	8.438	0.609	0.303	0.416	18	0.87	0.028	0.039	0.054
C3	8.084	0.533	0.307	0.429	14	0.80	0.088	0.051	0.061
D1	8.260	0.598	0.443	0.070	12	0.88	0.083	0.061	0.096
D2	8.286	0.591	0.155	0.207	58	0.85	0.076	0.020	0.027
E	8.284	0.686	0.321	0.439	20	0.84	0.075	0.035	0.048

Chromosome pair 2.

	RELATIVE LENGTH					CENTROMERE POSITION			
POP	Y	SD	CL95	CL99	N	Y	SD	CL95	CL99
A1	3.298	0.221	0.077	0.104	34	0.83	0.032	0.029	0.038
A2	3.231	0.221	0.093	0.128	26	0.86	0.067	0.027	0.038
B1	3.320	0.223	0.078	0.104	34	0.83	0.094	0.033	0.044
B2	3.350	0.232	0.087	0.117	30	0.88	0.081	0.030	0.041
C1	3.298	0.247	0.088	0.120	32	0.83	0.081	0.030	0.041
C2	3.302	0.294	0.146	0.201	18	0.85	0.080	0.040	0.054
C3	3.434	0.242	0.014	0.095	14	0.79	0.060	0.035	0.046
D1	3.298	0.273	0.202	0.318	12	0.79	0.060	0.035	0.048
D2	3.291	0.228	0.061	0.087	58	0.87	0.060	0.019	0.026
E	3.472	0.235	0.111	0.015	20	0.83	0.064	0.030	0.041

Chromosome pair 3.

	RELATIVE LENGTH					CENTROMERE POSITION			
POP	Y	SD	CL95	CL99	N	Y	SD	CL95	CL99
A1	2.767	0.328	0.115	0.154	34	0.33	0.054	0.019	0.025
A2	3.231	0.388	0.093	0.126	26	0.37	0.068	0.027	0.037
B1	2.670	0.276	0.096	0.129	34	0.40	0.082	0.029	0.038
B2	2.671	0.289	0.108	0.145	30	0.39	0.066	0.025	0.033
C1	2.724	0.281	0.101	0.136	32	0.40	0.092	0.033	0.044
C2	2.670	0.256	0.127	0.175	18	0.40	0.063	0.031	0.043
C3	2.848	0.307	0.177	0.247	14	0.40	0.116	0.067	0.093
D1	2.538	0.300	0.220	0.345	12	0.44	0.068	0.051	0.080
D2	2.608	0.324	0.085	0.114	58	0.38	0.067	0.018	0.023
E	2.679	0.271	0.127	0.173	20	0.39	0.112	0.052	0.071

RELATIVE LENGTH The absolute length as a percentage of the total length of the karyotype.
CENTROMERE POSITION R The length of the short arm divided by the length of the long arm.
N number of chromosomes measured
CL Confidence limits 95 percent and 99 percent.

Table 6A. The results of the analysis of variance for chromosome pairs 1 to 3 from populations of C.nemoralis from the western Berkshire Downs.

PAIR	LENGTH			R VALUE		
	Fs	P		Fs	P	
1	0.0216	0.75000	ns	0.7003	0.7500	ns
2	0.5135	0.7500	ns	0.4759	0.7500	ns
3	0.6207	0.7500	ns	0.2433	0.7500	ns

F0.05 = 1.88
ns no significant difference

Table 7. The co-efficients of variation for chromosome pairs 1 to 3.

	PAIR 1		PAIR 2		PAIR 3	
POP	LENGTH	R VALUE	LENGTH	R VALUE	LENGTH	R VALUE
A1	6.687	8.636	6.701	9.896	11.865	16.163
A2	7.675	7.688	6.843	7.869	11.999	18.359
B1	6.324	8.590	6.711	11.401	10.337	20.159
B2	5.983	7.112	6.919	9.169	10.805	17.124
C1	9.303	7.065	7.522	9.803	10.308	23.127
C2	7.211	3.212	8.889	9.425	9.577	15.785
C3	6.593	10.900	7.041	7.554	10.783	29.262
D1	7.234	9.392	8.284	8.941	11.686	15.398
D2	7.130	8.925	6.928	6.873	12.439	17.712
E	8.281	8.919	6.809	7.658	10.101	28.837

Table 8. The frequency distribution of the relative lengths of the group C chromosomes from populations of C. nemoralis from the western Berkshire Downs.

	CLASS LIMITS							
POP	1.40 to 1.60	1.61 to 1.80	1.81 to 2.00	2.21 to 2.20	2.21 to 2.40	2.41 to 2.60	2.61 to 2.80	2.81 to 3.00	N
A1	125	192	151	73	50	34	19	2	646
A2	82	177	114	43	35	27	14	2	494
B1	107	217	155	71	39	27	24	6	646
B2	88	182	140	73	46	26	13	2	570
C1	88	209	147	79	46	22	16	1	608
C2	64	113	76	42	24	14	7	2	342
C3	45	79	73	33	14	15	5	2	266
D1	23	89	62	20	17	10	6	1	228
D2	224	344	250	114	60	64	38	8	1120
E	85	105	86	41	28	23	10	2	380

POP Populations

N Number of chromosomes measured

Table 9. The frequency distributuion of R values of the group C chromosomes from populations of C.nemoralis from the western Berkshire Downs.

	R VALUE CLASS LIMITS							
POP	0.31 to 0.40	0.41 to 0.50	0.51 to 0.60	0.61 to 0.70	0.71 to 0.80	0.81 to 0.90	0.91 to 1.00	N
A1	23	68	110	132	135	115	63	646
A2	9	39	86	109	132	74	45	494
B1	10	35	84	123	179	143	72	646
B2	9	29	80	140	161	120	31	570
C1	8	46	95	127	162	123	47	608
C2	8	22	46	82	89	64	31	342
C3	7	20	34	55	80	47	23	266
D1	3	10	31	61	54	51	18	228
D2	15	73	176	239	298	204	97	1102
E	14	24	64	99	88	60	31	380

Table 10 The frequency distribution of R values of the group C chromosomes from populations of C.nemoralis from the western Berkshire Downs.R values from each population within an area(A,B,C,D or E) are combined.

	R VALUE CLASS LIMITS							
AREA	0.31 to 0.40	0.41 to 0.50	0.51 to 0.60	0.61 to 0.70	0.71 to 0.80	0.81 to 0.90	0.91 to 1.00	N
A	32	107	196	241	267	189	108	1140
B	19	64	164	263	340	263	103	1216
C	23	88	175	264	331	234	101	1216
D	18	83	207	300	352	255	115	1330
E	14	24	64	99	88	60	31	380

N number of chromosomes measured

Table 11. The frequency distribution of R values of the group C chromosomes from populations of C.nemoralis from the western Berkshire downs. Class limits 0.51-0.60 and 0.61-0.70.

	CLASS LIMITS	
POP	0.51-0.60	0.61-0.70
A1	110	132
A2	86	109
B1	84	123
B2	80	140
C1	95	127
C2	46	82
C3	34	55
D1	31	61
D2	176	239
E	64	99

Table 12. The frequency distribution of R values of the group C chromosomes from populations of C.nemoralis from the western Berkshire Downs. Class limits 0.51-0.60 and 0.61-0.70 are ommited.

	CLASS LIMITS				
POP	0.31 to 0.40	0.41 to 0.50	0.71 to 0.80	0.81 to 0.90	0.91 to 1.00
A1	23	68	135	115	63
A2	9	39	132	74	45
B1	10	35	179	143	72
B2	9	29	161	120	31
C1	8	46	162	123	47
C2	8	22	89	64	31
C3	7	20	80	47	23
D1	3	10	54	51	18
D2	15	73	298	204	97
E	14	24	88	60	31

Plate 1
A representative karyotype from population A1 in the five-banded area effect on the Berkshire Downs.The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of sub-metacentric chromosomes.The mean chromosome number for this population is 26.

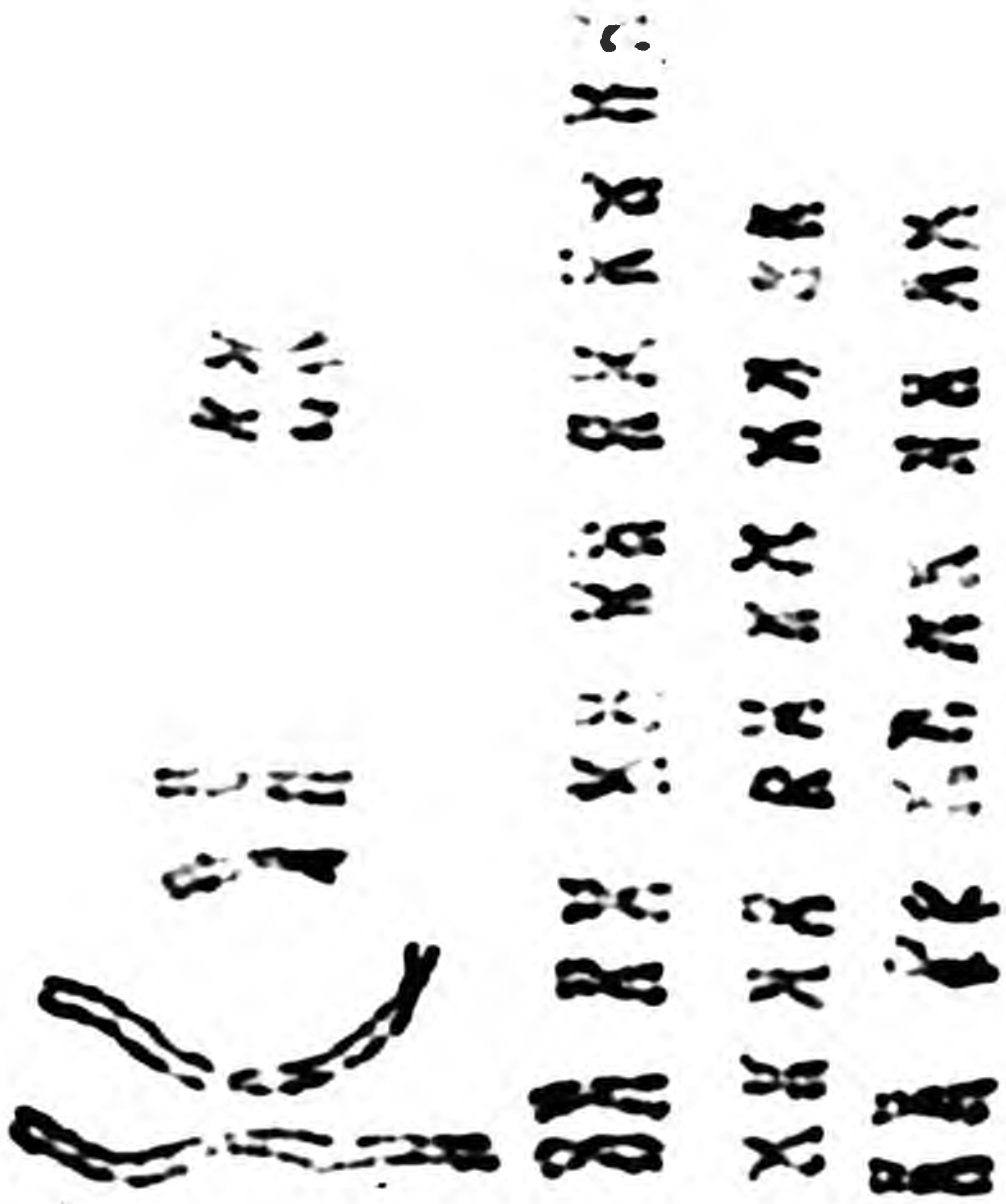


Plate 2

A representative karyotype from population A2 in the five-banded area effect on the Berkshire Downs. The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 28.

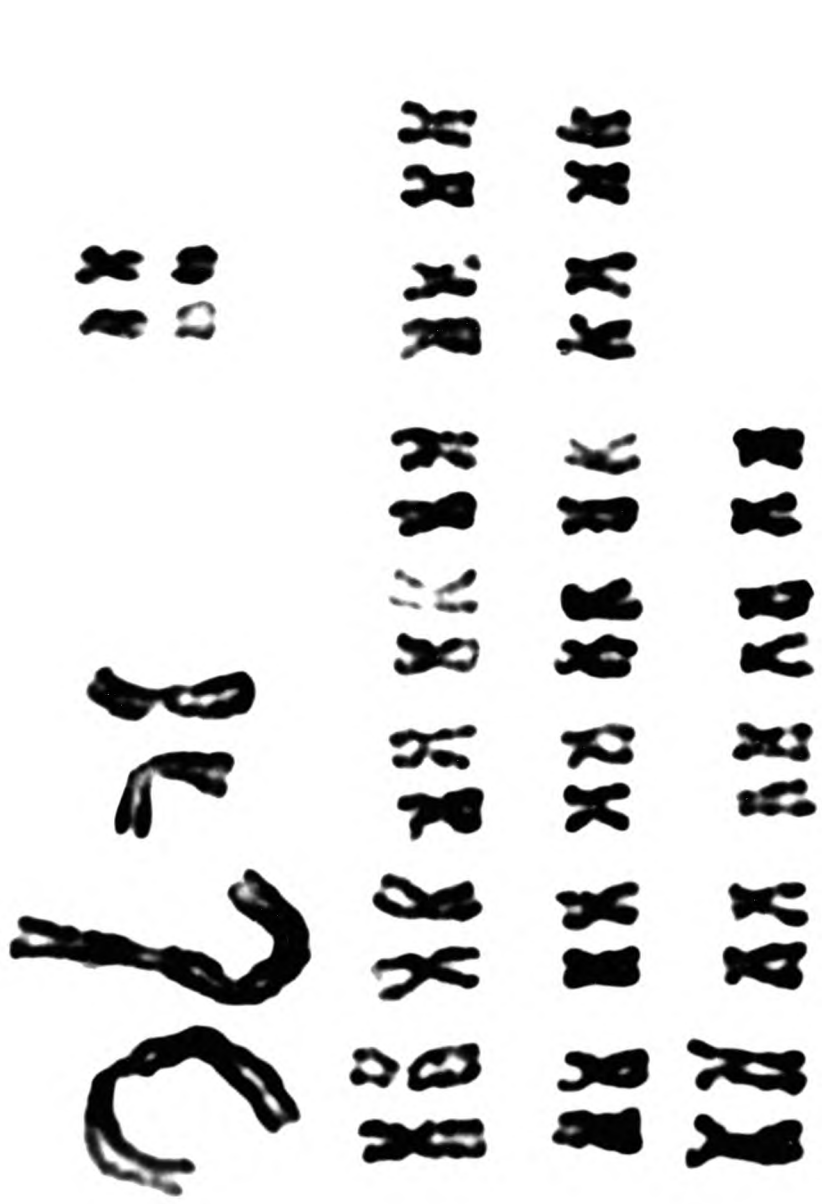


Plate 3
A representative karyotype from population B1 in the western transition zone on the Berkshire Downs. The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 30.

Plate 4
A representative karyotype from population B2 in the western transition zone in the Berkshire Downs.The chromosomes are arranged in three groups A,B and C. The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 30.

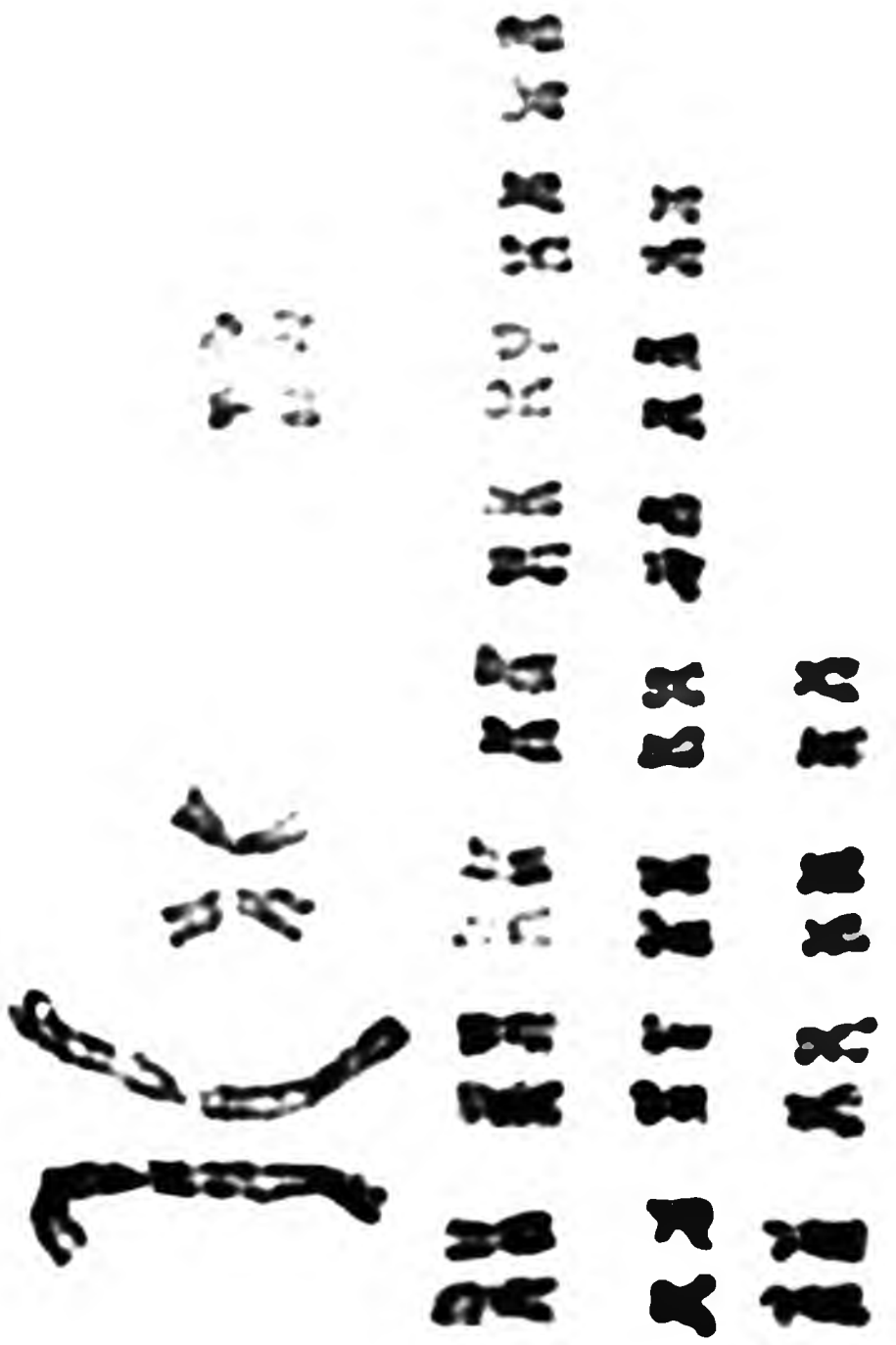


Plate 5
A representative karyotype from population C1 in the western midbanded area effect on the Berkshire Downs. The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 29.

Plate 6
A representative karyotype from population C2 in the western midbanded area effect on the Berkshire Downs. The chromosomes are arranged in three groups A,B andC.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 30.

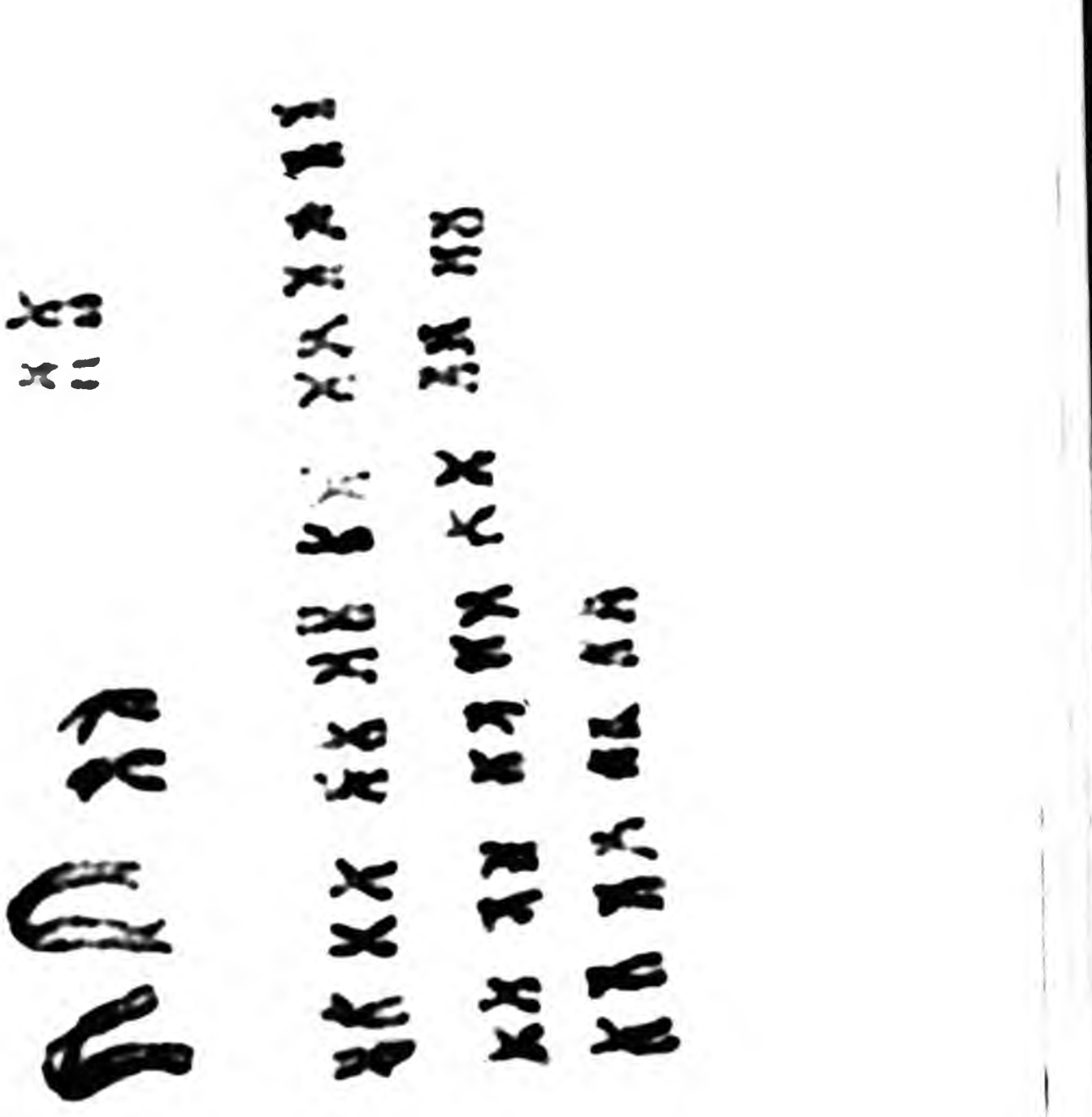


Plate 7
A representative karyotype from population C3 in the western midbanded area effect on the Berkshire Downs. The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 29.

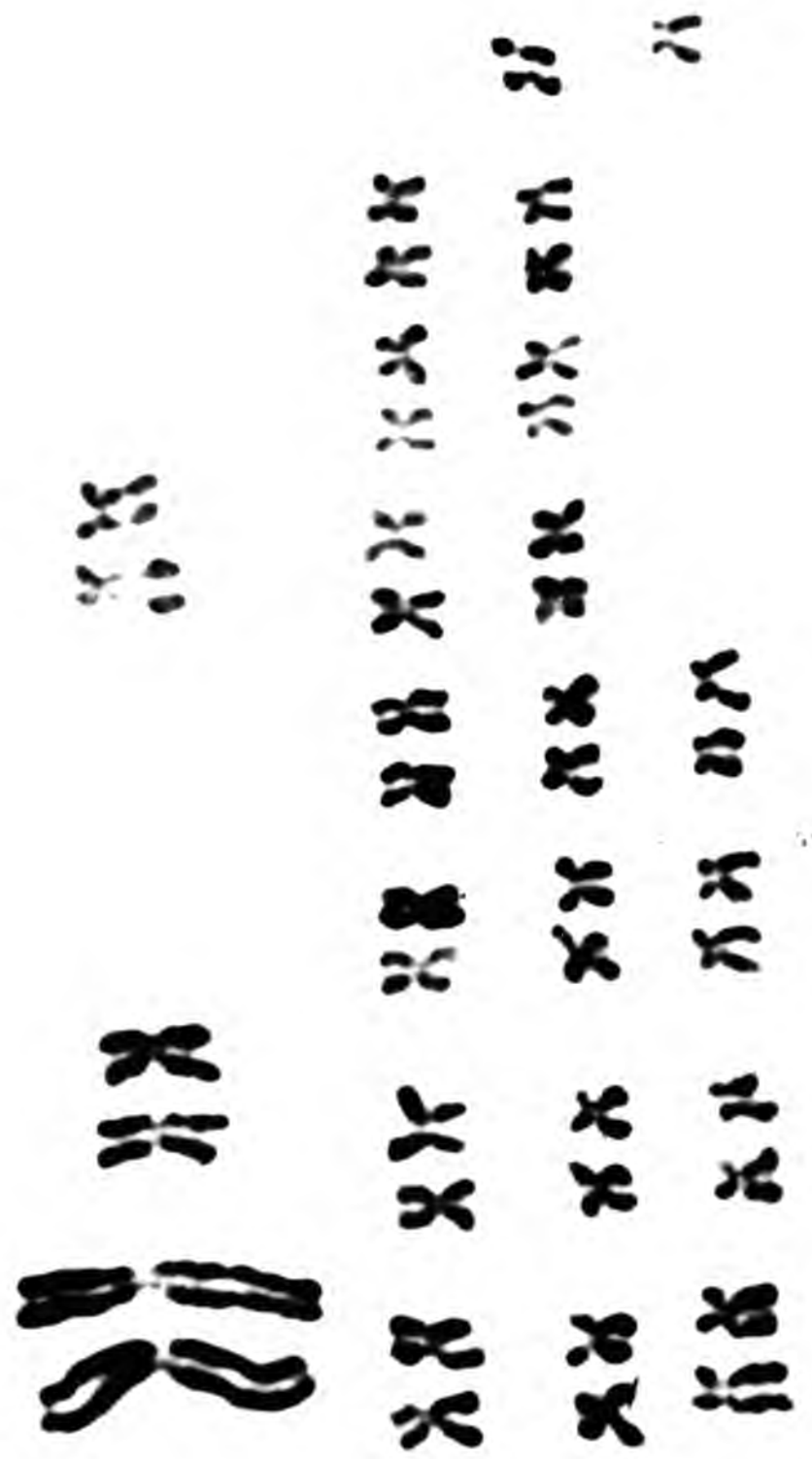


Plate 8
A representative karyotype from population D1 in the eastern midbanded and transition zone on the Berkshire Downs.The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number for this population is 31.

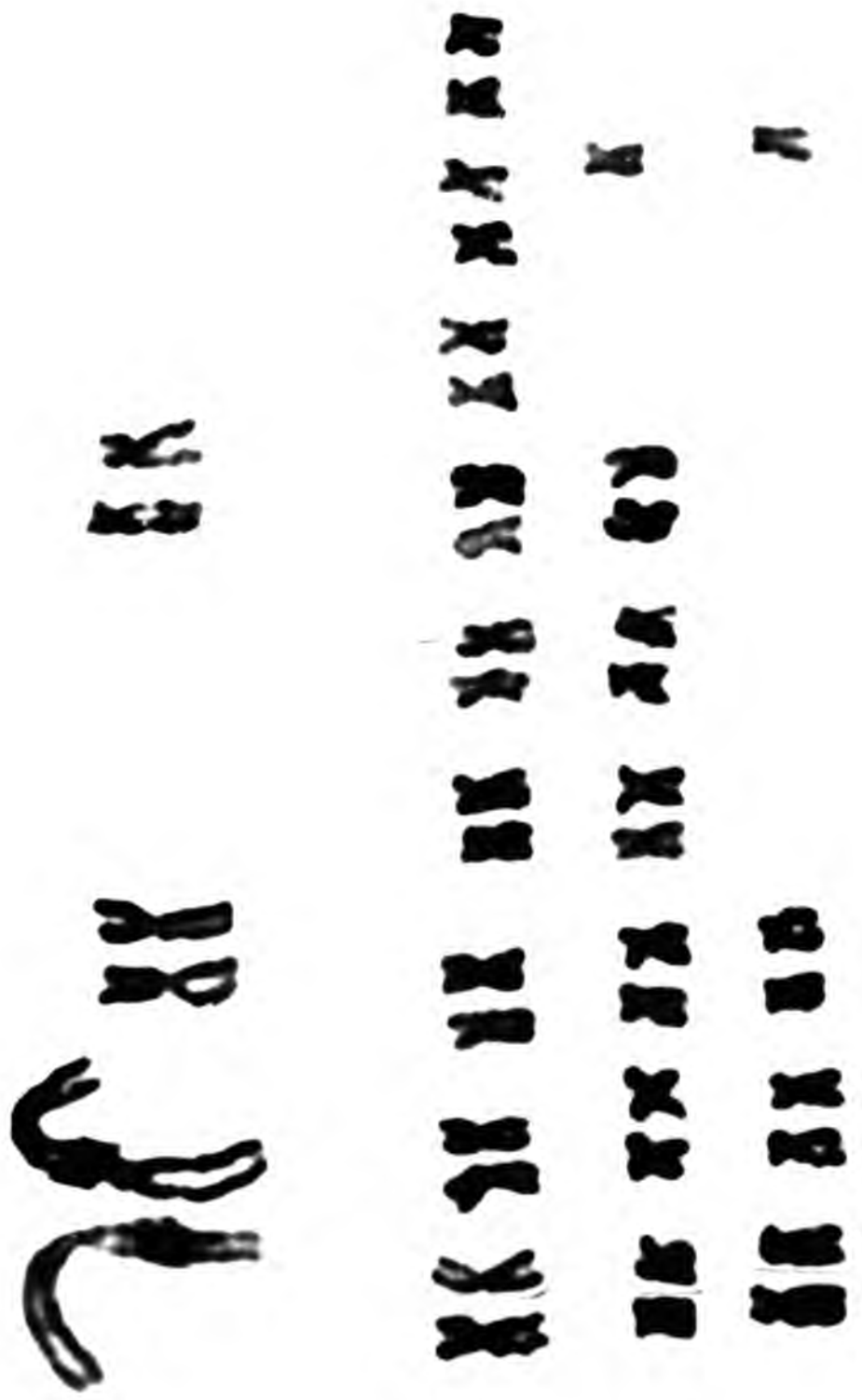


Plate 9
A representative karyotype from population D2 in the eastern midbanded and transition zone on the Berkshire Downs.The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows.The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number of this population is 29.

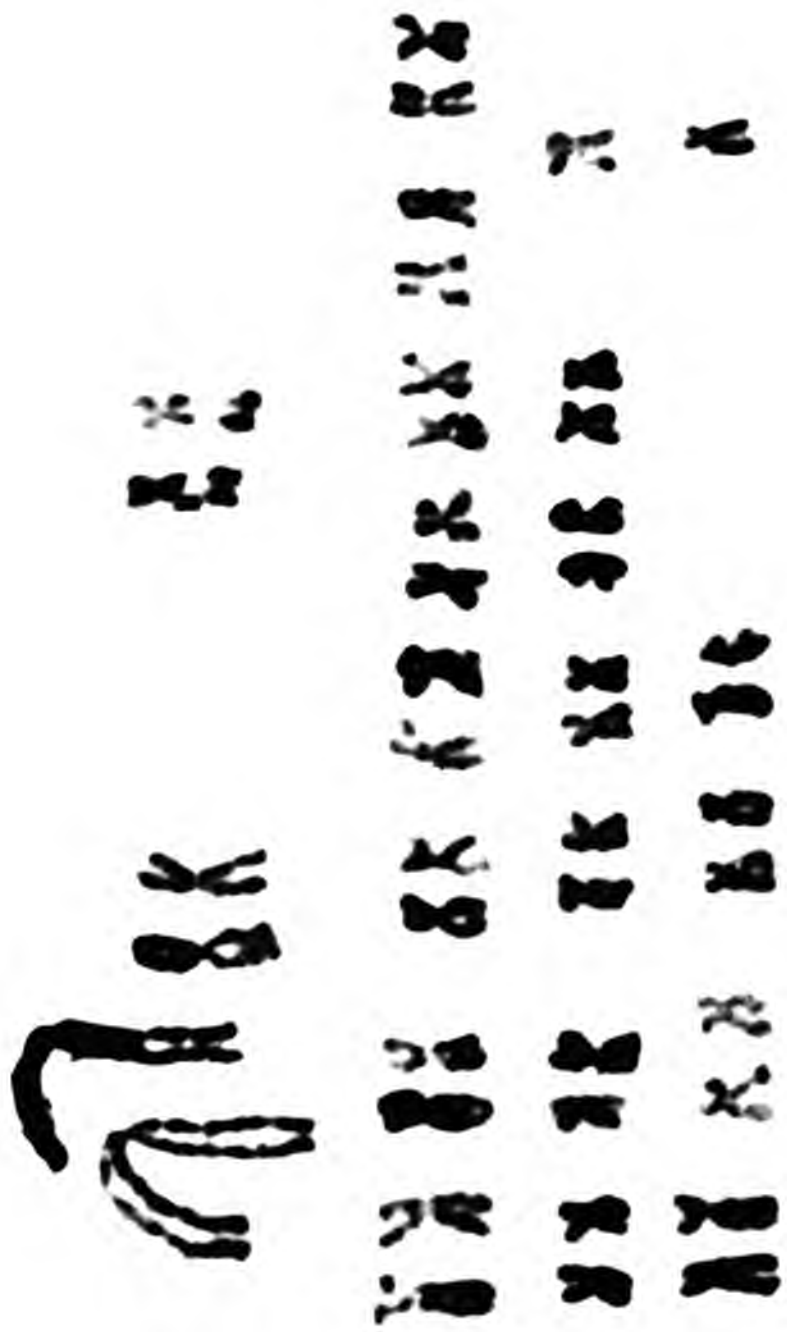
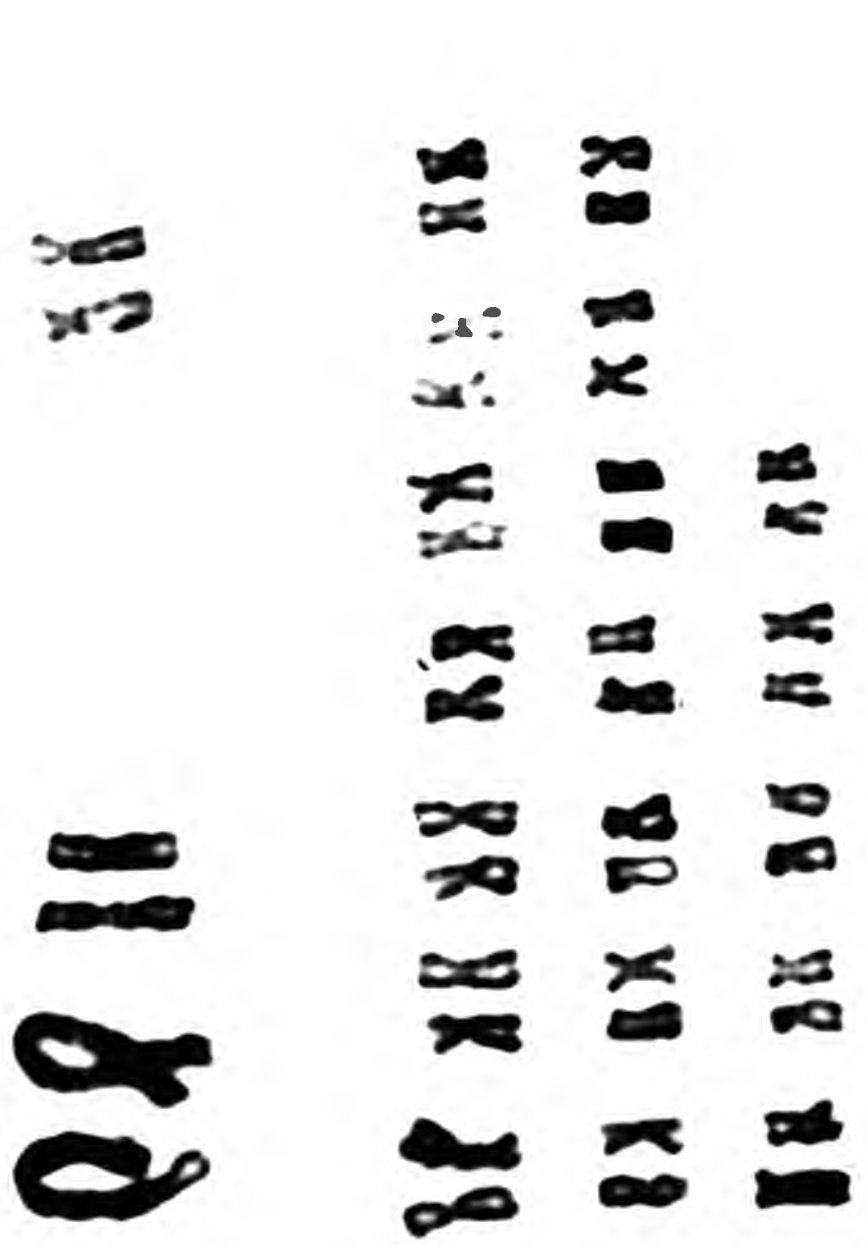


Plate 10
A representative karyotype from population E1 in the eastern non-midbanded area effect on the Berkshire Downs.The chromosomes are arranged in three groups A,B and C.The chromosomes of group C are arranged in three rows. The first two rows consist of metacentric chromosomes and the third row consists of submetacentric chromosomes.The mean chromosome number of this population is 28.



4. DISCUSSION

This study of Cepaea nemoralis from the Berkshire Downs (U.K.) has shown that there are marked interpopulational differences in the proportions of metacentric and submetacentric chromosomes in the C group. The differences fall within the range found previously in several widespread allopatric populations in the British Isles, Northern Europe and America (Page 1980) and are possibly conferred by pericentric inversions in at least three chromosome pairs. Alternative explanations are discussed below.

The survey region has been divided into five sampling areas, based on the morphological and genic area effects reported by Carter (1968) and Johnson (1976). The populations within the region form a series of karyomorphs which are characterized by a mean number of metacentric chromosomes within the C group. The degree to which the populations differ depends, in part, on the method of classification, but in all cases the most metacentric areas or populations show marked significant differences from the least metacentric ones. The mean chromosome number varies from 26 in population A^1 to 31 in population D^1.

There are no immediately obvious associations of differences in chromosome structure and any observable environmental variations, as seen for example in Thomomys bottae (Eydoux and Gervois) (Patton 1970), Caledia captiva (Moran and Shaw 1977) and the asiatic black rat Rattus rattus (Linn.) (Yosida et.al. 1971). The two populations of C. nemoralis from the present study showing the greatest chromosomal differences (A^1 and D^1) are both from a Beechwood habitat at the same altitude, whereas populations with similar chromosomal rearrangements, come from completely different altitudes. e.g. Population E^1 at 150 m. and A^2 at 230 m.

The overall distribution of the karyomorphs in the region appears, at first sight, to be random. There are however marked non random associations of the populations within areas A, B and C. Populations A^1 and A^2, B^1 and B^2 and C^1, C^2 and C^3 all show intra-area similarities in the mean

chromosome number. There are no significant differences between the proportions of metacentric and submetacentric chromosomes in the populations within these areas.

White (1978b) has suggested that species which exhibit area effects may also show particular chromosome rearrangements. In this modfied model of stasipatric speciation based on an idea proposed by Hall (1973) and developed by White (1978a), populations within an area are assumed to possess a co-adapted gene complex which is partially incompatible with those from other areas. A chromosomal rearrangement which arises within an area spreads until it is concordant with the limits of the effect, where in the homozygous state it protects the existing co-adapted genes against intro gression from neighbouring but different populations. If such a situation exists in the "area effect populations" of C. nemoralis from the Berkshire Downs it would be expected that the five sampling areas A to E would be characterized by different chromosomal arrangements.

Populations within areas A, B and C all show strong intra-area association with respect to chromosome structure. The most significant difference in chromosome constitution occurs between the Western midbanded area A and the transition zone B. There is no evidence to suggest that the gradual cline (area B) in shell characters, which runs Westward for five kilometres from the midbanded area effect (C) to the five banded area effect (A) is accompanied by a similar variation in chromosome structure, as might be expected if, for example, the chromosome rearrangement had been present during the initiation and spread of the visible are effect. The difference between these two areas is, however, consistent with the expectations of the "area effect model" of speciation in as much as clines between two already co-adapted area effect populations need not necessarily be accompanied by a similar cline in karyotypic variation.

Only two areas show clearly significant differences in chromosome structure but there are several other similarities in the distribution of the chromosomal variation and the visible area effects. Johnson (1976)

has shown that genotypic frequencies show a sharp transition to the east. This is reflected in the chromosomal variation, if some what displaced to the west, in that differences in the central populations and those to the east are less well defined than the very significant difference in the west between populations areas in A and B.

Morph frequency variation alone (Carter 1968) also shows a strong east/west axis. Variation with habitat is less marked to the west where the most pronounced area effects occur and gradual to the east where variation with habitat is greatest.

The analysis of co-variation of the morphological and allozyme alleles indicate that, as with chromosomal variation two of the five sampling areas A and E are closely associated with each other. In both areas the midbanded morph occurs at low frequencies, however, increases in the midbanded gene elsewhere are not accompanied by similar increases in the metacentricity of the karyomorphs.

The results of the present investigation suggest that at least two (A and B) and possibly three (including area C) "area effect populations" are characterized by a particular chromosome arrangement. The absence of clines between the major visible area effects i.e. in areas B and D suggest that the arrangements have originated after the area effects were established. The lack of significant differences between some of the areas, however, in particular area C which shows the strongest visible and genotypic area effects, suggest that the rearrangements may not be "protective" as envisaged by White's area effect model, but may have some unknown adaptive value. Whether or not the differences in chromosome rearrangements between the "area effect model" of speciation are therefore, debatable. There are already several theoretical difficulties associated with this model regarding the method by which a chromosomal arrangement whose only adaptive value is that of negative heterosis, can become established and spread within a population. (Templeton 1981, Futuyama & Mayer 1980, Bickham & Baker 1980).

It is possible for a chromosomal arrangement of this kind to become fixed in a very small population where inter-breeding is intense (Lande 1979), or in populations that have experienced a severe reduction in population size at some time in their history (Wright 1941, 1978). Whites model however "does not invoke founder effects, local extinctions of populations or invasions of occupied or unoccupied territory by individuals" but, it is suggested that drift may be involved in the initial establishment of the chromosomal rearrangement in a "population isolate". It is difficult to envisage an isolated population, that would provide the conditions favourable to the fixation of a neutral or even slightly deleterious chromosome rearrangement in a large already co-adapted population which is part of an established area effect.

It is possible that meiotic drive may provide a mechanism by which negative heterosis can be overcome (White 1978). Several models provided by Hedrick (1980) illustrate that meiotic drive alone, or in conjunction with genetic drift can be of particular importance in the fixation of a chromosomal rearrangement. Differential selection of the new chromosome in the hetero-karyotype may well facilitate the spread and fixation of the arrangement but the role of meiotic drive either in speciation or in the protection of an existing area effect is improbable. The very process that allows the rearrangement to spread would presumably act in a similar way at the boundaries between different "area effect populations" or chromosomal races such that the isolation afforded by chromosomal differences would be removed.

In addition to the theoretical objections to the area effect model of speciation, there is some evidence, from the mean chromosome number in some populations of C. nemoralis, and from the considerable (but not significant) variation in R value between individuals of the same population, that at least one but possibly more of the chromosome pairs involved in the chromosomal rearrangements are heterozygous and are maintained in a polymorphic state within each population.

Many other species show intra-population polymorphisms which are probably maintained by hetero karyotypic advantage (Lewontin 1974). For example populations of Gerbillus cheesmani (Thomas) regularly show individuals with two, three or four telocentric chromosomes in an otherwise metacentric karyotype (Badr et al. 1980). The relative frequencies of the specific chromosome pairs were not reported in this study but the authors suggest that the high frequency of individuals with three telocentric chromosomes might reflect a certain adaptive advantage.

Intrapopulation variation in chromosome structure in populations from the present investigation and from several other colonies of C. nemoralis (Page 1980) indicate that the variations are geographically widespread and occur in many different habitat types. The relative frequencies of the chromosome pairs involved in the variation,however, cannot be established and until this is possible it seems unlikely that a clear association can be made between the chromosomal inversions and environmental variables.

Not withstanding the theoretical problems associated with this "area effect model" and the possibility that the chromosomal inversions are maintained in a polymorphic state within populations, it is entirely possible that the visible area effects shown in the populations of C. nemoralis from the Berkshire Downs are accompanied by chromosomal rearrangements which cannot be readily determined using the limited cytological methods available for molluscan chromosomes. Inter-and intra-population differences in the number of acrocentric chromosomes of Peromyscus species were originally thought to be due to pericentric inversions. (Hsu et al.1966, 1968, Arakaki et al. 1970) but the use of advanced chromosomal identification techniques (e.g. C. banding) have demonstrated that several differences in the number of chromosome arms were due to additions of heterochromatin (Hsu et al. 1971, Pathak et al. 1973). It is possible that the chromosomal rearrangements found in C. nemoralis are due to heterochromatic additions. Large increases in heterochromatin, whether or not involving concomitant changes in centromere position

can result in changes in total chromosome length. The overall length of the karyotypes measured in the present and other studies (Page 1978, 1980) show little variation. This suggest that if changes in heterochromatin do occur they are those involving the redistribution within the genome as seen in Meriones species (Korobitsyna et al.1980), rather than those involving substantial gains or losses in heterochromatin.

5. CONCLUSION

The role of the chromosomal rearrangements found in populations of C. nemoralis are not clear. The non random association of different karyomorphs in the area effect populations of the Berkshire Downs and the lack of chromosomal clines between them suggests that the chromosomal rearrangements have been initiated after the area effects were established. The lack of significant differences between all but two areas A and B, however, suggests that the role of such chromosome rearrangements may not be "protective" as envisaged by Whites area effect model of speciation but may confer some other adaptive advantage.

It is possible that in some populations the chromosomal rearrangements are maintained in a polymorphic state and as such represent some adaptive advantage of the heterozygote. The specific chromosome pairs involved in the polymorphism cannot be identified using the present cytological methods, so that the relative frequencies of different inversions cannot be established.

Whether or not the chromosomal rearrangements found in populations of C. nemoralis are polymorphic within populations or represent polytypic differences between them, there are no immediately obvious relationships between the distribution of the inversions and any environmental variables. The east/west axis of variation, however, of both morphological and genic polymorphisms and that of chromosomal variation suggests that the selective force or interaction of forces may act similarly on all three variables.

The lack of an unequivocal association of the chromosomal inversions and the visible area effects, however, does not exclude the possibility that chromosomal arrangements other than those found in the present study are associated with the area effects.

Clearly more extensive cytological investigations of Cepaea populations both within area effect and other populations will be necessary to determine the exact function and maintenance of the chromosomal variation system which occurs in Cepaea nemoralis.

PART 11

The investigation of chromosomal variation in Nucella lapillus.

INTRODUCTION

Nucella lapillus is a carnivorous intertidal snail found on rocky shores in Europe and North East America (Cooke 1915). In common with its close relatives of the subgenus Thais found in the Pacific, it shows considerable variation in shell sculpture and colour. Variation in shell colour between different populations may be due to differences in diet (Moore 1936). There are also great variations in the thickness, shape and size of the shell. In many investigations, this variation has been related to the degree of exposure to wave action of the foreshore, such that short squat shells are found on "open sea" exposed sites and tall elongated shells are found in sheltered areas (Colton 1922, Moore 1936). The origin and maintenance of these shell shape gradations has been attributed to the differential effects of selection by wave action. In some populations there is a direct relationship between wave action and shell morphology. (Berry et al 1968, Crothers 1983) whilst in others no direct associations are found (Crothers 1975, 1981, Kitching 1977).

Chromosomal polymorphism in Nucella lapillus was first reported by Staiger (1950) who later completed a detailed study of chromosomal variation in two regions on the North coast of France (1954, 1957). He established the existence of a range of chromosome forms whose diploid chromosome number varies from 2n = 26 to 2n = 36 by means of Robertsonian variation in five metacentric chromosome pairs. The remaining eight chromosome pairs, although numerically constant, often form heteromorphic bivalents in meiosis which may result from pericentric inversions in one or more chromosome pairs.

Individuals of each chromosomal type (2n = 26 or 2n = 36) are fully interfertile so that heterozygotes form trivalents at meiosis. There is however, a slight loss in fecundity due to non-disjunction of the trivalents and the formation of aneuploid gametes (Staiger 1954).

The three possible genotypic arrangements for each of the five chromosome pairs results in 3^5 or 243 possible diploid chromosome constitutions. The microgeographical

distribution of Nucella at Roscoff (Brittany) varies in a simple way such that the 2n = 26 form occupies exposed locations and the 2n = 18 type occupies sheltered shores and bays. More over, intermediate shores between the two types are occupied by chromosomally intermediate populations. In contrast the second region (Primel Locquirez) showed complete monomorphism for the 2n = 26 type for both exposed and intermediate locations. Hoxmark (1970) re-examined four locations at Roscoff and confirmed Staigers earlier findings. In addition he examined five populations forming an exposure gradient on the Western coast of Norway. These too were monomorphic for the 2n = 26 type irrespective of the degree of exposure. Bantock and Cockayne (1974) reported the overall distribution of chromosomal polymorphism in S.E. England and found that most populations monomorphic for the 2n = 26 form. The polymorphism, however, occurs regularly in bays to the South West. Two areas where the acrocentrics reached high frequencies were studied in detail. The authors concluded that although polymorphic populations exhibit chromosome variation in a similar direction to those at Roscoff. i.e. the percentage of acrocentrics increases as wave exposure decreases, other factors relating to wave movements, such as tidal current and range may influence the distribution of the polymorphism.

In all the previous chromosomal investigations of Nucella lapillus chromosome number has been determined by chromosome counts from female (Staiger 1954, 57) or male meiotic cells. (Bantock et al 1975), Hoxmark 1970). Recently, however, Bantock and Page (1976) have extended the studies on Nucella by a detailed investigation of mitotic chromosomes from embryonic tissue. They established that 2n = 26 forms from three allopatric populations each showing different degrees of chromosomal polymorphism did not differ from each other. In addition they reported the existence of two inversion polymorphisms in the fourth and eighth or ninth largest chromosome pairs of the 2n = 26 karyotype. The relationship between the numerical and inversion polymorphism was not known.

It is generally agreed that chromosomal rearrangements such as inversions can alter the epistatic relationships of the genes within a genome and may protect certain co-adapted gene sequencies by repression of crossing over in the inverted region (Lewontin 1974). It is therefore possible that the chromosomal inversions found in some populations of Nucella lapillus may alter the adaptive response of the karyotype to particular environmental factors such that individuals of the same chromosome number, but different inversion polymorphisms, need not necessarily respond to similar environmental variables in the same way.

If, however, the chromosome pairs, involved in the inversion polymorphism are also part of the Robertsonian variation it is probable that meiotic irregularities could severely reduce the fertility in the heterozygote. There are six possible diploid constitutions for an individual polymorphic for both types of chromosome rearrangements. Heterozygotes for both arrangements will consist of two acrocentric chromosomes and an "inverted" metacentric chromosome neither arm of which will be linearly homologous with either of the acrocentrics. Misali gnment of chromosome arms or crossing over in the inverted segment in such individuals could produce a high proportion of aneuploid gametes and could result in an overall selection against the high (acrocentric) chromosome number.

There is already some evidence to suggest that one of the large chromosome pairs of the complement may be involved in both numerical and inversion polymorphisms (Bantock and Page 1977), In addition Staiger (1954) has also observed the regular occurence of an abnormal trivalent formation conferred by a possible pericentric inversion in the second largest chromosome pair involved in the Robertsonian variation.

Staiger was able to distinguish the chromosomes involved in the Robertsonian variation in female meiosis but the specific identification of the five chromosome pairs in mitotic chromosomes has not been determined.

The primary objectives of the present study were one; to identify as far as possible, the specific chromosome pairs involved in both the Robertsonian and inversion

polymorphisms in mitotic metaphase chromosomes and two, to determine the distribution of the two types of polymorphism in two populations showing different degrees of numerical and environmental variation.

In pursuit of the former, however, it was found that, given the present limited cytogenetic techniques available for molluscs (i) The unequivocal identification of the specific chromosome pairs involved in either polymorphism is not possible. (ii) The inversion polymorphism in the larger of the two chromosome pairs (pair 4) is absent in most populations and rare elsewhere. (iii) The inversion polymorphism in the smaller chromosome pair (8 or 9) is indistinguishable in most karyotypes where the largest chromosomes of the Robertsonian variation are also polymorphic.

In consequence, only one of the two populations selected for the investigations into the distribution of the two polymorphisms provided data suitable for this kind of analysis.

The survey of the two polymorphic populations, however, has provided information about the chromosomes involved in the Robertsonian variation and distribution of the numerical variation in response to exposure of the collecting sites in a coastal region which is generally monomorphic for the $2n = 26$ karyotype.

2. MATERIALS AND METHODS.

2.1. The identification of the chromosomes involved in the inversion polymorphism.

2.2. The identification of the chromosomes involved in the Robertsonian polymorphism.

2.3. The investigation of the distribution of the numerical and inversion polymorphisms at Rottingdean and Cuckmere Haven.

a. The populations used in the study.
   (i) Rottingdean.
   (ii) Cuckmere Haven.

b. Sampling and culture methods.

c. Cytological methods.

d. Karyotypes and karyotype analysis.

e. The analysis of variation within and between sampling areas.

2. MATERIALS AND METHODS

2.1. The identification of the chromosomes involved in the inversion polymorphism.

Several populations have been sampled by the author mainly in Sussex and Dorset but also in Pembrokeshire, South Wales and on the West coast of Scotland. The majority of populations are monomorphic for the 2n = 26 form.

The two areas chosen for the investigation of the distribution the numerical and inversion polymorphisms; Cuckmere Haven and Rottingdean, Sussex are polymorphic for both chromosome number and the presence of inversions in two chromosome pairs (Page unpublished). Details of the present surveys are given in Section 2.3.

In view of the problems involved in the identification of specific chromosome pairs of similar size and shape (see part 1 Section 2.7). It was decided, prior to the main investigation, to review the methods of chromosome analysis previously used by the author for the 2n = 26 karyotypes of Nucella lapillus.

The presence of inversion polymorphisms in two chromosome pairs gives the possibility of nine different arrangements in the 2n = 26 karyotype (see Table 1). The acrocentric form of the inversion in the smaller of the two pairs occurs frequently in both the homozygous and heterozygous form but the submetacentric form of the larger chromosome pair is absent in many populations and rare when it is present.

The most common arrangement in the majority of areas sampled by the author is one in which both chromosome pairs involved in the inversion polymorphisms are metacentric.

Four of the nine possible arrangements of the 2n = 26 karyotype are present in Nucella lapillus from Rottingdean, Sussex. The data from a combination of the four arrangements give information on the size and centromere position of both chromosome pairs involved in the inversion polymorphism.

Two representative karyotypes for each arrangement were measured and analysed using the methods described in Part 1 Section 2). It was obvious, even before the karyotypes were measured, that certain chromosome pairs were of similar size and centromere position. This was confirmed by the analysis of the measurement data which show that certain chromosome pairs overlap in both R value and relative length (e.g. Table 2). It therefore follows that although familiarity with the material makes it easy to arrange the chromosomes, exact homologues may not always be paired. This in turn leads to the difficulties in the accurate identification of the chromosomes involved in both the numerical and inversion polymorphism. The problem can be overcome in part, by dividing the chromosomes of the karyotype into groups of similar size and centromere position as follows:-

Group A: chromosome pairs 1 to 4
Group B: chromosome pairs 5 and 6
Group C: chromosome pairs 7 to 10
Group D: chromosome pair 11
Group E: chromosome pairs 12 and 13

In this particular arrangement of the karyotype the two inversions, previously attributed to the specific chromosome pairs four and eight or nine, now occur in groups A and C respectively.

Representative karyotypes for the four arrangements found at Rottingdean are given in Plates 1 to 4. The mean R values and relative lengths (RL) for each chromosome "pair" are also given in Tables 2 to 5.

2.2. The identification of the chromosome pairs involved in the Robertsonian polymorphism.

The number of possible chromosome arrangements in a Robertsonian system with five chromosome pairs is 3^5 or 243. The number and nature of the possible arrangements for each chromosome number are given in Table 6. The presence of an inversion polymorphism in two additional chromosome pairs (assumed at this stage not to be those involved in the numerical variation)

gives an additional eight rearrangements to each of the original karyotypes (3^7 or 2187 in total). In consequence, even for the low chromosome number of 2n = 27 there are forty five possible arrangements of the karyotype. (see also Table 6). This extreme variability presents problems in the identification of inversion polymorphisms, particularly in the C group, but the chromosomes involved in the Robertsonian variation are easier to detect.

Mitosis from several polymorphic populations in Britain were used to determine the five chromosome pairs involved in the Robertsonian variation. The karyotypes were arranged in groups A to E. Numerical heterozygotes are detectable by the presence of an "odd" metacentric or submetacentric chromosome belonging to one of the five chromosome groups, plus an additional two acrocentric or submetacentric chromosomes not found in the 2n = 26 karyotype. Comparisons of chromosome measurements (R and RL) of specific chromosome pairs between karyotypes is not possible because exact homologies cannot be determined. The relative lengths and R values may, however, provide useful information for the arrangement and analysis of individual karyomorphs and so help to identify the chromosome pairs involved in the numerical polymorphism. Where appropriate both visual and measurement data were used to analyse the karyotypes.

2.3. The investigation of the distribution of the numerical and inversion polymorphisms at Rottingdean and Cuckmere Haven.

a. The populations used in the study.

The two areas selected for the investigation of the distribution of the numerical and inversion polymorphisms are situated on a coastal region of S.E. England along which populations of Nucella lapillus are usually monomorphic for the 2n = 26 form, irrespective of the degree of exposure of the foreshore. Both areas in the present investigation,

however are polymorphic for chromosome number and the presence of inversions in the chromosomes of groups A and C.

(i) The first area, Rottingdean (Grid ref. 020375) is situated on the chalk cliffed coastline of Sussex which runs almost continuously from Eastbourne to Brighton (Fig. 1). The cliffs are brick and concrete faced in this area and a series of groynes extend into the sea at regular intervals. A stretch of beach, approximately 150 m., in width, between two groynes was selected as representative of the area. The upper and lower limits of N. lapillus were marked and a transect of ten by ten metre squares, numbered from west to east was marked out at 40 metres below the upper limit of this species (Fig. 2).

There have been several attempts to standardize the methods of estimating the degree of exposure of shorelines(e.g. Ballantine 1961). The methods, for the most part, are not applicable to the soft chalk shoreline in this area where many of the indicator species are absent irrespective of the exposure of the site. (Bantock and Cockayne 1975). The estimation of exposure of the survey area was therefore made on a purely subjective basis. In comparison with other sites along the coastline this area was considered to be intermediate for exposure. Sites such as Beachy Head and Seaford Haven are exposed and New Haven Bay and Eastbourne are sheltered. The mean tidal range is large (14.70 metres) compared with 7.5 metres at Cuckmere Haven and an average of 3.5 metres between Brighton and New Haven (Reed 1977). Tidal currents in the area are weak, except at the mainheadlands, and in conjunction with tidal stream give an average tidal flow of 0.70 knots (maximum 1 knot and minimum 0.25 knots) in both ebb and flood tides in spite of the prevailing south westerly winds.

Chromosome number in the area varies from 2n = 26 to 2n = 28. Both inversion polymorphisms are present

but the acrocentric form of the group A inversion is rare.

(ii) The second area; Cuckmere Haven (Grid ref. 985 515) is situated approximately 15 kilometres east of Rottingdean (see Fig. 1). The area has been previously sampled by Bantock and Cockayne 1975 and Bantock and Page 1976). Chromosome number varies from 2n = 26 to 2n = 30, both inversions are present in the 2n = 26 form but, the submetacentric form of the group A inversion is rare. In contrast to the rather uniform coastline at Rottingdean, this area shows varying degrees of exposure of the foreshore. Two ten metre square sampling areas were made at 100 metre intervals along a transect running for approximately 500 metres below the upper limit of Nucella lapillus. The position of the transect was placed to reflect differences in exposure of the collecting sites which varies from sheltered at the mouth of the River Cuckmere to exposed on the extreme western head of the bay. (Fig. 3.)

(b) Sampling and Culture Methods.

Where possible egg capsules were collected from each ten metre square. N. lapillus females tend to congregate in sheltered crevices for egg laying so that up to twenty adults can be found at any one egg laying site. It is not possible, therefore, to distinguish separate egg clutches. The capsules are very firmly attached to the substrate and in both areas it is impossible to remove them from the rock without damage to the embryos. In most cases a small section of chalk was chisled out with the egg capsule mass. Care was taken to select recently laid capsules which contain a mass of yolky eggs (Fig. 4a). In later stages of development (Fig. 4c and d) distinct embryos are clearly visible and are not suitable for chromosome preparation. Five to twelve samples were collected from each ten metre square depending on the abundance of Nucella in the area. Each sample was at least one metre from any other to reduce the possibility of repeated sampling of egg capsules laid by the same adult.

The capsules were placed in plastic bags to reduce dehydration, in transit, and returned to the laboratory where they were maintained at 5°C in aerated sea water.

c. Cytological Methods.

Embryonic development is far slower in Nucella lapillus than in C. nemoralis. It can take up to four months for the fully formed juveniles to hatch. Newly laid egg capsules contain a large number of yolky eggs (Colton 1916, Pelseneer 1935) many of which are not fertilised but act as nutrient of "nurse eggs" to the developing embryos. Development is arrested from four to six weeks while the eggs are injested. (Fig. 4a-b). When this is complete small embryos can be seen floating freely within the capsule (Fig. 4c). At this stage (Fig. 5c), the embryos are suitable for chromosome preparation.

The chromosome preparation technique is as follows:-

(i) Five to six egg capsules were slit open and the embryos washed in filtered sea water.

(ii) The nutrient egg mass and shell were removed and the remaining tissue transferred to a watch glass.

(iii) The watchglass containing the disected embryos was filled with 0.005% aqueous colchicine and left for 15 minutes.

(iv) The colchicine/tissue mixture was transferred to a $5mm^3$ glass centrifuge tube and spun at 1000 r.p.m. for 2 minutes. The supernatant was removed.

(v) The remaining pellet was resuspended in 3: 1 Methanol and glacial acetic acid fixative and agitated using a rotamix.

(vi) The fixative was changed three times.

(vii) The cell pellet was resuspended in fresh fixative and left to stand at room temperature for 30 minutes; spun down and the tissue pellet resuspended in 45% acetic acid.

(viii) Heat dried slides were made on a hot plate. (40°C).

(ix) The slides were allowed to cool and were stored at room temperature in slide boxes.

Staining technique.

The slides were stained in a 2% solution of Giemsa (G.T.Gurr) in phosphate buffer p H. 6.8 for 2 minutes. The slides were rinsed in buffer soaked in michrome essence and mounted in michrome.

Slide preparations from each sampling site were scanned using a Ziess photo-microscope mark 111 and clear well defined metaphases were counted and scored, where possible, for the presence of the metacentric and acrocentric forms of each inversion.

d. Karyotypes and karyotype analysis.

Photographic prints from several 2n = 26 and 2n = 30 mitosis were karyotyped using the methods described in Part 1 Section 2. Each chromosome from every karyotype was measured using Jocal digital calipers. The relative length and R value were calculated using the methods described in Part 1 Section 2.5.).

2. 3e. <u>The analysis of variation within and between sampling areas</u>.

The statistical analysis of the differences in both chromosome number and structure between sampling areas is not easy. The predominant chromosome number at both Rottingdean and Cuckmere Haven is 26 in which both inversion polymorphisms are homozygous for the metacentric form. In consequence the frequency of the rarer karyotypes are normally insufficient to complete the usual statistical tests, for example, to test departures from the Hardy Wienberg equilibrium or to test differences in the distribution of homozygotes and heterozygotes from different sample areas.

The situation is further complicated by the fact that at Cuckmere Haven it is not always possible to identify the presence of the group C inversion in the karyotypes of chromosome number greater than 2n = 26. The accurate distribution of the inversion, therefore, cannot be determined. Nor is it possible to identify the specific chromosome pairs involved in the numerical polymorphism, consequently the relative frequencies of the specific homozygotes and heterozygotes in the range 2n = 26 to 2n = 30 cannot be estimated.

Chromosome analysis was therefore restricted to:-

1. Variation within sampling areas.

Variation in chromosome number, at Cuckmere Haven and chromosome number and structure, at Rottingdean between the sampling sites from each area were tested using the Kruskal-Wallis one way analysis of variance (see Part 1 Section 2).Where appropriate the data from each sampling site within the area were used to calculate

(i) The expected frequencies of chromosome number.

(ii) The expected frequencies of homozygotes and heterozygotes for each inversion for each chromosome number.

(iii) The frequency of the metacentric (A) form and the acrocentric of submetacentric (B) forms of both inversions for each chromosome number.

2. Variation between sampling areas.

Variation in chromosome structure and number between sampling areas at both Rottingdean and Cuckmere Haven were tested using the Kruskal-Wallis one way analysis of variance.

In addition, where possible, differences in the distribution of the metacentric (A) and acrocentric or submetacentric (B) forms of the inversion for each chromosome number and for each area as a whole were tested using the log likelihood ratio (G test).

In the absence of significant differences in the above tests, the data from each sampling area were pooled to give the overall distribution in chromosome number and structure for each region. Differences in the proportions of homozygotes and heterozygotes for each chromosome number can be tested using the χ^2 statistic (Siegel 1956). The low frequency of rare chromosomal arrangements in the present investigation usually makes the results of this test invalid and in these circumstances the non-parametric Kruskal Wallis analysis of variance may be used.

Differences between the observed and expected frequencies for both chromosome number and the group C inversion polymorphism were tested, where possible, using χ^2 (Siegel loc cit).

3. RESULTS

3.1. The identification of the chromosome pairs involved in the inversion polymorphism.

3.2. The identification of the chromosome pairs involved in the Robertsonian polymorphism.

3.3. The investigation of the distribution of the numerical and structural polymorphisms at Rottingdean and Cuckmere Haven.

a. Sample collection.
   (i) Rottingdean.
   (ii) Cuckmere Haven.
b. Slide preparation and metaphase analysis.
c. Karyotypes and karyotype analysis.
   (i) The 2n = 26 karyotype.
   (ii) The 2n = 27 karyotype.
   (iii)The 2n = 28 karyotype.
   (iv) The 2n = 29 and 2n = 30 karyotype.
d. The analysis of variation within and between sampling areas.
   (i) Within areas.
   (ii) Between areas.

3.4. The analysis of the chromosomes pairs involved in the Robertsonian polymorphism in populations from Cuckmere Haven and Rottingdean, Sussex.

3. RESULTS

3.1. The results of the identification of the chromosome pairs involved in the inversion polymorphism.

The results of this investigation are given in detail in section 2.1. The results demonstrate that the specific chromosome pairs involved in the inversion polymorphism cannot be identified. In consequence, the inversions can be identified only by reference to the group in which they occur. The largest of the two chromosome pairs involved in the inversion polymorphism is from group A and the smaller occurs in group C.

3.2. The identification of the chromosome pairs involved in the Robertsonian polymorphism.

Karyotypes from the following populations were used in the analysis.

Cuckmere Haven	Grid ref: 985 515 Sussex
Isle of Cumbrae	Grid ref: 170 540 Fyrth of Clyde
St. Brides Haven	Grid ref: 110 802 Pembrokeshire
Castlebeach Bay	Grid ref: 048 819 Pembrokeshire
Osmington Mills	Grid ref: 743 735 Dorset
Lulworth Cove	Grid ref: 728 829 Dorset

All the populations were polymorphic for chromosome number with the exception of Lulworth Cove which was monomorphic for 2n = 36.

The chromosomes in each karyotype were rearranged in five chromosome groups A to E. The metacentrics, submetacentrics, acrocentrics or telocentrics thought to contribute to the polymorphism were placed below the other chromosomes in the appropriate group. The absolute and relative measurements for each karyotype measured are given in full in Appendix B. The relative measurements for specific chromosome pairs, where necessary are given with the karyotype plates.

Measurement data and visual arrangement of the 2n = 27 karyotypes from Cuckmere Haven and the Isle of Cumbrae indicate that the unpaired metacentric is from group A. The exact identification of the

chromosome is not possible, however, the two additional chromosomes found in both areas are not always the same in each karyotype(see Plates 8 and 9) suggesting that two different chromosome pairs from group A are involved in the numerical polymorphism.

The two karyotypes also highlight the difficulties in distinguishing the acrocentric form of the group C inversion from the chromosomes involved in the numerical polymorphism. In both karyotypes one (8) or two (9) of the additional chromosomes are indistinguishable from the acrocentric form of the inversion in group C. In other karyotypes (Plates 10 to 11) the inversion is easily detected in the heterozygous (10) and homozygous (acrocentric) state. (11). In addition some of the chromosomes involved in the numerical polymorphism appear to have substantial short arms, so that, for example in Plate 8 one of the additional chromosomes; 2.50 (RL) and 0.33 (R) is indistinguishable from the other submetacentrics in group C.

Several arrangements of the 2n = 28 karyotype are presented in Plates 12, 13 and 14. Plates 12 and 13 suggest in conjunction with the 2n = 27 karyotypes that two different chromosome pairs from group A contribute to the numerical polymorphism. Plate 14 shows a karyotype in which one of the polymorphic group A chromosomes is represented by two submeta-centric and two acrocentric chromosomes.

Plates 15 to 20 indicate the involvement of two different chromosome pairs in the Robertsonian variation. One pair in group B (plates 15 to 17) and the other in group C (plates 18 to 20). In plates 21 (2n = 32), 22 (2n = 32), 23 (2n = 33) and 24 (2n = 30) chromosomes pairs from groups A, B and C all contribute to the numerical polymorphism.

Karyotypes from Osmington Mills and Lulworth Cove (both from the Dorset coast) show high chromosome numbers. Plate 25 (2n = 34) from Osmington and plate 26 (2n = 36) from Lulworth Cove (rearranged from Bantock and Cockayne 1975) suggest that the

"fifth" chromosome pair involved in the numerical polymorphism is also from group C.

The re-arrangement of the 2n=26 karyotype given in plate 27 shows the five chromosome pairs most likely to contribute to the numerical polymorphism.

3.3. The investigation of the distribution of the numerical and structural polymorphisms at Rottingdean and Cuckmere Haven.

a. Sample collection

(i) Rottingdean

The distribution of N. lapillus at Rottingdean is not uniform. Several of the fifteen possible sampling sites contained few or no Nucella adults. In sampling areas 3,4,6,8,9,10,11 and 14 no egg capsules were found (Fig. 2). The absence extended to the adjacent areas above and below the sampling square. In most of these areas in particular 8,9, 10 and 11 a fine silt covers the underlying chalk substrate. Several of the beaches in this area have patches of fine silt, deposited since the extensive construction of the Brighton Marina approximately 12 km. west of Rottingdean. Local information from piddock collectors, suggest that, prior to the construction work at Brighton, the beaches in the Rottingdean area were entirely rocky in the intertidal region. It is probable that the isolation of sampling areas 5 and 7 and the complete absence of Nucella from sampling areas 8 to 11 is recent and only temporary. The number of samples collected from each area are given below.

Area	Samples collected
1	10
2	10
5	5
7	6
12	8
13	11
15	2

(ii) Cuckmere Haven

Adult N. lapillus were found in all the sampling squares but egg capsules were found only in eight of the ten squares. The remaining two squares 9 and 10 (see Fig. 3) represent the most exposed section of the transect and probably provide all but a few suitable sites for egg laying. The number of samples collected from each square are given below.

Area	Samples collected
1	5
2	10
3	3
4	3
5	5
6	5
7	5
8	5

b. Slide preparation and metaphase analysis.

The number of slides prepared for each sample and the origin of each metaphase analysed are given in Appendix B. At Rottingdean all the sampling squares provided material suitable for chromosome analysis. At Cuckmere Haven, however, only six of the eight sampling squares provided suitable material.

c. Karyotypes and karyotype analysis.

(i) The 2n = 26 karyotype.

Five of the nine possible arrangements of the 2n = 26 karyotype were found at Cuckmere Haven and only four at Rottingdean. This was due to the rarity of the submetacentric form of the group A inversion. Two heterozygotes for this inversion were found at Rottingdean and one homozygote and one heterozygote were found at Cuckmere Haven. Representative karyotypes for each of the five arrangements are given in Plates 1 to 5.

(ii) The 2n = 27 karyotype.

Only one arrangement of the forty five possible arrangements of the 2n = 27 karyotype was found at Rottingdean. In all individuals both inversions (from group A and group C) were homozygous for the metacentric form and the chromosome pair involved

in the numerical polymorphism was from group C. The two additional chromosomes involved in the numerical polymorphism are small and unequal in size. The larger of these has very small short arms (acrocentric) and in some preparations no arms are visible at all. (telocentric). The smaller chromosome is metacentric or submetacentric. A representative karyotype is presented in Plate 6.

In contrast to the Rottingdean area several of the 2n = 27 karyotype were found at Cuckmere Haven. In all individuals the chromosomes involved in the numerical variation are from group A. The acrocentric form of the group C inversion occurs in several karyotypes. It is not always possible, however, to identify the inversion because of the similarity in size and shape of the inverted chromosomes and those involved in the numerical polymorphism. (see also Part 11 section 2.1.) and Plates 8,9 and 10.

In both areas all 2n = 27 individuals were homozygous for the metacentric form of the group A inversion.

(iii) The 2n = 28 karyotype.

Only one arrangement of the 2n = 28 karyotype was found at Rottingdean. In this arrangement the chromosome pair involved in the numerical polymorphism was from group C and the group C inversion was homozygous for the metacentric form. A representative karyotype is presented in Plate 7.

Several 2n = 28 karyotypes were present at Cuckmere Haven. In some instances the acrocentric form of the group C inversion could be identified whilst in others it could not. Two typical karyotypes are presented in Plates 13 and 14.

(iv) The 2n = 29 and 2n = 30 karyotypes

One 2n = 29 and three 2n = 30 individuals were present at Cuckmere Haven. In all four karyotypes from these individuals the chromosome or chromosomes

involved in the numerical variation were from group A. A representative karyotype of the 2n = 30 arrangement is given in Plate 18.

The relative length and R value for the photographic Plates are given in Appendix B.

d. The analysis of variation within and between sampling areas.

(i) Analysis of variation within sampling areas.

Variations in chromosome number (Cuckmere Haven) and in chromosome number and structure (Rottingdean) between clutches within a sampling square were tested using the Kruskal-Wallis test. The results, given in Tables 7 and 8 were consistently non-significant and suggest that there are no appreciable differences between the clutches. The data from each clutch were pooled and used as follows:-

(ii) Analysis of variation between the sampling areas.

The chromosome number (Cuckmere Haven) and the chromosome number and structure (Rottingdean) for each sampling square are given in Tables 9 and 10.

Only two of the 164 individuals analysed at Rottingdean possessed the acrocentric form of the group A inversion. One was located in sampling square five and the other in sampling square thirteen. In view of the rarity of this inversion polymorphism it was omitted from any further analysis.

The observed and expected frequencies of homozygotes and heterozygotes for chromosome number and the group C inversion are given in Tables 11 and 12.

Departures from the Hardy-Wienberg equilibrium are usually detected using the χ^2 statistic. The expected frequencies of the rarer homozygotes for both chromosome number and the group C inversion, however, are less than one so that in order to validate the test, adjacent categories must be

combined until the expected frequency is equal to or greater than one. (Snedecor and Cochran 1969). In both cases the combination of chromosome numbers 27 and 28 or the inversion types AB and BB meet the requirement of the statistical test but results in the loss of useful information as regards the polymorphisms.

The differences in the observed and expected frequency of the heterozygotes for chromosome number 2n = 27 are small. The observed frequencies are slightly more than expected in five of the six areas. The deviations of the expected frequencies are probably insufficient to represent a significant deviation from the observed values.

In contrast the observed numbers of heterozygotes (AB) for the group C inversion for both chromosome number 2n = 26 and 2n = 26 to 2n = 28 are less than expected and are accompanied by greater than expected frequencies in both homozygous types in five of the seven areas. In the two remaining areas, one and fifteen, the observed frequencies are slightly above expectation. It is of interest to note that both these sampling areas are adjacent to groynes (Fig. 2) which may provide local protection. The magnitude of the deviations in the two areas, however is far less than those showing a deficiency of heterozygotes.

Variations in chromosome number (Cuckmere Haven) and chromosome number and structure (Rottingdean) were tested using the Kruskal-Wallis one way analysis of variance. $(H_{(5)} = 9.343\ (0.1 > P > 0.05)$ for Cuckmere Haven. This result suggests that there is little variation in chromosome number between the populations in the Cuckmere Haven area, irrespective of the varying degrees of exposure of the sampling sites.

The result of the Kruskal-Wallis analysis of variation in chromosome number and structure for

Rottingdean $H_{(6)} = 5.201$ ($0.97 > P > 0.5$) is not significant. Variations within five of the sampling squares are less than those between them whereas in squares five and twelve the variation within is slightly greater. In all cases the differences are not significant.

The frequencies of homo and heterozygotes for the group C inversion are given in Table 13. In all the sampling areas for each chromosome number the metacentric (AA) homozygote is the most common form. The frequencies of the heterozygote (AB) and the other homozygote (BB) are substantially less in the 2n = 26 form and totally absent from 2n = 27 and 2n = 28 individuals.

Statistical comparisons of the frequencies (using χ^2 based methods e.g. the G test) are not possible because more than twenty per cent of the expected cell frequencies in the contingency tables are less than 5. (Siegel 1956). It is possible however to compare the frequencies of the metacentric (A) and acrocentric (B) form of the inversions between sampling areas. The frequencies for each type are given in Table 14. Comparisons of both chromosome number 2n = 26; $G_{(6)} = 11.232$ ($0.1 > P > 0.05$) and 2n = 26 to 2n = 28 $G_{(6)} = 8.937$ ($0.5 > P > 0.1$) suggest there are no significant differences in the proportions of the two inversion types between the sampling squares.

This test gives no information on the distribution of the inversion types in either the homozygous or heterozygous form but this result in conjunction with the Kruskal-Wallis analysis suggests that there are no significant differences in chromosome number or structure between the seven sampling squares.

The data for each area at Rottingdean were therefore combined to give the overall frequencies of chromosome number; 2n = 26, 2n = 27 and 2n = 28.

The proportions of homozygotes (AA and BB) and the heterozygotes (AB) of the group C inversion for each chromosome number were compared using the Kruskal-Wallis one way analysis of variance. ($H_{(2)}$ = 2.403 $0.5 > P > 0.2$. This result indicates that there are no significant differences in the proportions of heterozygotes and homozygotes between chromosome numbers 2n = 26, 2n = 27 and 2n = 28 The test of independence could not be used in this instance because five of the nine expected frequencies are less than five. (see Table 15).

The observed and expected frequencies of the pooled data for chromosome number and for the group C are given in Tables 16A and 16B.

It is not possible to test the significance of deviations from the expected frequencies for each chromosome number (see also page 94). The small differences between the observed and expected frequencies, however, suggest that the populations of Nucella in this region are in Hardy-Wienberg equilibrium for chromosome number.

In contrast the comparison of the observed and expected frequencies for the group C inversion show a highly significant deficiency of heterozygotes accompanied by an increase in the proportions of both homozygous types for individuals of chromosome number 2 n = 26: $\chi^2_{(2)} = 24.779$ ($P < 0.001$) and for chromosome number 2n = 26 to 2n = 28. $\chi^2_{(2)} = 30.877$ ($P < 0.001$).

The fact that chromosome number is in genetic equilibrium but the inversion polymorphism, scored from the same sample of individuals is not, suggests that the two chromosomal polymorphisms occur independently of each other.

The implications of these results are discussed in section 4.

The information from sections 3.2. and 3.3. suggest that the chromosome pairs involved in the Robertsonian variation at Rottingdean and Cuckmere

Haven are different and are restricted to one or two chromosome pairs. The investigation of polymorphic populations from the coast of France, however, have revealed that, even in populations of low chromosome number, all five of the chromosome pairs involved in the numerical variation may be polymorphic (Staiger 1954). In view of the possible differences in the distribution of the chromosomes involved in the Robertsonian polymorphism between different regions, the data from Rottingdean and Cuckmere Haven were analysed as follows:-

3.4. The analysis of the chromosome pairs involved in the Robertsonian polymorphism in populations from Cuckmere Haven and Rottingdean, Sussex.

The results from section 3.2. indicate that the five chromosome pairs involved in the Robertsonian polymorphism are as follows:- Two from group A, one from group B and two from group C (see Plate 27). In most mitotic metaphases it is not possible to distinguish the specific chromosome pairs involved in the polymorphism within the groups. In some metaphases, however, it is obvious from the differences in size and centromere position of both the odd metacentric and the four additional acrocentrics that two different chromosome pairs contribute to the polymorphism (e.g. Plates 12 and 13).

The chromosome pairs involved in the Robertsonian variation at Cuckmere Haven and Rottingdean were scored as follows:-

Metaphases with one chromosome pair involved in the polymorphism were scored $A_{(1)}$ $B_{(1)}$ or $C_{(1)}$ depending upon in which group the odd metacentric or lack of metacentrics occurs. For example Plate 8 would be scored 26 (for chromosome number) $A_{(1)}$ and Plate 17 would be scored 30 $A_{(1)}$ $B_{(1)}$. In cells where two chromosome pairs were distinguishable within a group the scoring was as follows:-

Metaphases with one chromosome pair involved in the polymorphism were scored $A_{(1)}$ $B_{(1)}$ or $C_{(1)}$ depending upon in which group the odd metacentric or lack of metacentrics occurs. For example Plate 8 would be scored 26 (for chromosome number) $A_{(1)}$ and Plate 17 would be scored 30 $A_{(1)}$ $B_{(1)}$. In cells where two chromosome pairs were distinguishable within a group the scoring was as follows:- $A_{(2)}$ or $C_{(2)}$. For example Plate 15; 29 $A_{(2)}$ $B_{(1)}$ and for Plate 25; 34, $A_{(2)}$ $B_{(1)}$ $C_{(2)}$. Each cell of chromosome number greater than 2 = 26 from the original analysis of the numerical and structural variation between the areas was scored using the method described above.

Details of chromosome number and the chromosome pairs involved in the numerical polymorphism are given in Appendix B and summarized (for both areas) in Tables 17 and 18.

The results show that, without exception

(1) Only one chromosome pair from group C is involved in the numerical polymorphism at Rottingdean.

(ii) Two different chromosome pairs, both from group A, are involved in the numerical polymorphism at Cuckmere Haven.

The differences between the two areas with respect to the chromosome pairs involved in the Robertsonian polymorphism are discussed in section 4.

Fig. 1. A map of the S.E. coast of England to show the location of the two sampling areas at Rottingdean, Sussex and Cuckmere Haven, Sussex.

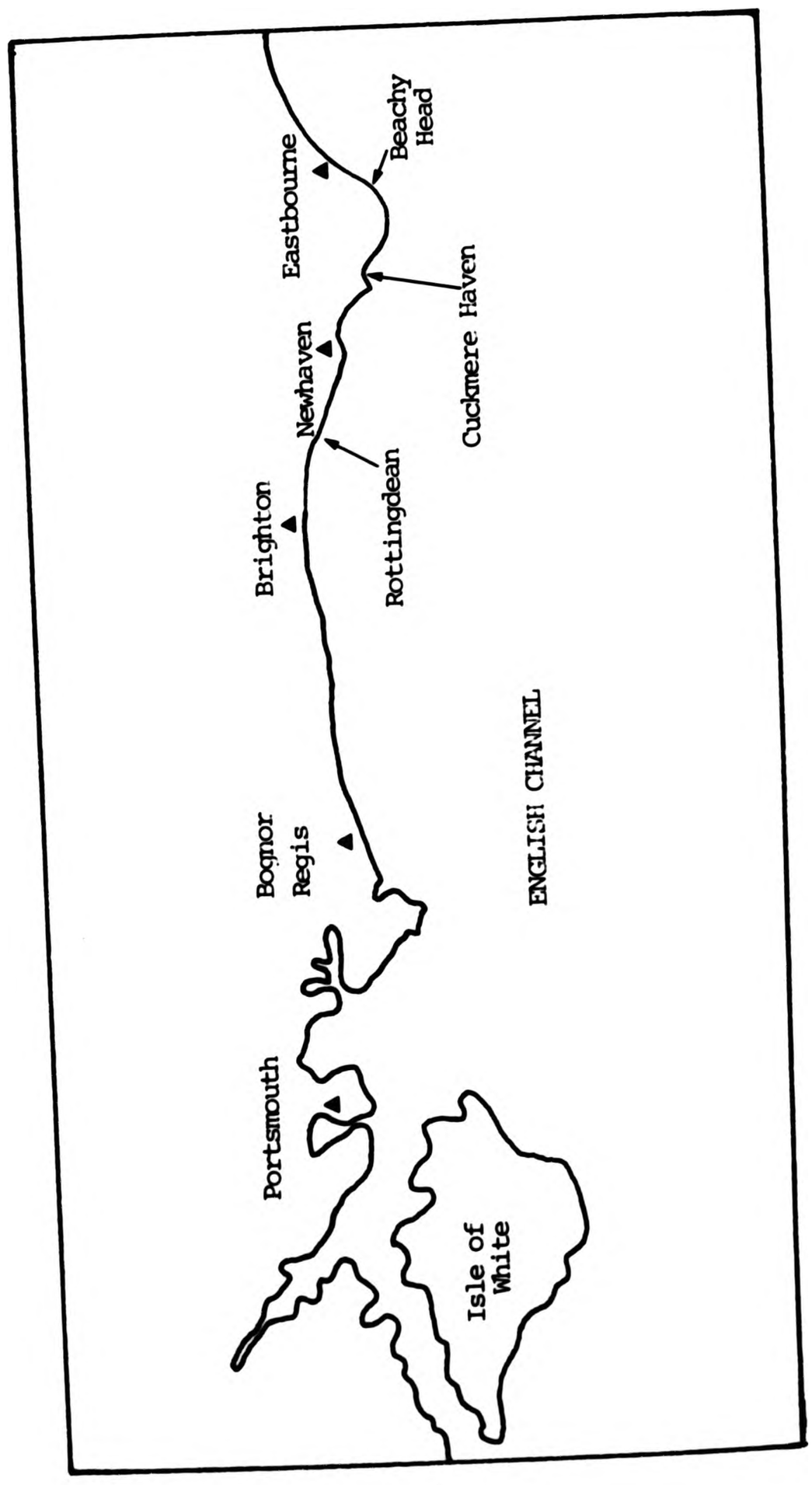


Fig. 2. A map of the sampling area at Rottingdean, Sussex to show the position of the transect.

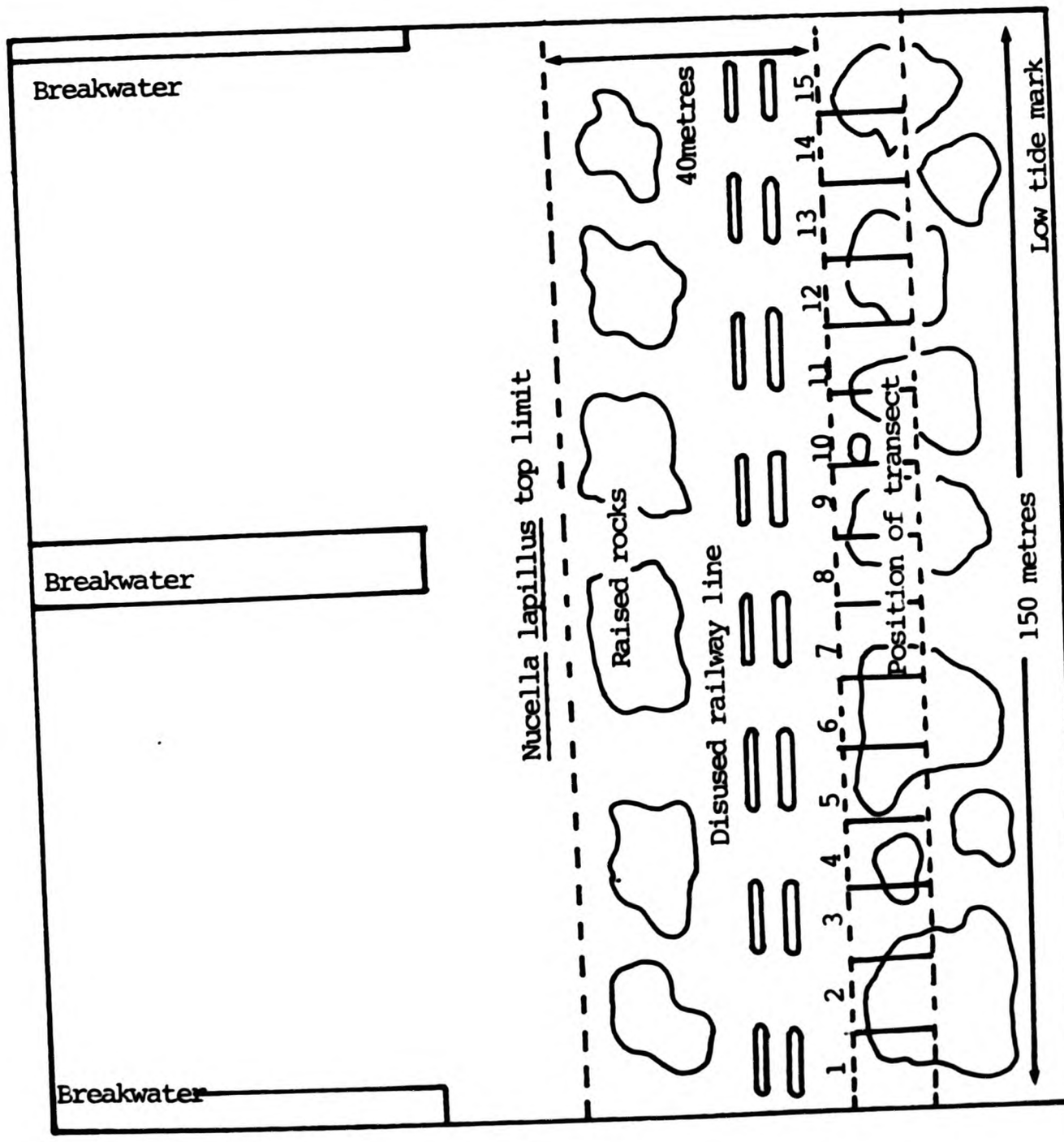


Fig. 3. A map of the sampling area at Cuckmere Haven, Sussex to show the position of the transect.

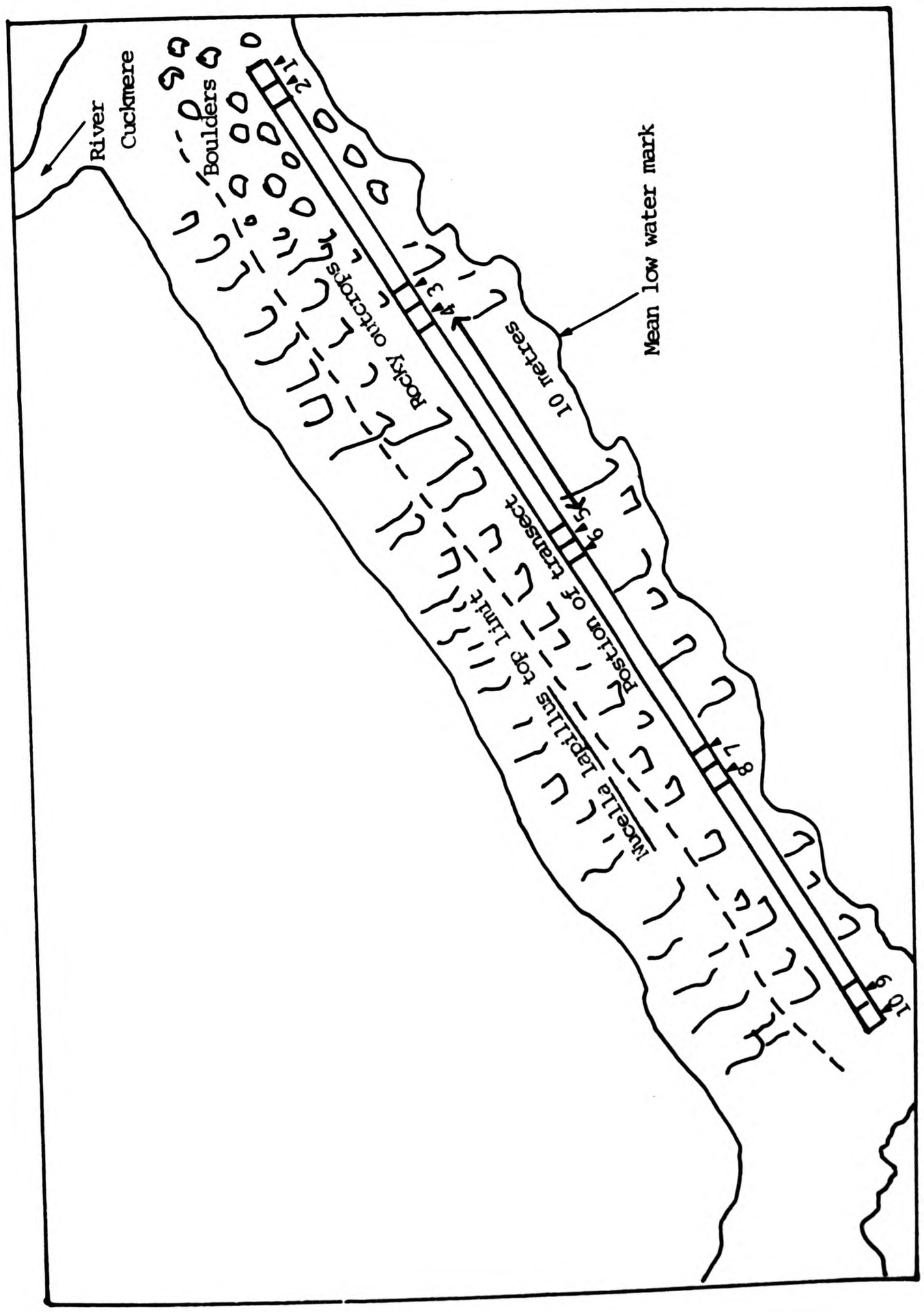
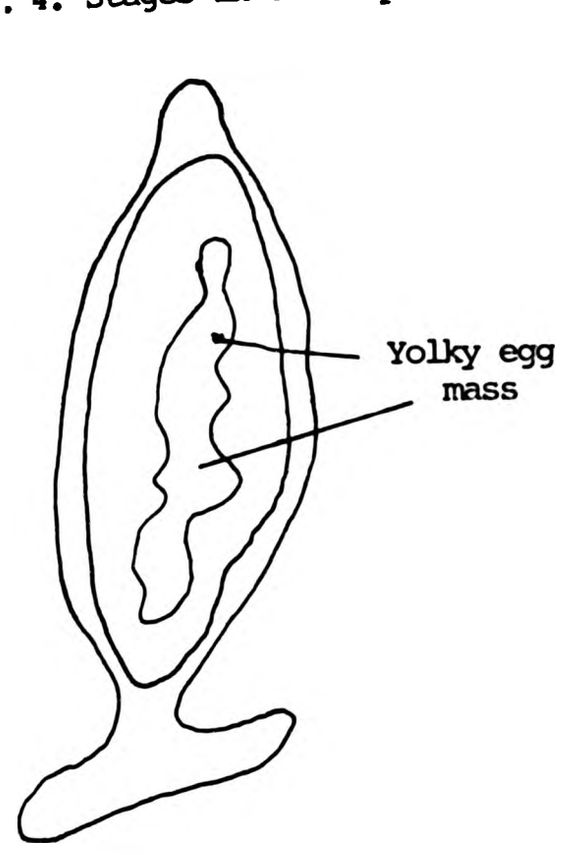
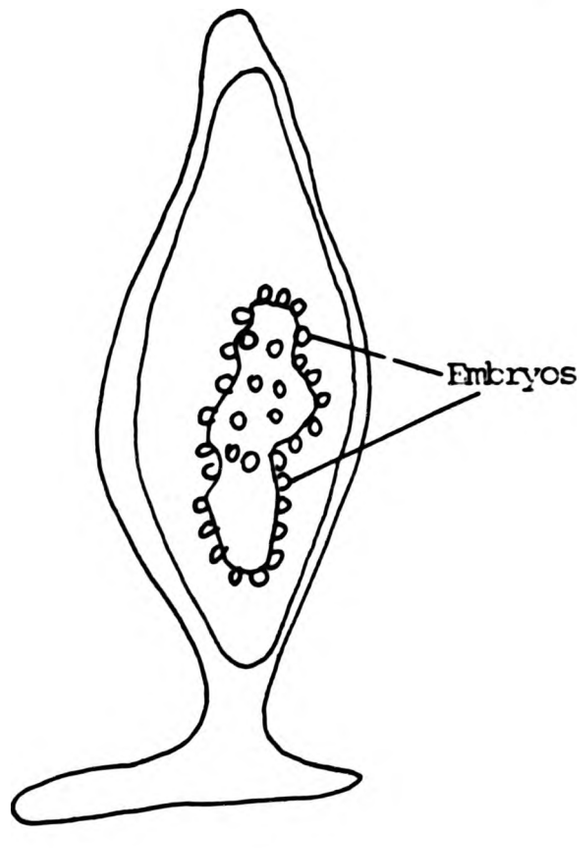


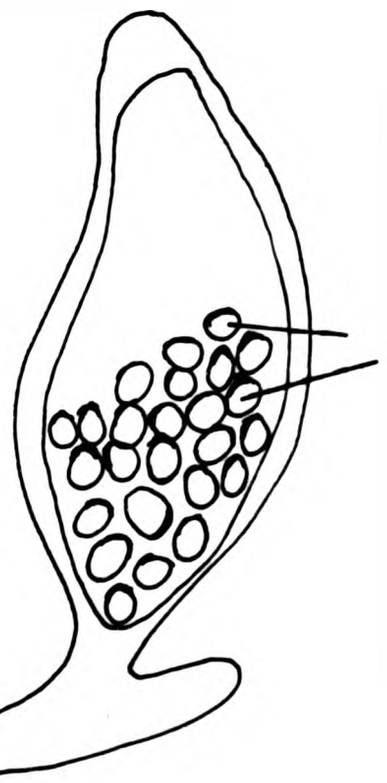
Fig. 4. Stages in developement of the egg capsules of Nucella lapillus.



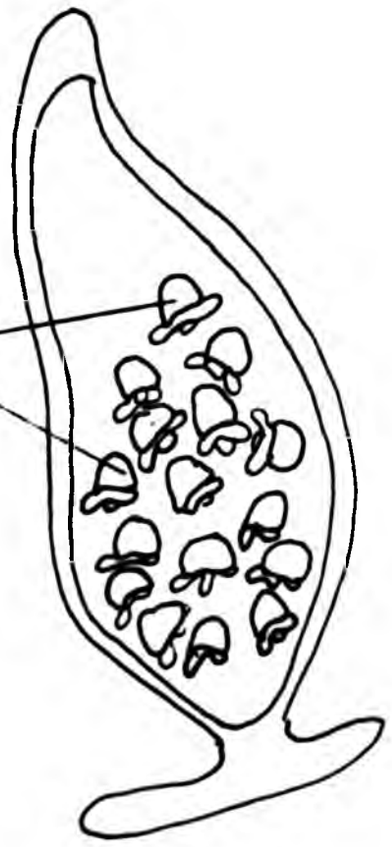
4a.



4b.



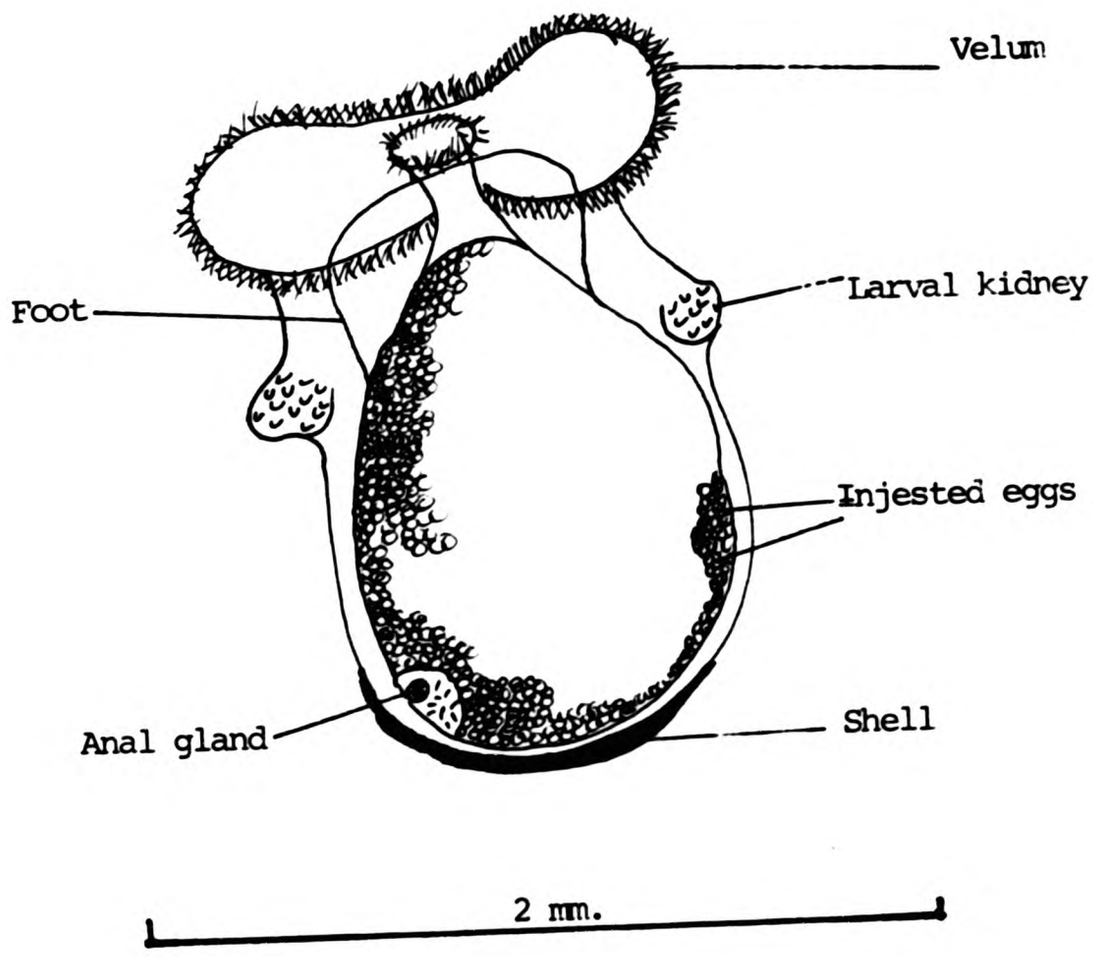
4c.



4d.

Fig. 5. Stages in the developement of the embyo of Nucella lapillus.

Stage c.



Stage d.

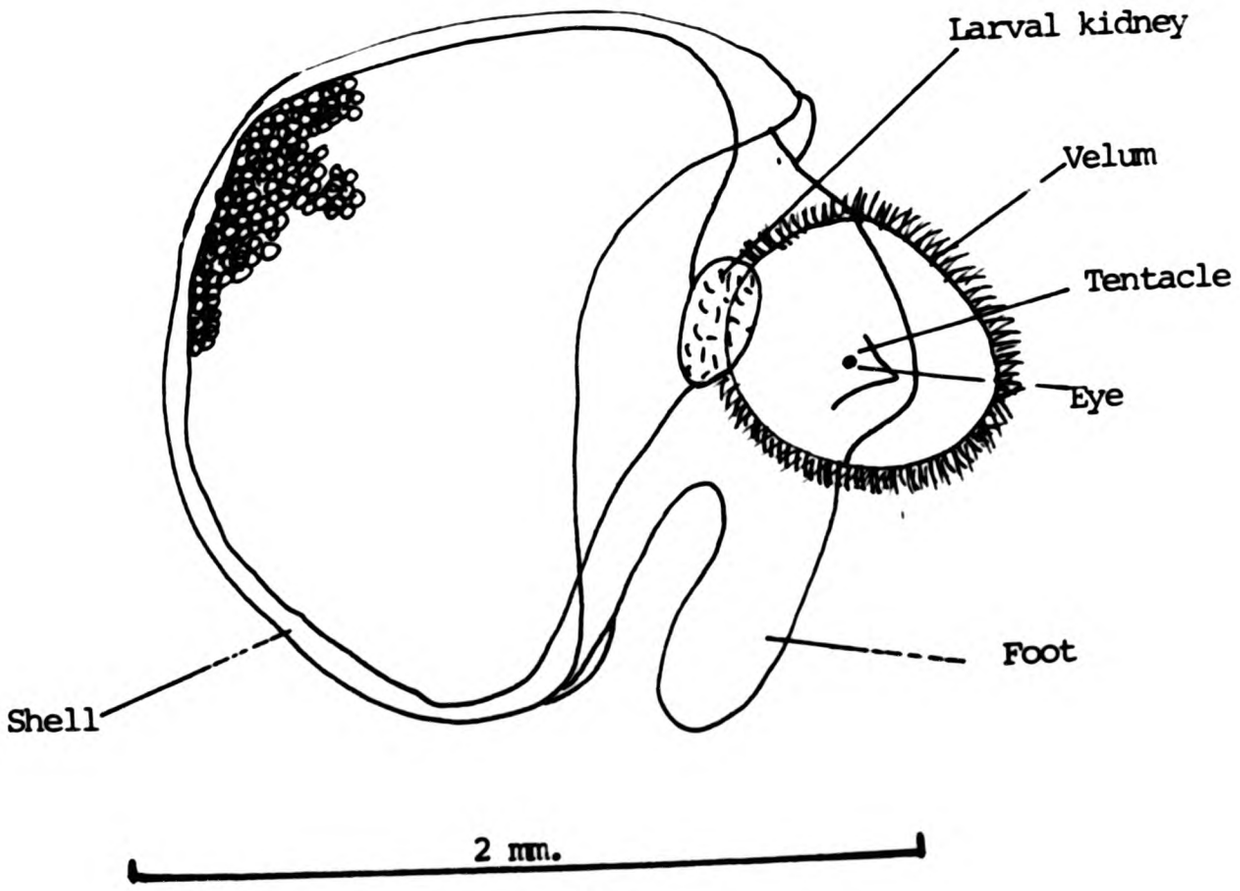


Table 1. The nine possible arrangements of the 2n = 26 karyotype with inversion polymorphisms in two chromosome pairs.

Inversion in chromosome pair 9 (Group A)	Inversion in chromosome pair 8 or 9 (Group C)	
MM	MM	*
MM	MA	*
MM	AA	*
M SM	MM	
M SM	MA	
M SM	AA	*
SM SM	MM	
SM SM	MA	
SM SM	AA	

M metacentric
SM submetacentric
A acrocentric

* Karyotypes found at Rottingdean, Sussex.

Table 2. The Mean and Standard deviation (SD) for relative length and R value from 2n = 26 karyotypes from Rottingdean,Sussex. The chromosomes involved in the group C inversion are homozygous for the metacentric arrangement.

Chromosome pair	Length		R value		Chromosome type	Group
	Mean	SD	Mean	SD		
1	7.12	0.40	0.79	0.07	M	
2	5.88	0.35	0.87	0.04	M	A
3	5.76	0.31	0.60	0.07	SM	
4	5.10	0.27	0.70	0.13	M	
5	4.45	0.10	0.42	0.009	SM	B
6	3.82	0.29	0.40	0.03	SM	
7	3.52	0.45	0.63	0.15	M	
8	3.22	0.26	0.79	0.19	M	C
9	3.07	0.09	0.61	0.06	M	
10	2.69	0.10	0.65	0.05	M	
11	2.30	0.16	0.28	0.005	A	D
12	1.79	0.04	0.88	0.16	M	E
13	1.13	0.27	0.36	0.41	SM	

Table 3. The Mean and Standard deviation (SD) for the relative length and R value from 2n = 26 karyotypes from Rottingdean,Sussex. The chromsomes involved in the group C inversion are heterozygous.

Chromosome pair	Length		R value		Chromosome type	Group
	Mean	SD	Mean	SD		
1	7.20	0.39	0.74	0.17	M	
2	6.17	0.19	0.98	0.03	M	A
3	7.82	0.30	0.67	0.08	M	
4	5.41	0.30	0.62	0.09	M	
5	4.65	0.27	0.34	0.06	SM	B
6	3.64	0.16	0.35	0.04	SM	
7	3.27	0.21	0.80	0.15	M	
8	3.11	0.13	0.60	0.10	SM	
9	2.58	0.56	0.59	0.07	SM	
			0.25	0.03	A	C
10	2.91	0.56	0.81	0.15	M	
11	2.61	0.46	0.81	0.15	M	D
12	1.52	0.11	0.90	0.04	M	
13	1.04	0.18	0.43	0.30	SM	E

M Metcentric , SM submetacentric , A acrocentric.

Table 4. The Mean and Standard deviation (SD) for the relative length and R value from 2n = 26 karyotype from Rottingdean, Sussex. The chromosomes involved in the group C inversion are homozygous for the acrocentric arrangement.

Chromosome pair	Length		R value		Chromosome type	Group
	Mean	SD	Mean	SD		
1	6.36	0.47	0.77	0.10	M	
2	5.77	0.41	0.92	0.07	M	A
3	4.94	0.33	0.62	0.07	M	
4	4.49	0.21	0.62	0.07	M	
5	4.17	0.43	0.40	0.05	SM	B
6	3.64	0.27	0.37	0.02	SM	
7	3.14	0.29	0.56	0.05	SM	
8	3.11	0.34	0.80	0.04	M	
9	2.86	0.41	0.32	0.04	A	C
10	2.62	0.24	0.78	0.05	SM	
11	2.54	0.50	0.32	0.03	A	D
12	1.78	0.16	0.95	0.06	M	
13	1.25	0.17	0.51	0.34	SM	E

Table 5. The Mean and Standard deviation (SD) for the relative length and R value from 2n = 26 karyotypes from Rottingdean,Sussex. The chromosomes involved in the group A inversion are heterozygous and the group C inversion is homozygous for the acrocentric arrangement.

Chromosome pair	Length		R value		Chromosome type	Group
	Mean	SD	Mean	SD		
1	6.51	0.38	0.82	0.08	M	
2	5.95	0.28	0.85	0.16	M	A
3	5.57	0.18	0.67	0.06	M	
4	5.44	0.43	0.78	0.15	M	
			0.37	0.06	SM	
5	4.36	0.21	0.43	0.04	SM	B
6	3.51	0.32	0.43	0.05	SM	
7	3.71	0.24	0.78	0.09	M	
8	3.01	0.11	0.62	0.09	M	C
9	3.16	0.28	0.29	0.04	A	
10	2.71	0.15	0.73	0.10	M	
11	2.58	0.25	0.32	0.02	A	D
12	1.99	0.17	0.81	0.10	m	E
13	1.26	0.26	0.51	0.34	SM	

Table 6. The number and structure of the possible arrangements of the five chromosome pairs involved in the Robertsonian variation in Nucella lapillus.

Grand total : The number of arrangements when two additional chromosome pairs are involved in a structural(inversion)polymorphism.

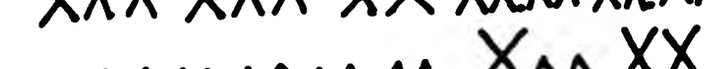
Chromosome number	Basic structure	no.	Total	Grand Total
26		1	1	9
27		5	5	45
28		5		
		10	15	135
29		10		
		25	35	315
30		10		
		5		
		25	40	360
31		25		
		1		
		25	51	459
32		10		
		5		
		25	40	360
33		25		
		10	35	315
34		5		
		10	15	135
35		5	5	45
36		1	1	9
		TOTAL	243	2187
			5	7
			3	3

Table 7. The results of the Kruskal Wallis analysis of variation within the sampling squares at Rottingdean,Sussex.

Sampling square					
1	$H_{(3)}$ = 2.207	0.9	P	0.5	ns
2	$H_{(7)}$ = 1.569	0.995	P	0.975	ns
5	$H_{(3)}$ = 3.542	0.5	P	0.1	ns
7	$H_{(4)}$ = 1.770	0.9	P	0.5	ns
12	$H_{(3)}$ = 5.887	0.5	P	0.1	ns
13	$H_{(8)}$ = 4.949	0.9	P	0.5	ns
15	$H_{(1)}$ = 0.068	0.9	P	0.5	ns

Table 8. The results of the Kruskal Wallis analysis of variation within the sampling squares at Cuckmere Haven,Sussex.

Sampling square					
1	$H_{(1)}$ = 1.110	0.5	P	0.1	ns
2	$H_{(8)}$ = 4.380	0.9	P	0.5	ns
5	$H_{(1)}$ = 2.977	0.1	P	0.05	ns
6	$H_{(2)}$ = 2.977	0.1	P	0.5	ns
7	$H_{(3)}$ = 0.744	0.975	P	0.90	ns
8	$H_{(4)}$ = 1.218	0.9	P	0.5	ns

Table 9. The chromosome numbers for the sampling squares at Cuckmere Haven, Sussex.

Sampling square	Chromosome number 26	27	28	29	30	n	Samples
1	18	-	1	-	-	19	2
2	40	2	-	-	1	54	9
5	9	3	2	-	-	14	2
6	10	2	-	-	-	12	3
7	8	2	2	-	1	13	4
8	10	3	1	1	1	16	5

Table 10. A summary of chromosome number and structure for each sampling square at Rottingdean, Sussex.

Sampling square	Chromosome number 26 A AA	AB	BB	26 C AA	AB	BB	27 A AA	AB	BB	27 C AA	AB	BB	28 A AA	AB	BB	28 C AA	AB	BB	Total
1	22	-	-	20	2	-	3	-	-	3	-	-	-	-	-	-	-	-	25
2	30	-	-	27	1	2	2	-	-	2	-	-	-	-	-	-	-	-	31
5	11	-	-	9	1	1	1	-	-	1	-	-	2	-	-	2	-	-	14
7	32	-	-	27	3	2	3	-	-	3	-	-	-	-	-	-	-	-	35
12	10	-	-	6	2	2	3	-	-	3	-	-	-	-	-	-	-	-	13
13	34	-	-	27	6	1	3	-	-	3	-	-	-	-	-	-	-	-	37
15	8	-	-	5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	8

A : Group A inversion

C : Group C inversion

Table 11. The observed and expected frequencies of chromosome numbers for each sampling square at Rottingdean,Sussex.

Sampling square		Chromosome number 26	27	28	Total
1	obs.	22	3	0	25
	exp.	22.09	2.82	0.09	
2	obs.	29	2	0	31
	exp.	29.14	1.83	0.03	
5	obs.	11	1	2	14
	exp.	10.84	2.96	0.20	
7	obs.	32	3	0	35
	exp.	32.5	2.69	0.05	
12	obs.	10	3	0	13
	exp.	10.06	2.75	0.19	
13	obs.	34	3	0	37
	exp.	34.09	2.84	0.06	
15	obs.	8	-	-	8
	-	-	-	-	

Table 12. The observed and expected frequencies of the group C inversion for each sampling square from Rottingdean,Sussex.

Sampling square		2n = 26 Inversion type AA	AB	BB	Total	2n=26 to 2n=28 Inversion type AA	AB	BB	Total
1	obs.	22	2	0	22	23	2	0	25
	exp.	20.04	1.91	0.05		23.04	1.92	0.04	
2	obs.	26	1	2	29	28	1	2	31
	exp.	24.22	4.28	0.50		26.20	4.59	0.20	
5	obs.	9	1	1	11	12	1	1	14
	exp.	8.20	2.59	0.20		10.28	4.43	0.28	
7	obs.	27	3	2	32	30	3	2	35
	exp.	25.38	6.24	0.38		28.35	6.30	0.35	
12	obs.	6	2	2	10	9	2	2	13
	exp.	4.90	4.20	0.90		9.47	4.62	0.69	
13	obs.	27	6	1	34	30	6	1	37
	exp.	26.47	7.05	0.46		29.43	7.12	0.43	
15	obs.	5	3	0	8	5	3	0	8
	exp.	5.28	2.43	0.28		5.28	2.44	0.28	

Table 13. The frequencies of the group C inversion from Rottingdean, Sussex.

Sampling square	Chromosome number 26			27			28		
	AA	AB	BB	AA	AB	BB	AA	AB	BB
1	20	2	-	3	-	-	-	-	-
2	26	1	2	2	-	-	-	-	-
5	9	1	1	1	-	-	2	-	-
7	27	3	2	3	-	-	-	-	-
12	6	2	2	3	-	-	-	-	-
13	27	6	1	3	-	-	-	-	-
15	5	3	-	-	-	-	-	-	-

Table 14. The frequencies of the metacentric(A) and the acrocentric (B) of the group C inversion from Rottingdean,Sussex.

Sampling square	26		27		28		26 to 28	
	A	B	A	B	A	B	A	B
1	42	2	6	-	-	-	48	2
2	53	5	4	-	-	-	57	5
5	19	3	2	-	4	-	25	3
7	57	7	6	-	-	-	63	7
12	14	6	6	-	-	-	20	6
13	60	8	6	-	-	-	66	8
15	13	3	-	-	-	-	13	3

Table 15. The observed and expected f equencies of chromosome number and structure from Rottingdean,Sussex.

Inversion type		Chromosome number			Total
		26	27	28	
AA	observed	120	15	2	137
	expected	122.7	12.6	1.7	
AB	observed	18	0	0	18
	expected	16.1	1.7	0.2	
BB	observed	8	0	0	8
	expected	7.2	0.7	0.1	
Total		146	15	2	163

Table 16.A. The observed and expected frequencies for chromosome number from Rottingdean,Sussex.

	Chromosome number		
	26	27	28
observed	146	15	2
expected	143.44	18.91	0.65

Table. 16.B. The observed and expected frequencies of the group C inversion from Rottingdean, Sussex.

	Inversion type 2n = 26			Inversion type 2n=26 to 2n=28		
	AA	AB	BB	AA	AB	BB
observed	120	18	8	137	18	8
expected	114.03	30.08	1.89	130.89	30.32	1.79

Table 17. The chromosome number and structure of mitotic metaphases from populations of Nucella lapillus from Cuckmere Haven, Sussex.

Sampling square	Chromosome number	n	Chromosome type
1	26,	18	-
	28	1	$A_{(2)}$
2	26	40	-
	27	12	$A_{(1)}$
	28	1	$A_{(1)}$
	28	1	$A_{(2)}$
	30	1	$A_{(2)}$
5	26	9	-
	27	3	$A_{(1)}$
	28	2	$A_{(1)}$
6	26	10	
	27	2	$A_{(1)}$
7	26	8	-
	27	2	$A_{(1)}$
	28	1	$A_{(1)}$
	28	1	$A_{(2)}$
	30	1	$A_{(2)}$
8	26	10	-
	27	3	$A_{(1)}$
	28	1	$A_{(1)}$
	29	1	$A_{(2)}$
	30	1	$A_{(2)}$

Table 18. The chromosome number and structure of mitotic metaphases from populations of Nucella lapillus from Rottingdean, Sussex.

Sampling square	Chromosome number	n	Chromosome type
1	26	22	-
	27	3	$C_{(1)}$
2	26	29	$C_{(1)}$
	27	2	$C_{(1)}$
5	26	11	-
	27	1	$C_{(1)}$
	28	2	$C_{(1)}$
7	26	32	-
	27	3	$C_{(1)}$
12	26	10	-
	27	3	$C_{(1)}$
13	26	10	-
	27	3	$C_{(1)}$
15	26	8	-

Plate 1

A 2n=26 karyotype from Rottingdean,Sussex. The chromosome pairs involved in the inversions in groups A and C are homozygous for the metacentric form.

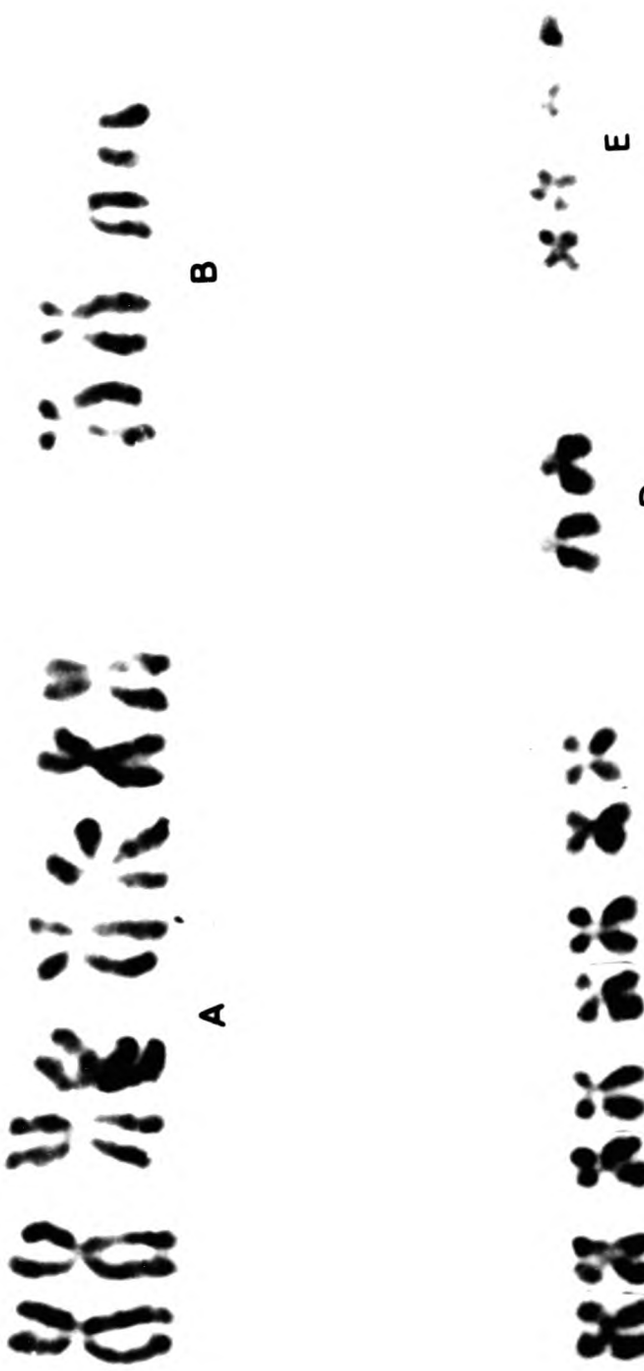


Plate 2
A 2n=26 karyotype from Rottingdean, Sussex. The chromosome pair involved in the group A inversion is homozygous for the metacentric form and the group C inversion is homozygous for the acrocentric form.

Plate 2
A 2n=26 karyotype from Rottingdean, Sussex. The chromosome pair involved in the group A inversion is homozygous for the metacentric form and the group C inversion is homozygous for the acrocentric form.

Plate 3

A 2n=26 karyotype from Rottingdean, Sussex. The chromosome pair involved in the group A inversionis is homozygous for the metacentric form and the group C inversion is heterozygous

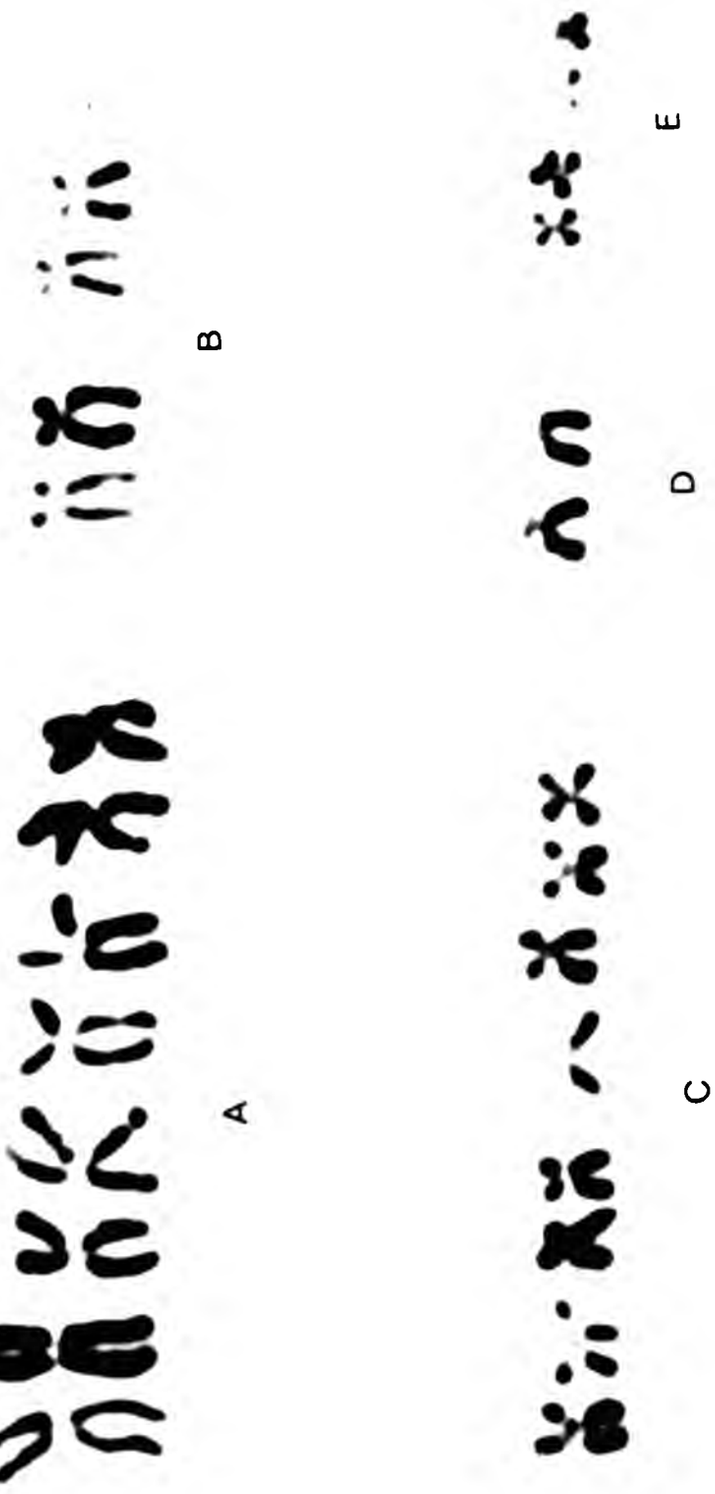


Plate 4
A2n=26 karyotype from Rottingdean, Sussex.The chromosome pair involved in the group A inversion is heterozygous and the group Cinversion is homozygous for the acrocentric form.

Plate 5
A 2n=26 karyotype from Cuckmere Haven, Sussex.The chromosome pair involved in the group A inversion is homozygous for the submetacentric form and the group C inversion is homozygous for the metacentric form.

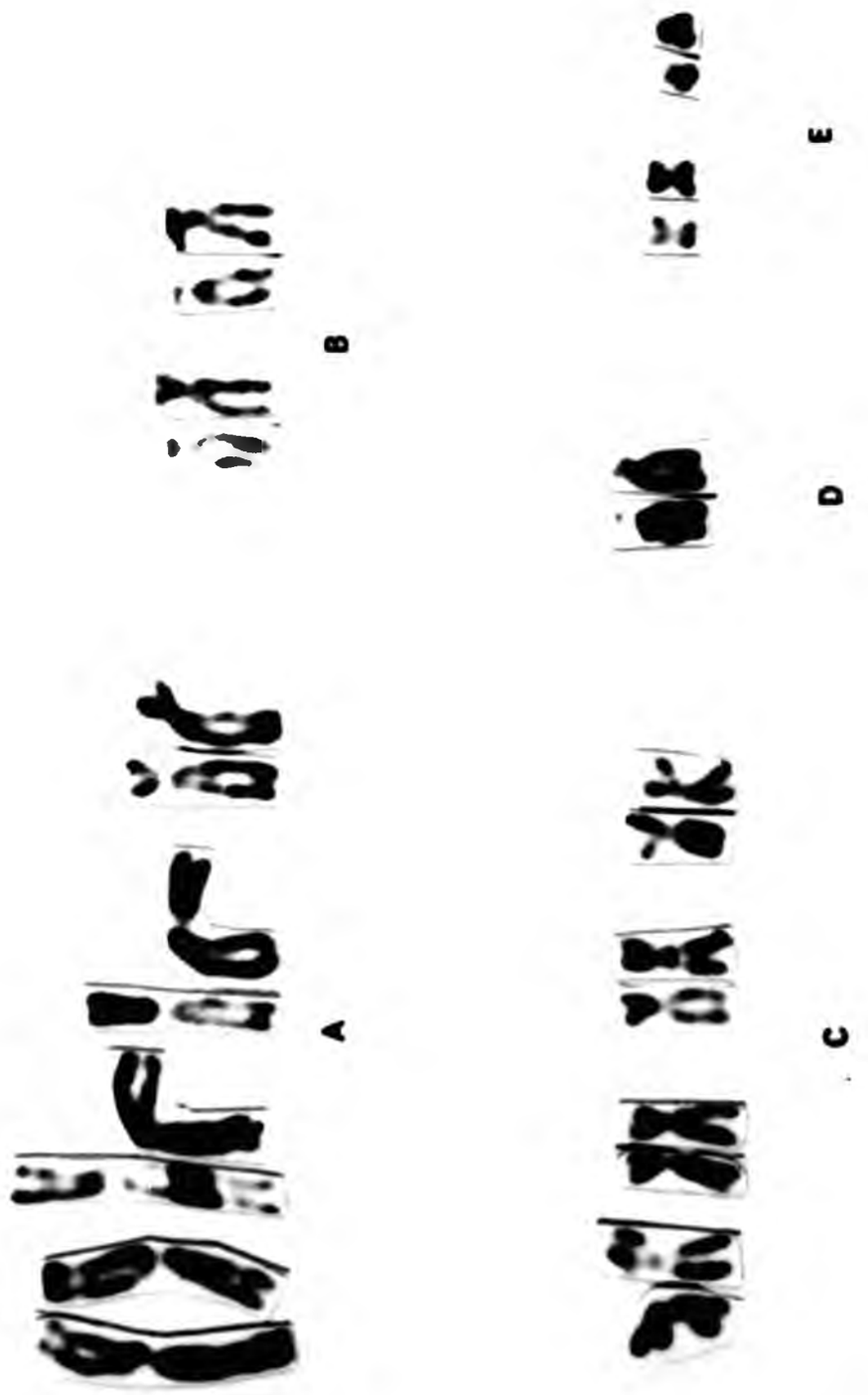


Plate 6
A 2n= 27 karyotype from Rottingdean, Sussex. The chromosome pairs involved in the group A inversion and the group C inversion are homozygous for the metacentric form.

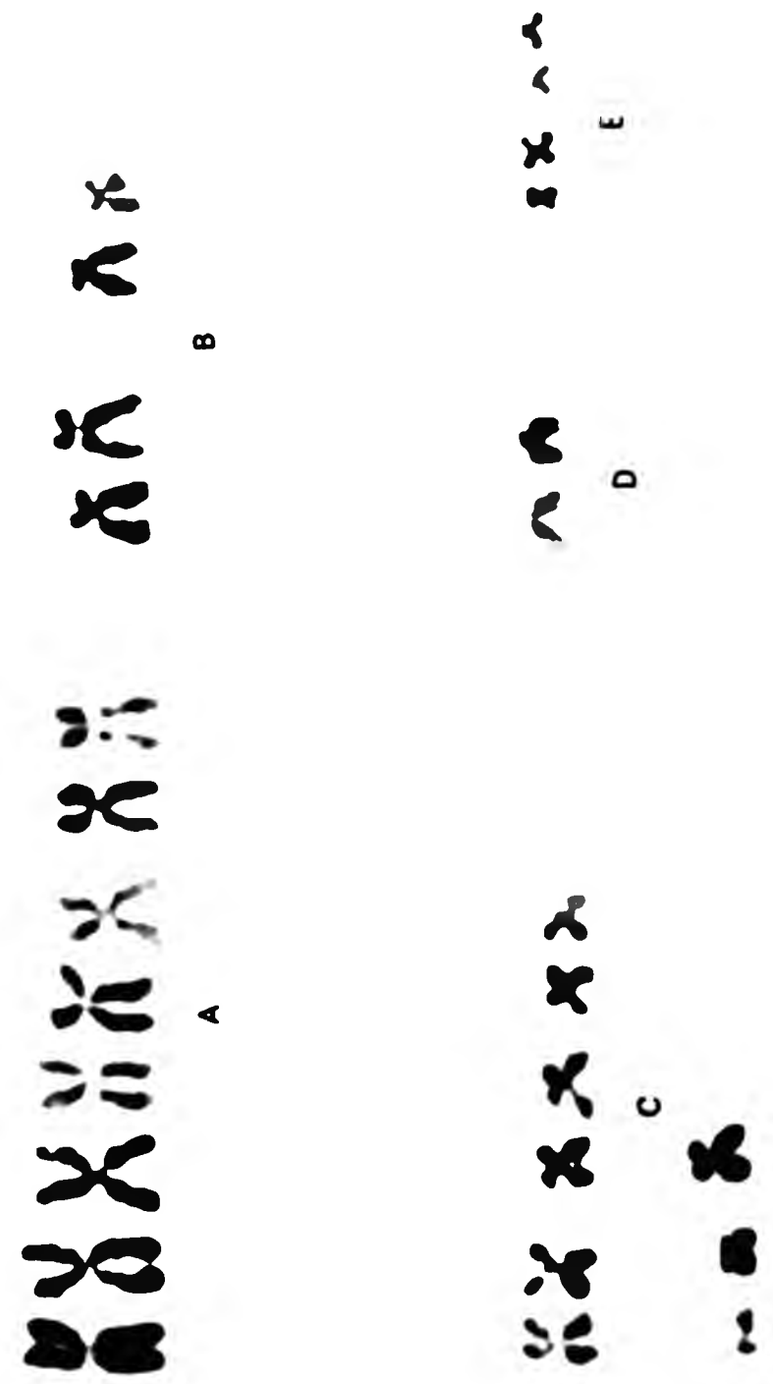


Plate 7
A 2n= 28 karyotype from Rottingdean, Sussex. The chromosome pairs involved in the goup A and group C inversion are homozygous for the metacentric form.

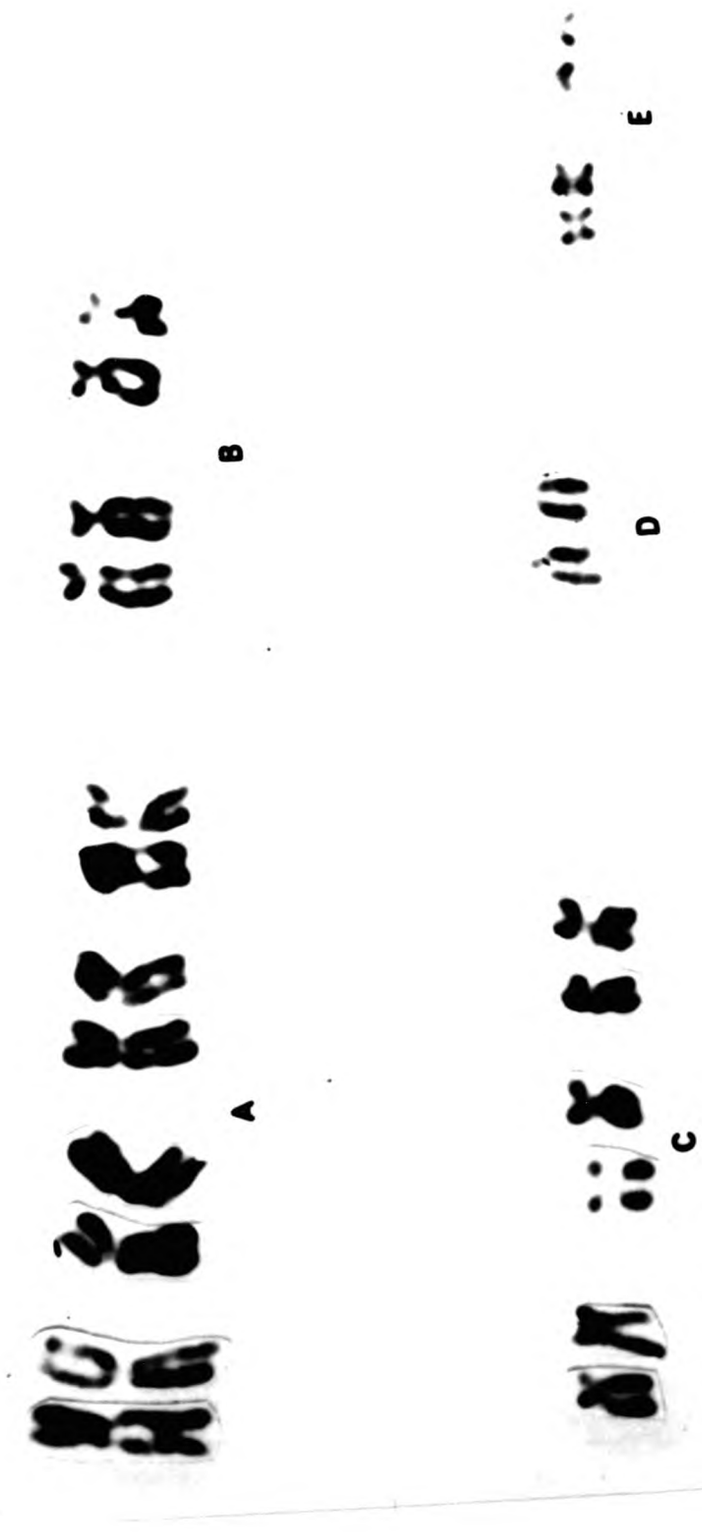


Plate 8
A 2n=27 karyotype from Cuckmere Haven,Sussex. The chromosome pair involved in the Robertsonian polymorphism is from group A.The relative length(RL) and the centromere position (R) for the chromosomes involved are as follows:- 5.53(RL), 0.82(R);2.29(RL),0.0(R);2.50(RL),0.43(R).

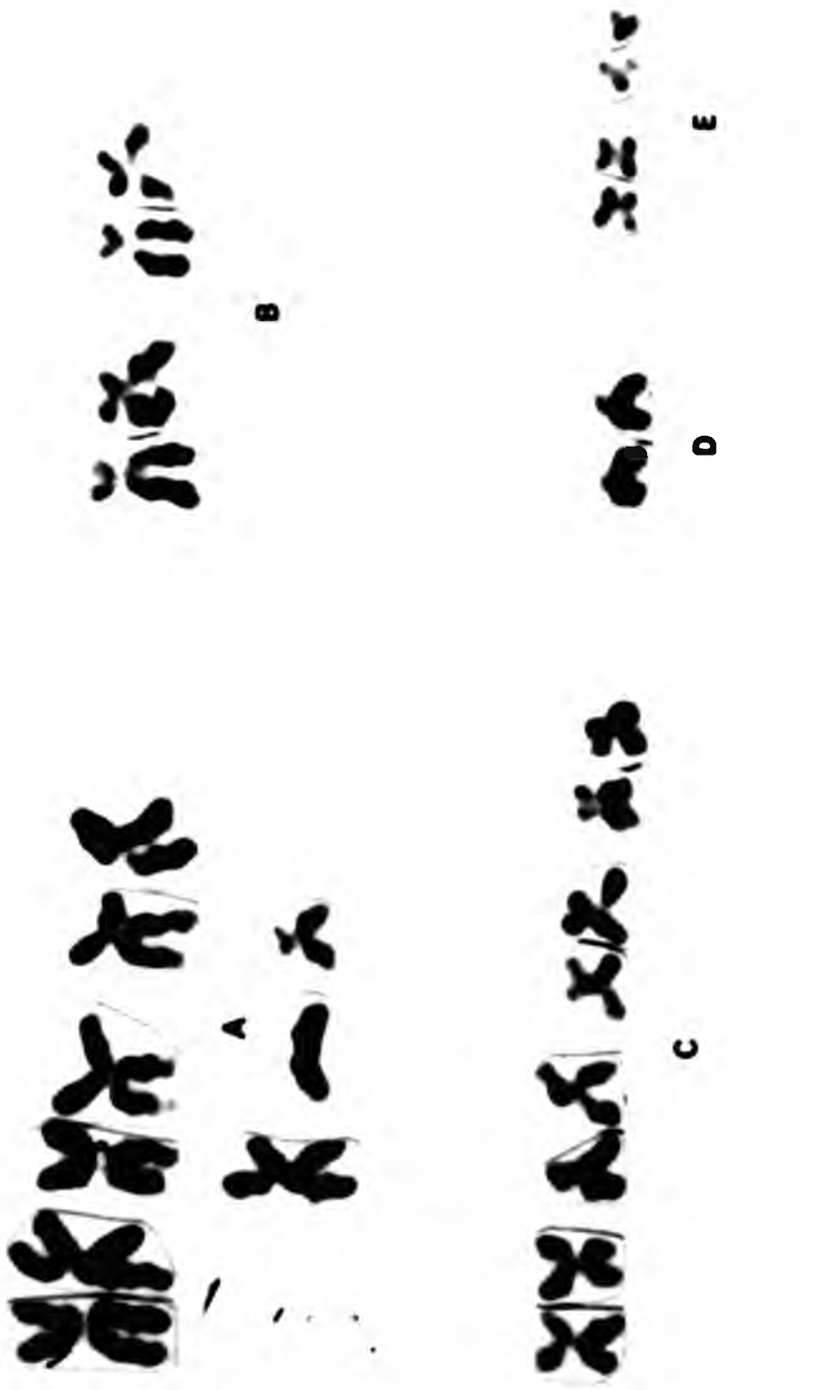


Plate 9
A 2n=27 karyotype from Cuckmere Haven, Sussex.The chromosome pair involved in the Robertsonian polymorphism is from group A.The relative length(RL) and centromere position (R) for the chromosomes involved are as follows:- 4.64(RL), 0.69(R);2.08(RL),0.20(R);2.39(RL),0.23.(R).

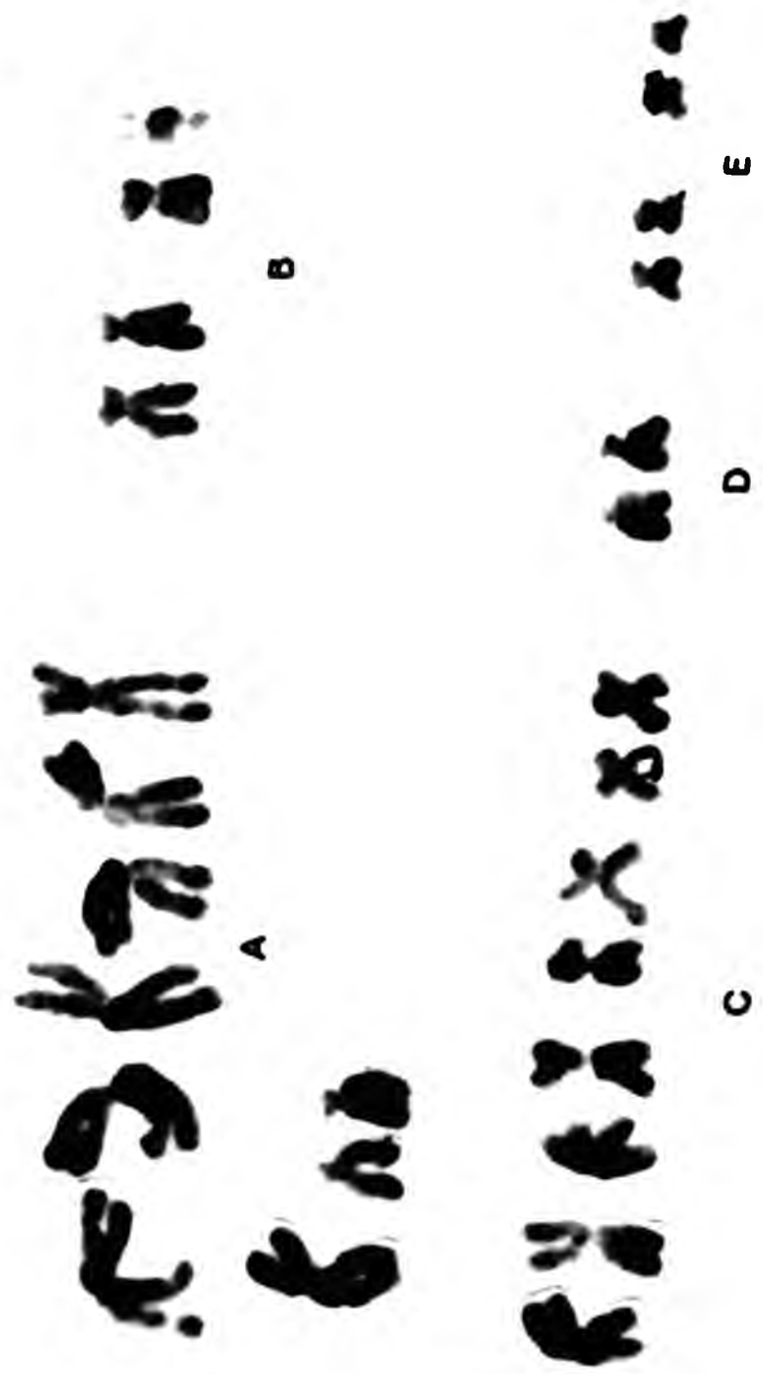


Plate 10

A 2n=27 karyotype from Cucumere Haven,Sussex.The chromosome pair involved in the Robertsonian polymorphism is from group A. The relative length (RL) and the centromere position(R) for the chromosomes involved are as follows:-
6.58(RL),0.92(R);3.65(RL),0.30(R);3.40(RL),0.23(R).

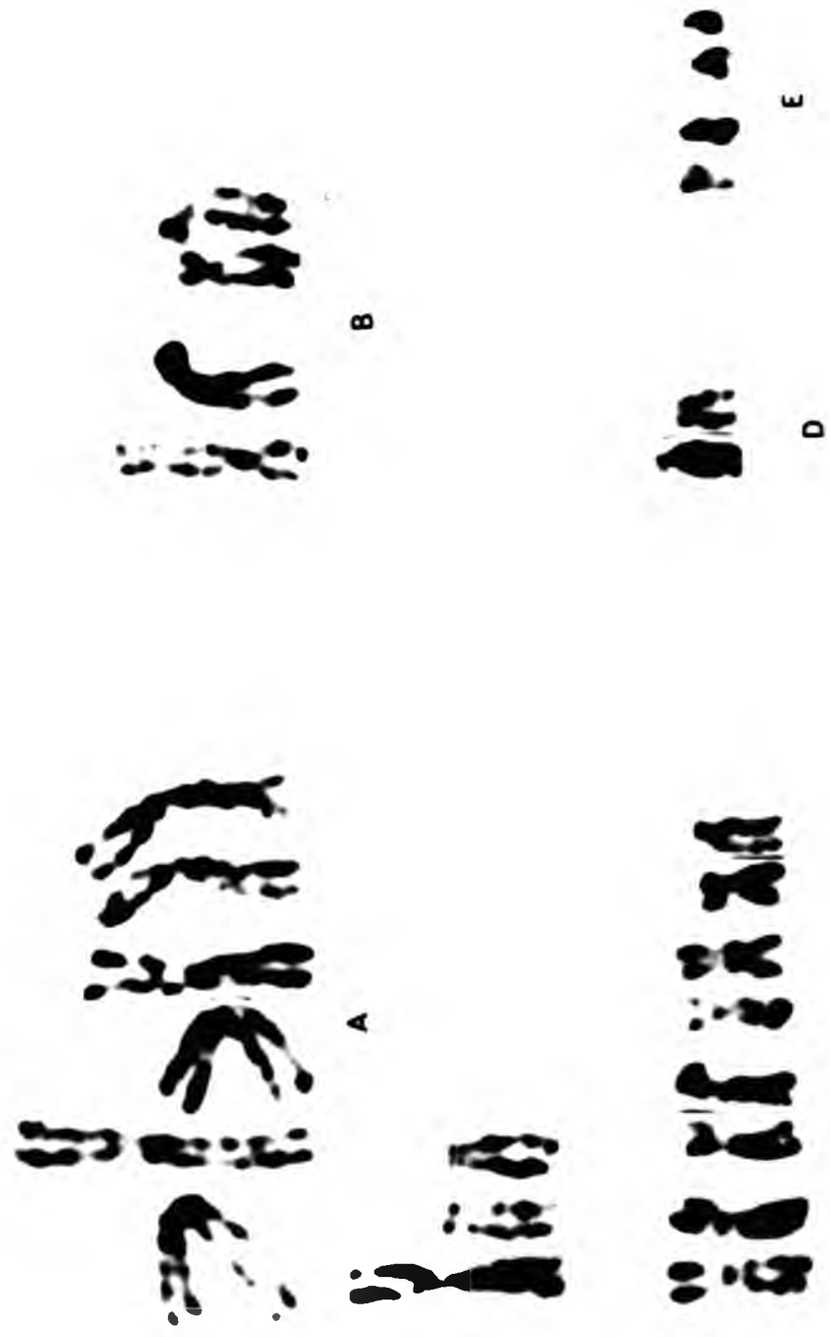


Plate 11

A 2n=27 karyotype from the Isle of Cumbrae,Firth of Clyde. The chromosome pair involved in the Robertsonian polymorphism is from group A. The relative length(RL) and the centromere position(R) for the chromosomes involved are as follows:-4.94(RL),0.79(R);2.60(RL),0.27(R);2.87(RL), 0.32(R).

Plate 12
A 2n=28 karyotype from the Isle of Cumbrae,Firth of Clyde. The chromosome pairs involved in the Robertsonian polymorphism are from group A.The relative length(RL) and centromere position(R) for the chromosomes involved are as follows:- Pair 1.6.82(RL),0.82(R);3.37(RL),0.36(R);4.25(RL) 0.42(R)Pair 2 6.53(RL),0.69(R);3.56(RL),0.43(R);3.22(RL), 0.27(R).

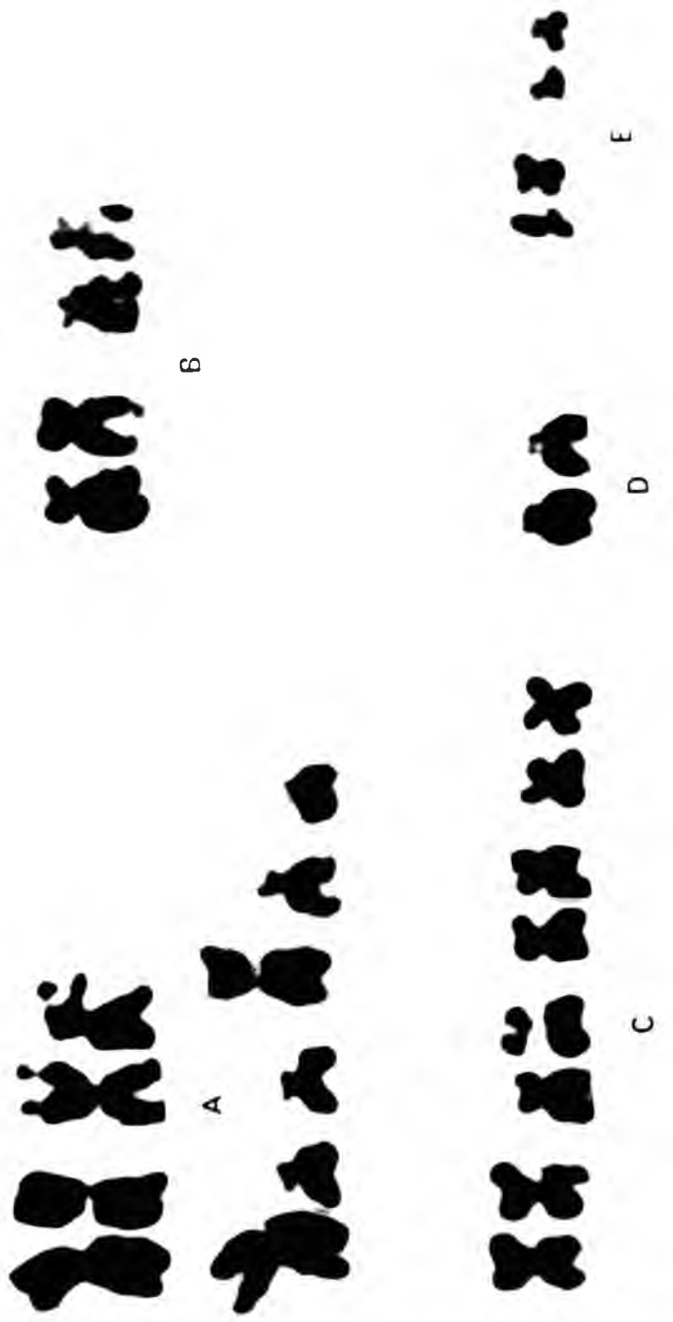


Plate 13
A 2n=28 karyotype from Cuckmere Haven,Sussex.The chromosomes involved in the Robertsonian polymorphism are from group A. The relative length(RL) and the centromere position(R) for the chromosomes involved are as follows:-
Pair 1.5.46(RL),0.82(R);3.37(RL),0.36(R);4.25(RL),0.42(R);
Pair 2. 6.53(RL),0.69(R);3.56(RL),0.43(R);3.22(RL),0.27(R).

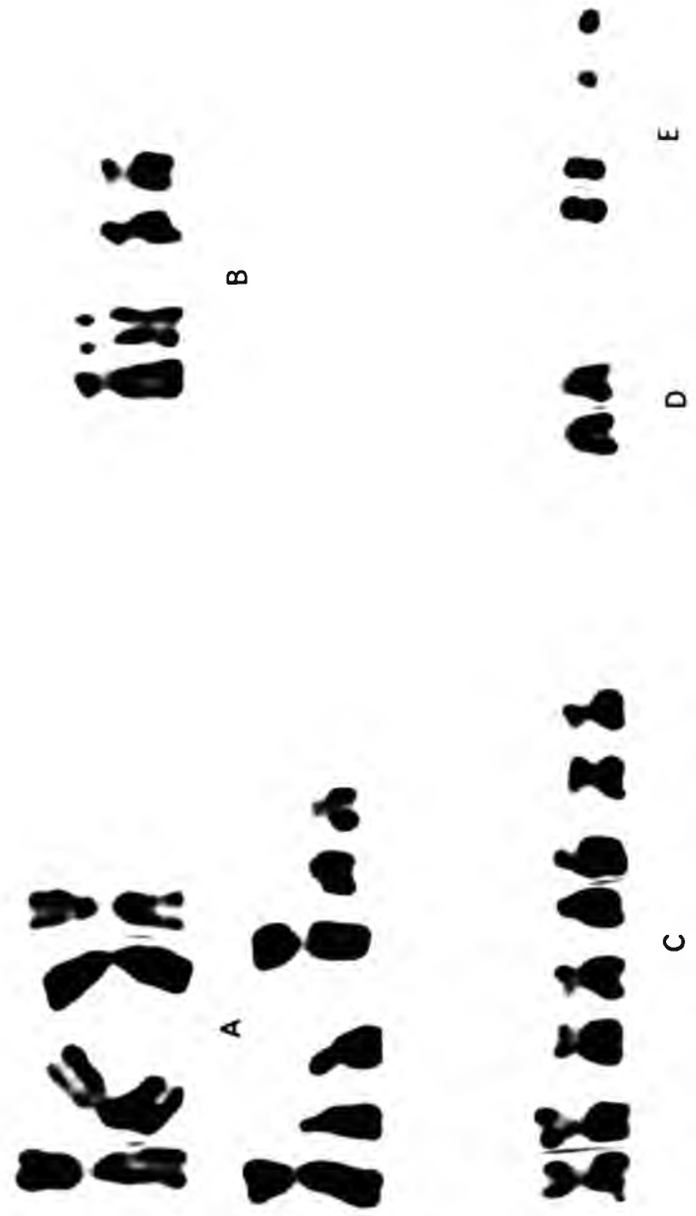


Plate 14

A 2n=28 karyotype from Cuckmere Haven,Sussex.The chromosomes involved in the Robertsonian polymorphism are from group A. The relative length(RL) and the centromere position(R) for the chromosomes involved are as follows:- 2.38(RL),0(R);2.38(RL),0(R);3.52(RL),0.27(R);2.11(RL),0.29 (R).

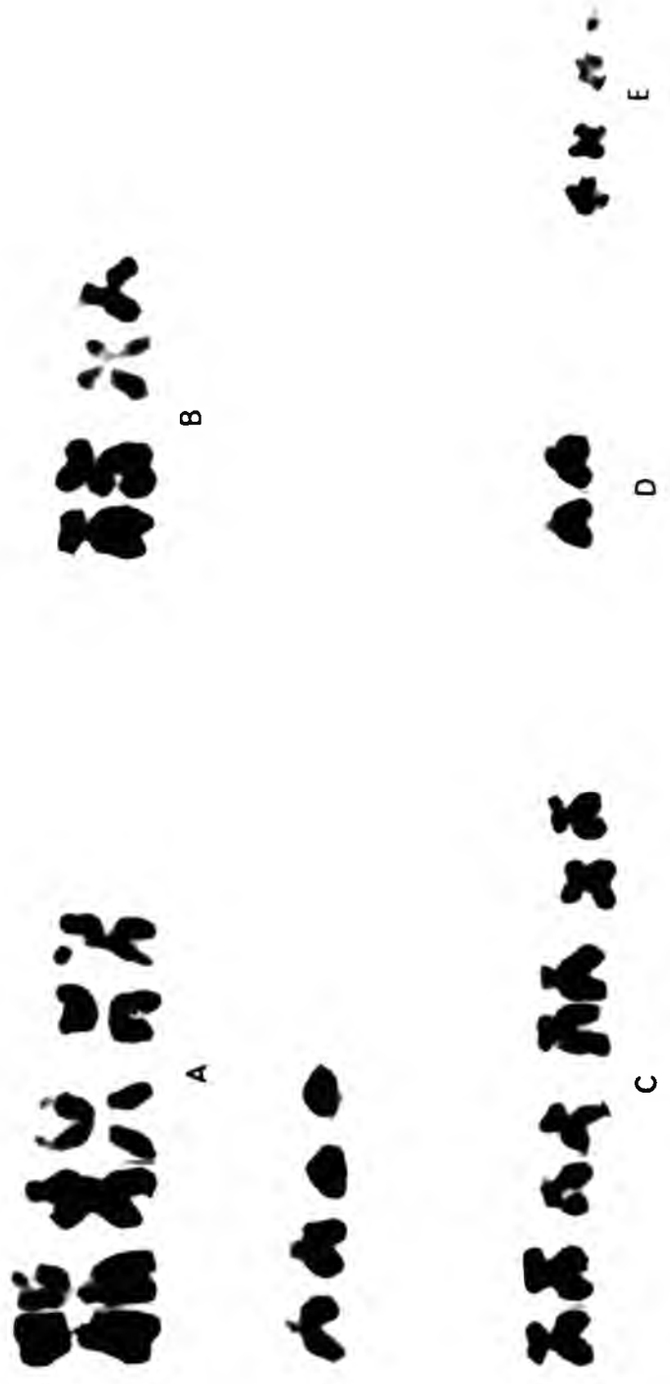


Plate 15
A 2n=29 karyotype from St. Brides Haven,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from groups A and B. The relative length (RL) and centromere position(R) for the chromosomes involved are as follows:-Group A,Pair 1.7.22(RL),0.68(R); 3.20(RL),0.24(R);3.61(RL),0.29(R). Pair 2 6.61(RL),0.79 (R);1.97(RL),0.60(R);3.05(RL),0.22(R).Group B 5.19(RL), 0.38(R);5.05(RL),0.62(R);1.37(RL),0(R).

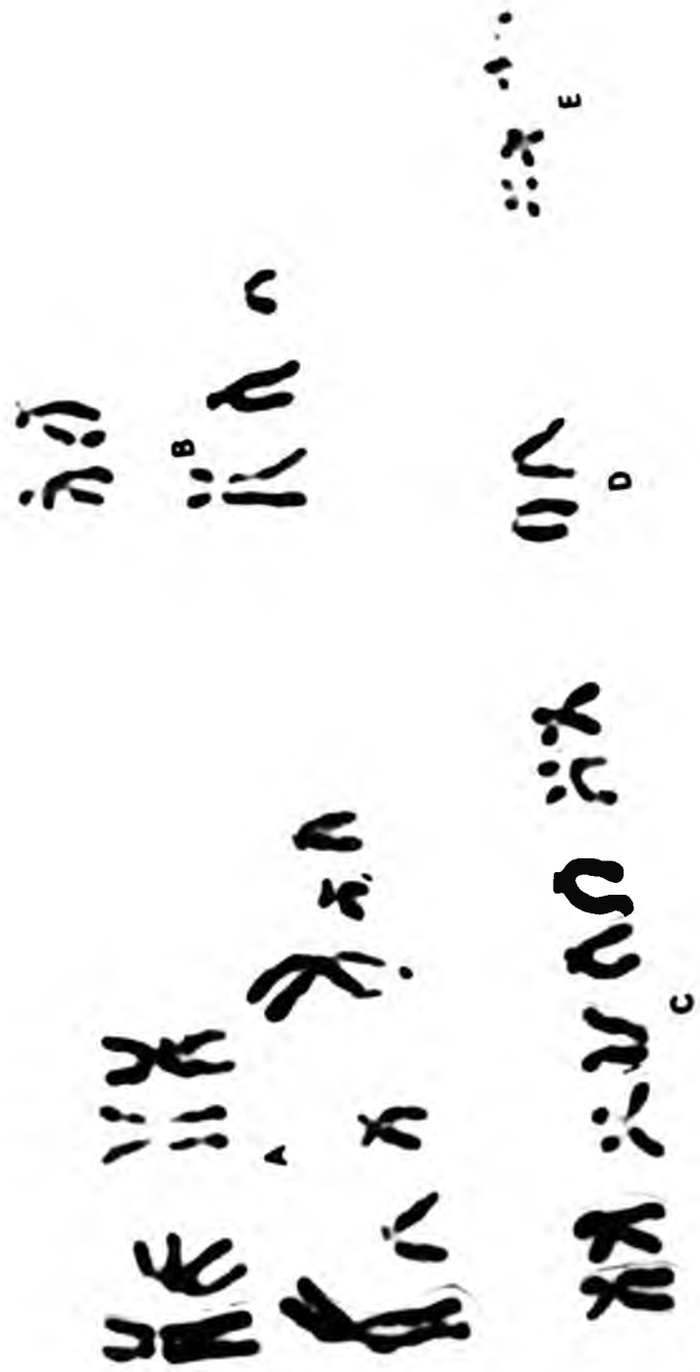


Plate 16
A 2n=31 karyotype from Castlebeach Bay,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from groups A and B.

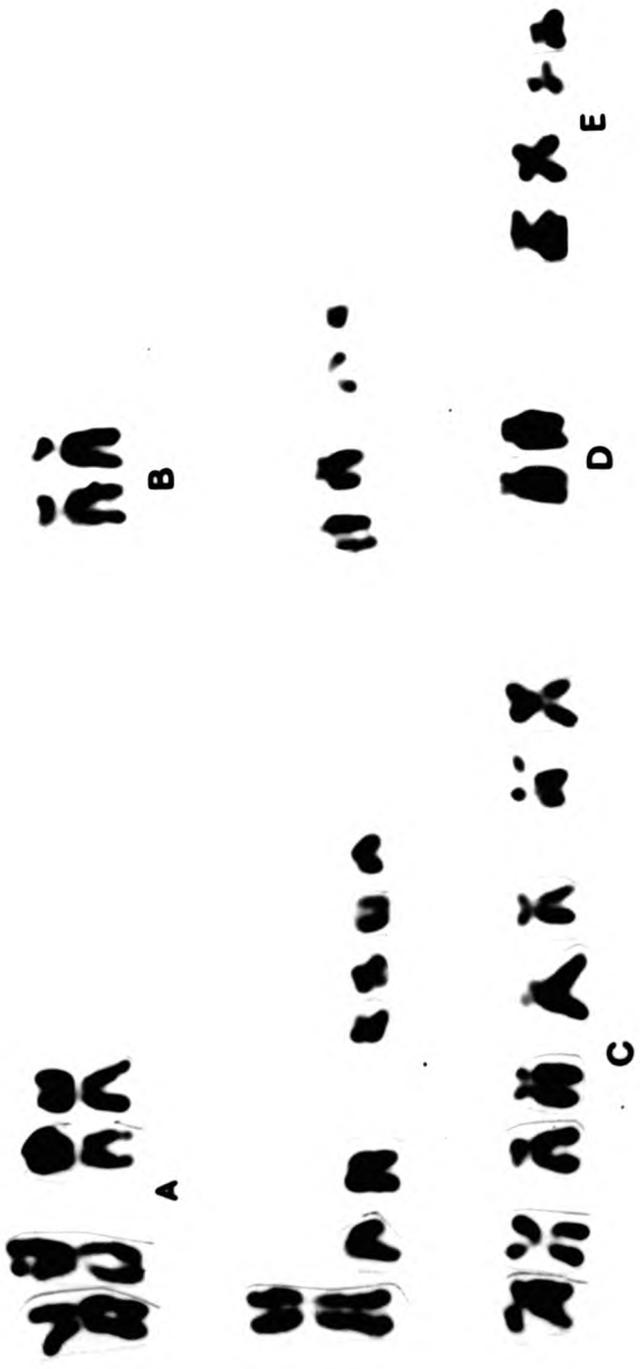


Plate 17

A 2n=30 karyotype from St.Brides Haven,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from groups A and B.

Plate 18
A 2n=30 karyotype from Castlebeach Bay,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from groups A and C.

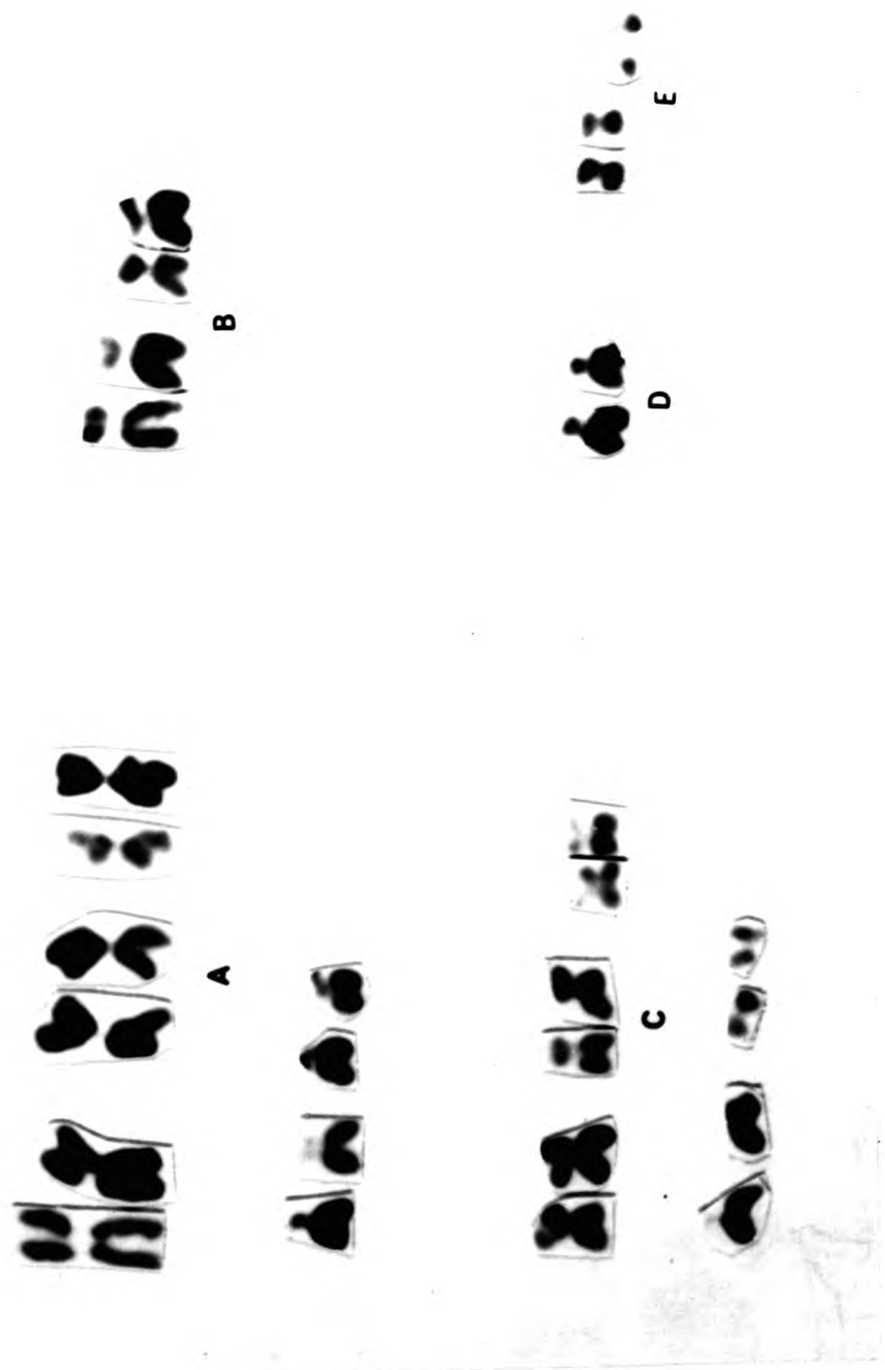


Plate 19
A 2n=29 karyotype from St.Brides Haven,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from groups A and C.The relative length (RL) and centromere position(RL) for the chromosomes involved are as follows:-Group A 5.65(RL),0.86(R);2.86(RL),0.25(R); 3.11(RL),0.43(R).Group C 2.49(RL),0(R);2.30(RL),0(R); 2.31(RL),0.52(R);1.33(RL),0(R).

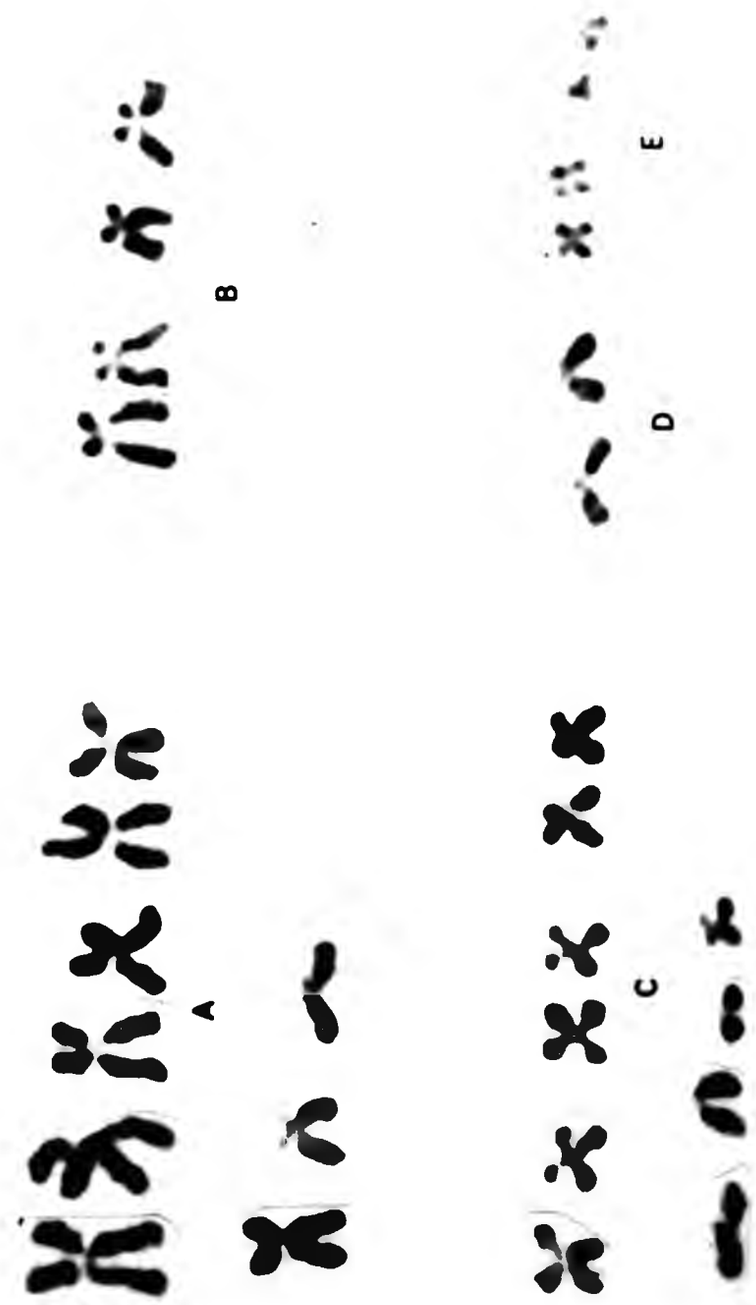


Plate 20
A 2n=32 karyotype from the Isle of Cumbrae,Firth of Clyde.The chromosome pairs involved in the Robertsonian polymorphism are from groups A and C.The relative length (RL) and the centromere position (R) for the chromosomes involved are as follows:- Group A 2.58(RL),0(R);2.97(RL), 0.28;3.11(RL)0.20(R);3.11(RL),0.22(R);2.52(RL),0(R);2.54 (RL),0(R),2.45(RL)0.28(R);2.20(RL),0.33(R). GroupC 1.86 (RL),0.56(R);1.81(RL),0.66(R);1.22(RL),0(R);1.39(RL),0(R).

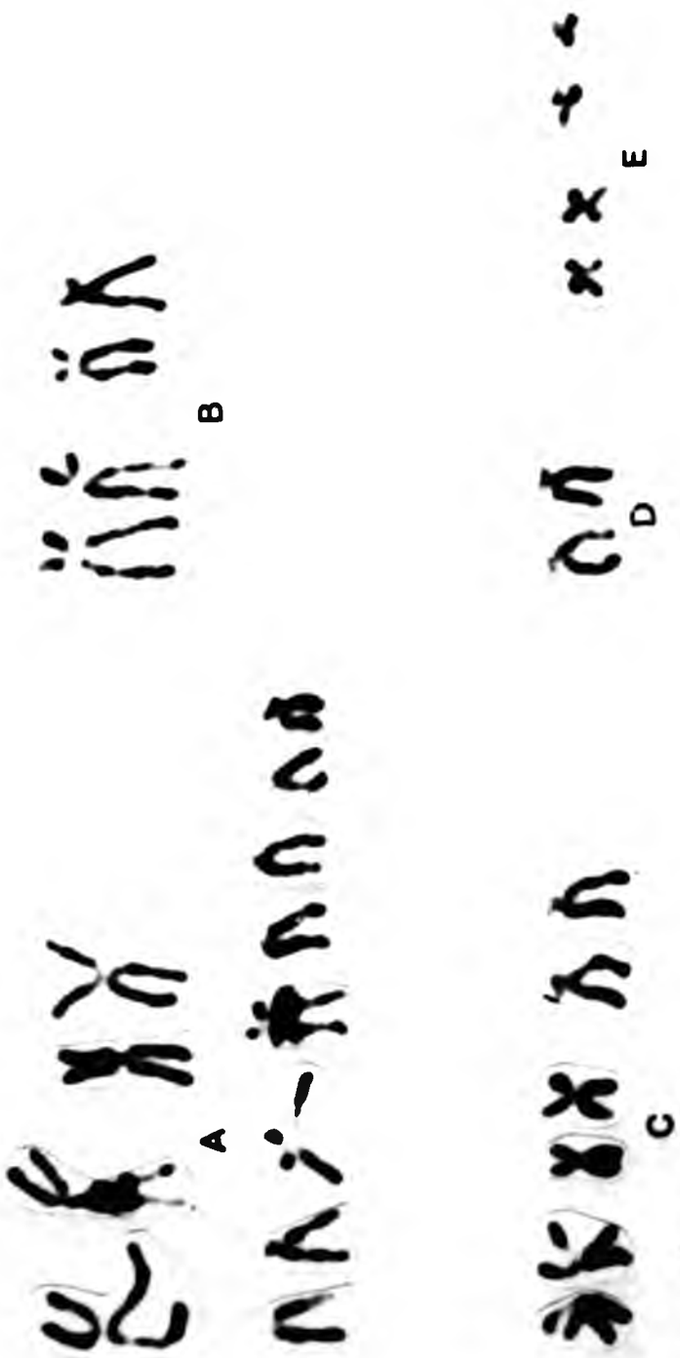


Plate 21
A 2n=32 karyotype from Castle beach Bay,Pembrokeshire. The chromosomes pairs involved in the Robertsonian polymorphism are from groups A,B and C.

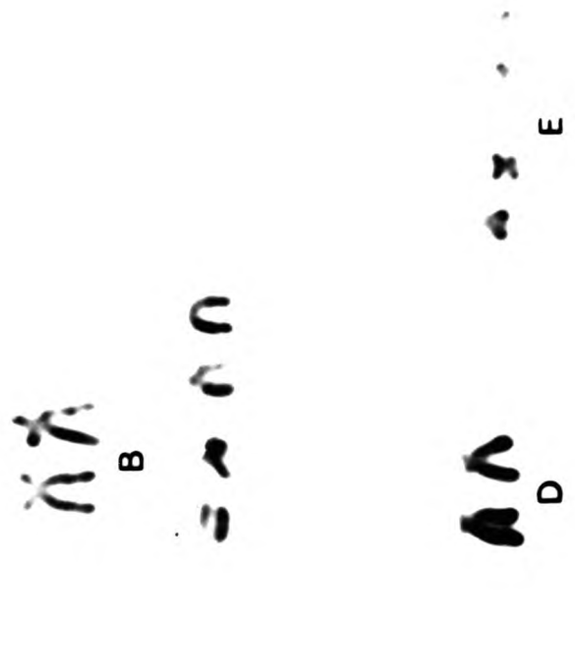


Plate 22
A 2n=32 karyotype from Castlebeach Bay,Pembrokeshire.
The chromosome pairs involved in the Robertsonian polymorphism are from Groups A,B and C.

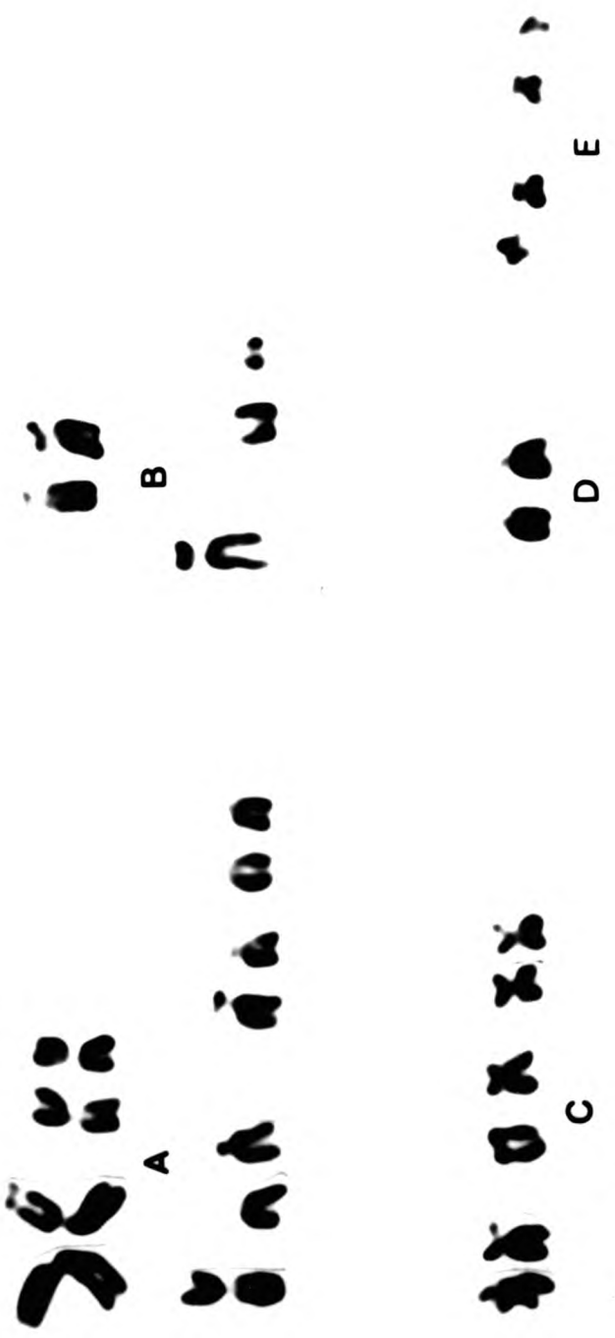


Plate 22
A 2n=32 karyotype from Castlebeach Bay,Pembrokeshire.
The chromosome pairs involved in the Robertsonian polymorphism are from Groups A,B and C.

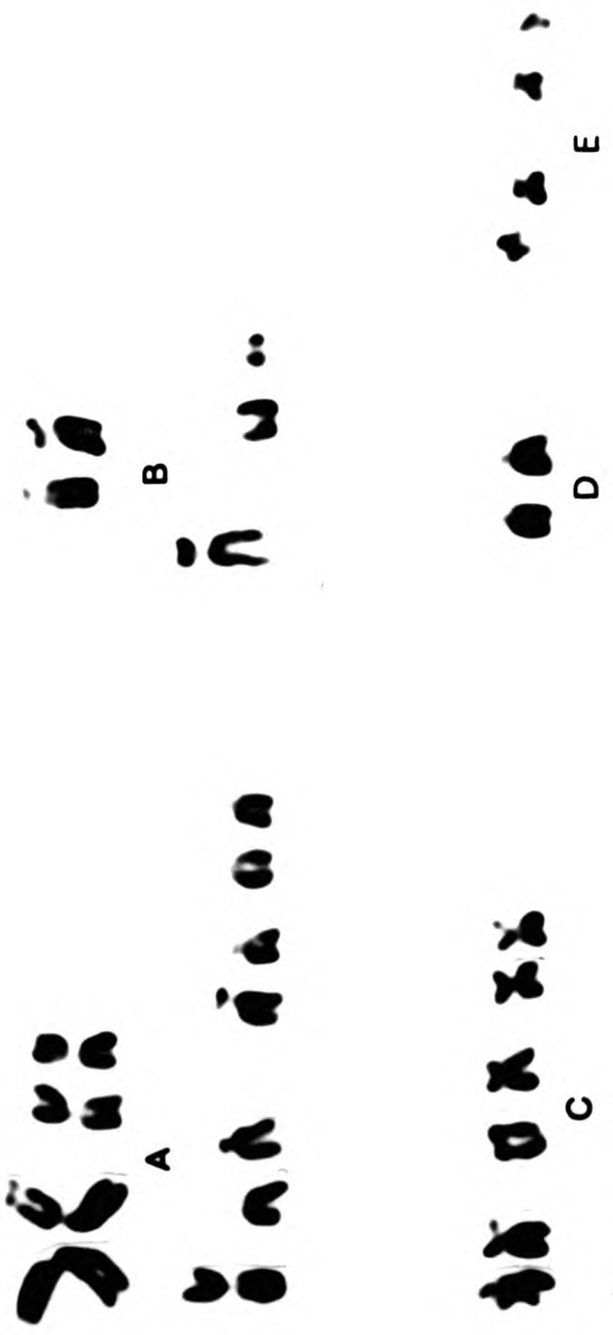


Plate 22
A 2n=32 karyotype from Castlebeach Bay,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from Groups A,B and C.

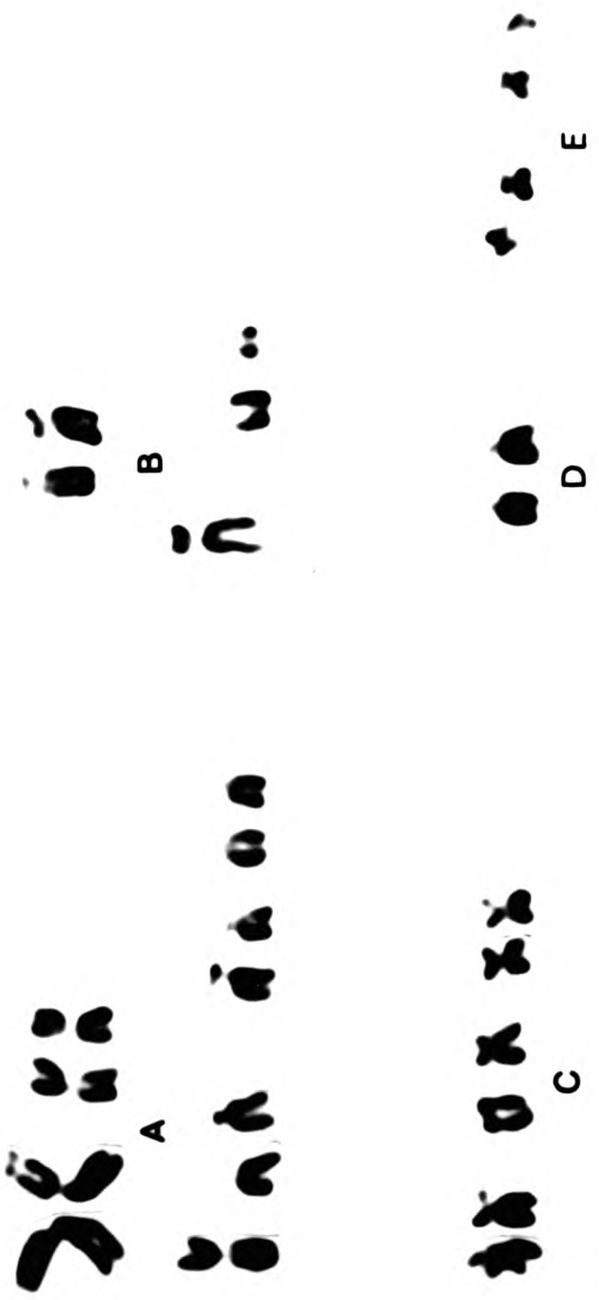


Plate 23
A 2n=33 karyotype from Castlebeach Bay,Pembrokeshire. The chromosome pairs involved in the Robertsonian polymorphism are from groups A,B and C.The relative length (RL) and the centromere position(R) for the chromosomes involved are as follows:-Group A 2.56(RL),0.27(R); 2.73(RL),0.33(R);3.15(RL),0.46(R);3.30(RL),0.57(R); 2.95(RL),0.38(R);2.97(RL),0.31(R);2.71(RL),0.46(R); 2.88(RL),0.33.Group B 4.36(RL),0.45(R);2.75(RL),0.19(R); 1.36(RL),0(R).Group C 1.45(RL),0.56(R);1.63(RL),0. 50(R); 1.46(RL),0(R);1.23(RL),0(R).

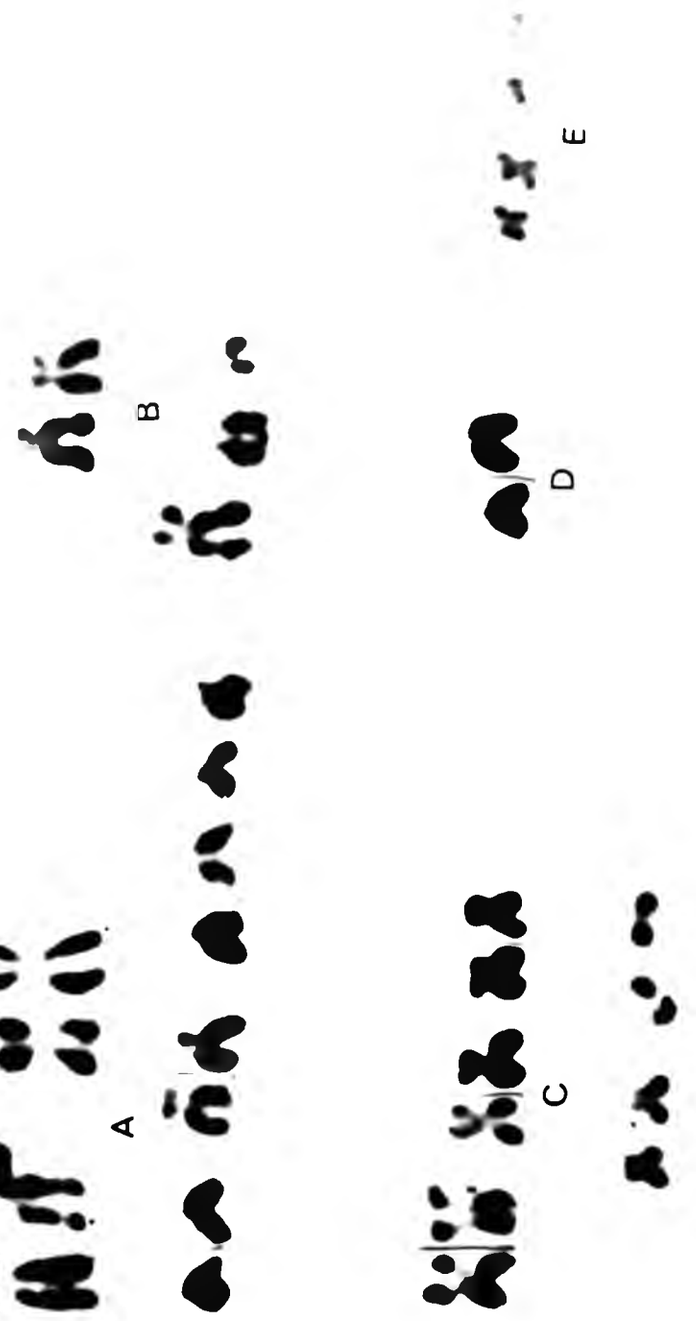


Plate 24

A 2n=30 karyotype from the Isle of Cumbrae,Firth of Clyde. The chromosome pairs involved in the Robertsonian polymorphism are from groups A,B and C.The relative length (RL) and the centromere position(R) for the chromoomes involve are as follows:- Group A 4.48(RL),0.76(R); 2.74(RL),0.32(R),2.87(RL),0.15(R).Group B 4.15(RL), 0.40(R);3.13(RL),0.21(R);1.09(RL),0(R). Group C 2.78(RL), 0.23(R);2.42(RL)0.42(R);1.67(RL),0.73(R);2.99(RL),0.40(R).

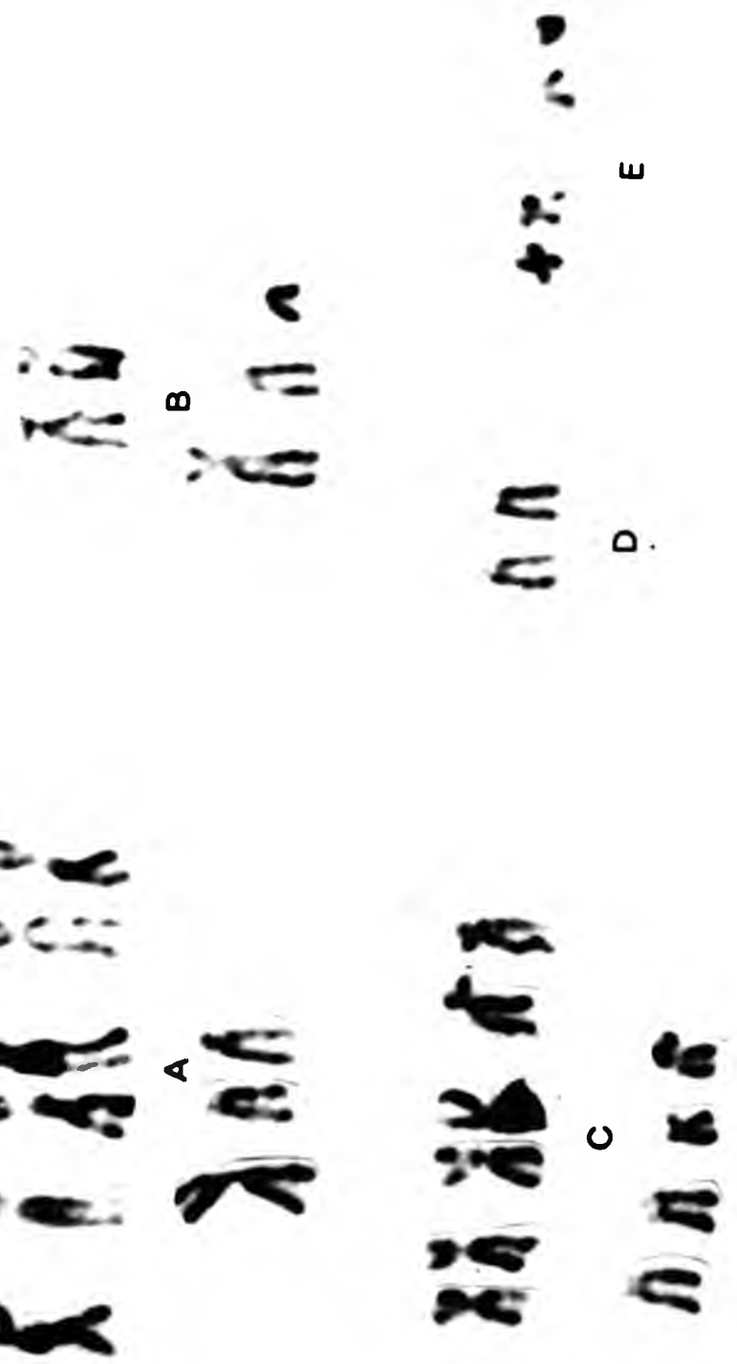


Plate 25
A 2n=34 karyotype form Osmington Mills,Dorset.
The chromosome pairs involved in the Robertsonian polymorphism are from Groups A,B and C.

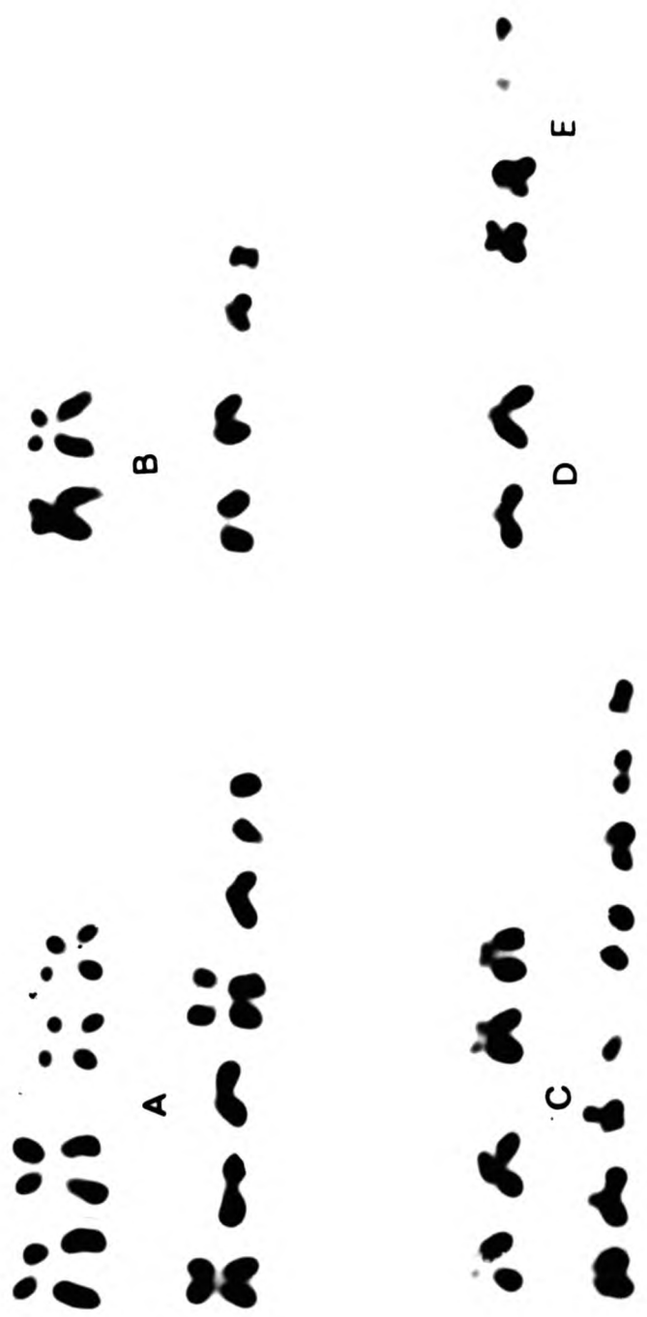


Plate 26
A 2n=36 karyotype from Lulworth Cove,Dorset.
The chromosome pairs involved in the Robertsonian polymorphism are from groups A,B and C.

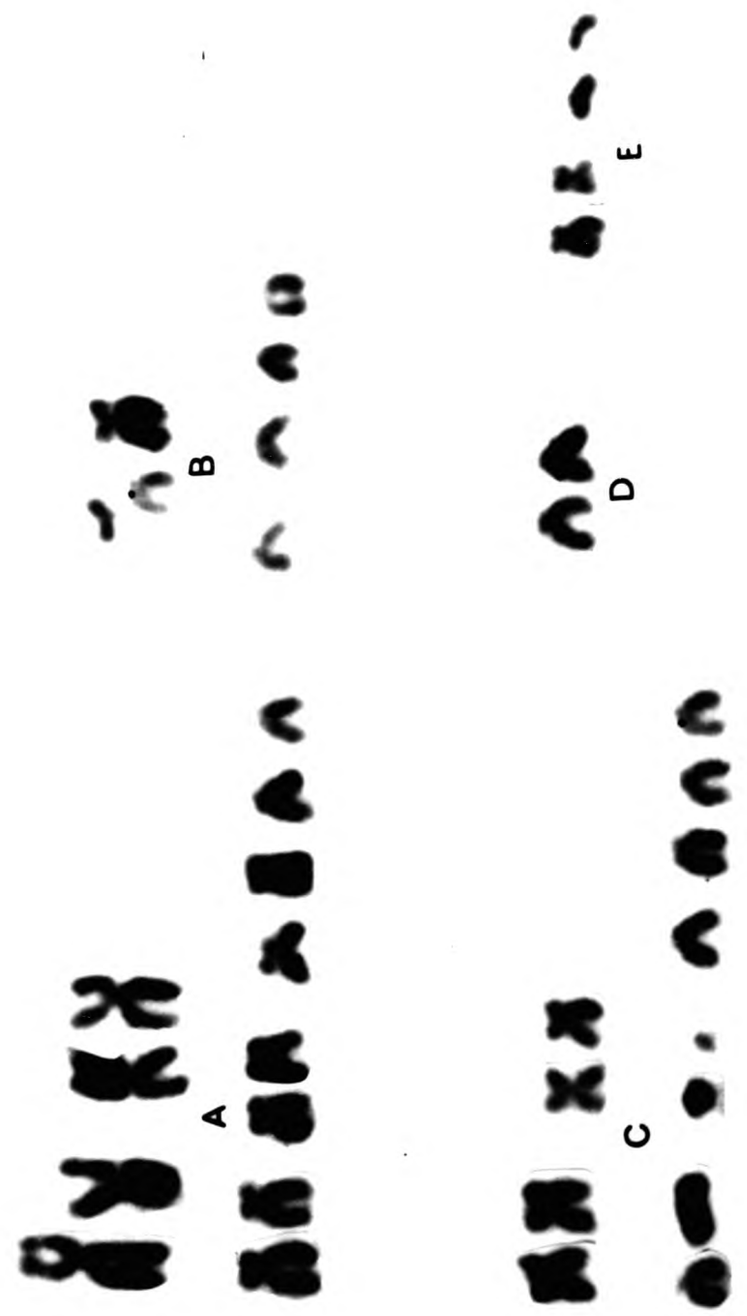


Plate 27
A 2n=26 karyotype from Rottingdean,Sussex.
The chromosome pairs thought to contribute to the Robertsonian poltmorphism are numbered from one to five as follows:- Group A Pairs 1 and 5. Group B; Pair 3. Group C;Pairs 4 and 5.

4. DISCUSSION

The information derived from the chromosomal analysis of the 2n = 26 karyotype from Rottingdean, (U.K.) has demonstrated that the specific chromosome pairs of the complement, with the exception of chromosome pair eleven, cannot be identified. The karyotype, however, can be divided into five distinct chromosomal groups based on the relative size and centromere position of each chromosome. Group A consists of the four largest chromosomes which are normally metacentric. Group B consists of the fourth and fifth largest chromosome pairs which are submetacentric. Group C consists of four chromosome pairs of similar size (pairs seven to ten) which are usually metacentric but are sometimes submetacentric. Group D consists of one chromosome pair (pair eleven) which is always acrocentric. Group E consists of the two smallest chromosome pairs which are either metacentric or submetacentric. The chromosomes within a group are indistinguishable from each other but chromosome pairs from different groups are easily identified.

The largest chromosome pair involved in the inversion polymorphism occurs in group A. This pair is normally metacentric but can be submetacentric. The submetacentric form is rare in both the homozygous and heterozygous state in the populations studied in the present investigation.

The smaller of the two chromosome pairs involved in the polymorphism occurs in group C. The chromosomes of this group are usually metacentric but the presence of the inversion results in one or two acrocentric chromosomes within the group. The most common form of the 2n = 26 karyotype is that in which both chromosome pairs involved in the inversion polymorphism are homozygous for the metacentric arrangement.

The chromosome pairs thought to contribute to the Robertsonian polymorphism occur in three of the five chromosome groups as follows:- Two chromosome pairs from group A, one chromosome from group B and a further two chromosome pairs from group C. It is therefore entirely possible that the chromosome pairs involved in the inversion polymorphism (groups A and C) are also part of the Robertsonian variation but unequivocal proof that this

is so is not available using the rather limited techniques available for molluscan chromosome analysis.

The present investigation of N. lapillus at Rottingdean and Cuckmere Haven has shown that there are no significant differences in chromosome number or structure of populations within each region.

The analysis of the distribution of the numerical and inversion polymorphisms at Rottingdean, Sussex, has demonstrated that in this region the acrocentric form of the group A inversion is rare. In the analysis of 165 individuals, 163 were metacentric for this inversion and the remaining two were heterozygotes. The group C inversion polymorphism however, has more equal frequencies. In addition only one of the five chromosome pairs involved in the Robertsonian variation is polymorphic. This chromosome pair also occurs in group C.

The frequency of the heterozygotes of the group C inversion at Rottingdean, show a marked and significant deficiency accompanied by an increase in both homozygous arrangements. This significant departure from genetic equilibrium suggests that the heterozygotes may be less fit in some way than either homozygote.

The cytogenetic investigations in the present study are based on the chromosome analysis of unhatched embryos. It could be argued, therefore, that the deficiency of the inversion heterozygotes is a consequence of prezygotic selection in which abnormal or incompatible chromosomal rearrangements fail to produce viable gametes. The alternative of postzygotic selection, however, cannot be excluded.

Most members of the subgenus Nucella, including Thais emarginata (Deshayes), T. canaliculata (Duclos) (Lyons et al. 1972), T.hippocastaneum (Lamark) and T.dubia (Krauss) (Bokenham et al. 1938) and N.lapillus (Thorsen 1946, Pelseneer 1916) produce tough walled egg capsules which contain large numbers of eggs. Only a small proportion of eggs are fertile, the remainder halt in early development and act as nutrient or nurse eggs to the remaining embryos. It has been suggested that the very high egg mortality in these species may be the result of

several abnormalities such as chromosome clumping and stickiness, fragmentation, multipolar and deformed spindles in mitosis and failure of cleavage (Ahmed et al. 1974). It is entirely possible, therefore, that at least some of the nurse eggs may be the zygotic products of abnormal gametes and as such are subject to elimination due to, for example, developmental problems in embryogenesis. This process is well documented in chromosomal heterozygotes of Mus in which aneuploid gametes regularly pass through gametogenesis but produce abnormal zygotes which fail to reach term. (Cattanach and Mosely 1973, Gropp and Winking 1981).

Departures from the Hardy Weinberg equilibrium may also be a result of inbreeding. The panmitic unit of Nucella is not known but must be restricted by the distance the animal is able to crawl. Adult Nucella may remain on the same rock (within a few metres) for over a year. (personal comm. to Bantock et al. 1975). Investigations of a close relative of N.lapillus have shown that adult snails return to the same breeding areas each year. (Spight 1976) and that apparently continuous populations of whelks are divided into a series of partially isolated interbreeding colonies of ten to seven hundred snails (Spight 1974).

An apparent excess of structural homozygotes could occur when an inclusive sample is taken in a population sub-divided into small and separate breeding units. This is known as the Wahlund effect (Wallace 1968). The lack of homozygotic excess from the same sample, for chromosome number however, suggest this type of sampling error is not responsible for the deficiency of heterozygotes for the group C inversion.

It is also possible that the homozygous excess demonstrated in the prehatched embryos of Nucella will diminish in the subsequent stages of development. In the scallop Chlamys perculans (L.), individuals of less than one year deviate only slightly from the Hardy Weinberg expectation in the proportions of electrophoretic phenotypes, whereas the whole population of all age classes show a significant excess of homozygotes (Crisp 1974). Mortality rates of juvenilles in several species of Thais are extremely high.

Within two months of hatching ninety to ninety nine per cent of the snails die and only ten to thirty five per cent of the survivors live for a further ten months. In consequence, of 1,000 eggs produced annually by any one female, it is rare that even ten will reach the age of one year. (Spight 1975).

Whether the differential survival of different inversion types occurs different stages in the life cycle of *N. lapillus*, is not known.

In contrast to the genetic disequilibrium of frequencies of the group C inversion polymorphism, data from the distribution of the numerical polymorphism suggest that, although there is a slight deficiency of the heterozygotes (2n = 27), this is well within the deviation which could be expected by chance and is not of biological significance. This result alone suggests that the two chromosomal polymorphisms are independent from each other and provides indirect evidence that the polymorphisms occur on two different chromosome pairs of group C.

It seems unlikely, therefore, that the presence of these two particular chromosomal arrangements affect fitness by altering the epistatic interactions in the genome as for example is demonstrated in both the morabine grass hopper *Moraba scurra* (Lewontin and White 1961) and some *Drosophila* species (Wallace 1955, Lin *et al.* 1948). The result of the present investigation, however, does not exclude the possibility that combinations of other chromosomal re-arrangements in other polymorphic populations of *Nucella* may produce differences in fitness.

The adaptive significance of the group C inversion is not known, and in the absence of any detailed analysis of its distribution in either monomorphic (2n = 26) populations or in populations in which chromosomes other than those in group C, it is difficult to reach any firm conclusions as to the exact relationships between the structural and numerical chromosomal rearrangements.

The results of the present study show that the chromosome pairs involved in the Robertsonian variation at Rottingdean and Cuckmere Haven are restricted to one chromosome pair (from group C) and two chromosome pairs (both from group A)

from each area respectively. In addition at Cuckmere Haven, the chromosome numbers both within and between each sampling square are homogeneous irrespective of degree of exposure of the sampling sites.

The lack of an association between chromosome number and the degree of exposure of the shoreline has been reported in several populations of N. lapillus in Norway, France and the south of England, but in contrast to the results of the present investigations, the populations concerned were monomorphic for chromosome number 2n = 26.

It was the opinion of Staiger (1954, 1957,)and Mayr(1963) that there are two distinct chromosomal forms of Nucella lapillus of chromosome number 2n = 26 and the other of 2n = 36. The two forms are adapted to specific environmental conditions and readily hybridize in areas intermediate for wave exposure. The wide range of chromosomal arrangements found in such areas suggests widespread intro gression of both chromosome types.

In consequence the lack of acrocentric chromosomes (those involved in the Robertsonian polymorphism) from regions which are exclusively monomorphic for the 2n = 26 form has been attributed to the absence of sheltered locations suitable for the establishment of the 2n = 36 type. Even in the presence of sheltered locations (Hoxmark 1970, Bantock et al. 1974) other factors such as strong tidal currents or large overall water movement may prevent colonization by the 2n = 36 form.

This explanation may apply to regions of complete monomorphism but it does not readily explain the rather limited polymorphism found in the two areas of Rottingdean and Cuckmere Haven.

It is possible that both populations are the remnants of a previously large hetero-geneous population, similar to those found in both the Roscoff region of France and in the major bays in the south east of England. There is indirect evidence, that in regions where chromosome number varies between 2n = 26 and 2n = 36, selection acts against fused chromosomes in sheltered locations and against unfused chromosomes in exposed locations. It is equally true, however, that in many areas where one might expect to find

polymorphic populations only 2n = 26 forms are present. The widespread distribution of the 2n = 26 form and the limited distribution of the 2n = 36 form suggests that individuals of low chromosome number may be better adapted to a greater range of environmental conditions.

An unequal colonization of the region by two chromosomal types, in this case a high proportion of the 2n = 26 form, could swamp the adaptive advantage of both homozygotes (2n = 36 form) and some heterozygous combinations, to both sheltered and intermediate conditions.

In addition it is generally believed that the five chromosome pairs involved in the Robertsonian polymorphism have the same adaptive value (White 1978) so that, for example, in populations of low chromosome number all five chromosome pairs have an equal chance of occuring in the polymorphic state. There is some evidence, however, to suggest that at least two chromosome pairs (pairs 111 and V using Staiger's 1954 nomenclature) do not occur at random either with respect to one another or with respect to the heterogeneity of the population (Staiger 1954). In consequence, the adaptive value of each chromosome pair or combination of chromosome pairs may be different.

The presence of one or two numerically polymorphic chromosome pairs in the two populations from the present study and the fact that they are different in each region suggests that the occurrence is not arbitary but may represent an adaptive response to differing environmental variables.

It is not known whether centric fusion or fission has been responsible for the formation of the two chromosomal types (2n = 26 and 2n = 36). It seems likely, however, that the 2n = 26 form is derived from the 2n = 36 form by fusion of the acrocentric chromosomes. Firstly, because all the other members of the subgenus have chromosome numbers in excess of 2n = 18 and secondly if centric fusion were to occur, there is no readily available explanation for the quite considerable short arms observed in many of the acrocentrics involved in the polymorphism (White 1978).

The preceeding discussion on the possible origins of the numerical polymorphism in Nucella has invoked the theory

that the chromosome forms have evolved in some previous period of isolation so that the heterogeneous populations are the result of secondary contact. In common with several boreal gastropods, the genus Nucella is thought to have originated in the north Pacific and entered the north A tlantic during a warm period when it was possible to pass the Arctic ocean. In glacial times Nucella probably suffered severe local extinction especially in the north east Atlantic and was probably entirely eliminated from the North Sea. It is possible, however, that the north west Atlantic population survived the recent glacial maximum by moving into deeper water. In the post glacial amelioration of climate, Europe was probably recolonized from the north before the English Channel was ice free. (France Merril 1980, Cambridge and Kitching 1982). Under such conditions it is possible to envisage the establishment of two chromosomal races one distributed to the north and the other to the south. If the separation of the two forms has been insufficient to lead to reproductive is olation chromosome heterozygotes would be expected in regions where their distribution overlaps. Nucella on the Atlantic coast of North America is monomorphic for the 2n = 26 form (Mayr 1963) as are some populations in northern Europe (Hoxmark 1970). Little is known of the distribution of chromosome number in Nucella from southern Europe but populations in northern France and the south east coast of England are polymorphic and could represent the region in which the two distributions coincide. In the present study, however polymorphic populations have also been found in both south Wales and as far north as the Isle of Cumbrae on the west coast of Scotland.

Clearly until more data are available on the numerical polymorphism in other regions, it is premature to make any further speculation as to the origin of the distribution of Nucella in Europe.

It is possible that the chromosomal fusions have arisen independently within different populations as seen for example in the domestic house mouse Mus musculus (L.) (Gropp 1975, Capanna et al. 1976, 1977). In this species a total of forty eight different Robertsonian translocations

have been reported in wild populations so that each acrocentric autosome involved in the polymorphism can form one or more different Robertsonian metacentrics (Baranov 1980). There is no evidence to suggest that chromosome fusion involving different acrocentric chromosomes has occurred in Nucella. The results from the present investigation demonstrate a remarkable similarity between the chromosome pairs involved in the Robertsonian polymorphism in several widespread populations. Bantock and Page (1976) could find no significant differences in the 2n = 26 karyotypes from Scotland, Dorset and Cuckmere Haven, Sussex and Staiger (per. comm. to Dr. C.R. Bantock) could find no differences in the chromosome structure between polymorphic populations from France, Scotland or America with respect to the overall size, arm ratios or chiasma localization. In addition, the majority of meiotic figures in polymorphic populations are composed of bivalents and trivalents. There are no multivalents, which might be expected to occur if the acrocentric autosomes are involved in more than one Robertsonian fusion.

It seems, unlikely, therefore that the same chromosome fusions found in both populations, at Cuckmere Haven and Rottingdean, Sussex have arisen independently.

Whatever the origin of the numerical variation at Rottingdean and Cuckmere Haven, the distribution of chromosome number in the two areas is in general agreement with the hypothesis that total water movement may have a major affect on the proportion of acrocentric chromosomes within a population (Bantock and Cockayne 1975). There are two chromosomal pairs involved in the numerical polymorphism at Cuckmere Haven giving a chromosome number in the range 2n = 26 to 2n = 30. The mean tidal range is 7.5 metres in this region and in conjunction with the gradual slope of the shoreline the tidal currents are likely to be slight. In contrast the mean tidal range at Rottingdean is nearly double that at Cuckmere Haven (14.5 metres) and this is reflected in the lower chromosome number of 2n = 26 to 2n = 28 conferred by the Robertsonian polymorphism in one chromosome pair.

5. CONCLUSION

In spite of the many unforseen difficulties in the analysis of mitosis from polymorphic populations of Nucella lapillus, the results from the present investigation have provided substantial information on the chromosome pairs involved in both the numerical and structural polymorphisms.

The similarities in the five chromosome pairs involved in the Robertsonian polymorphism from several widespread populations suggest that they have a common rather than independent origin. A simple interpretation of the origins of this variation could be that it is the result of interbreeding between two previously isolated chromosomal races of chromosome number 2n = 26 and 2n = 36.

The analysis of the distribution of the structural and numerical polymorphisms is restricted, firstly because of the rarity of the group A inversion and secondly because there is difficulty in identifying the group C inversion in populations polymorphic for high chromosome number.

At Rottingdean,however, only one chromosome pair is involved in the numerical polymorphism and this is clearly distinguishable from the group C inversion. In this region there is a strong indication that the C group inversion heterozygotes are less fit than either homozygote. This results in a highly significant deviation from the Hardy Weinberg equilibrium. In contrast chromosome number is in genetic equilibrium and accordingly provides evidence to suggest that the two chromosomal rearrangements in this region occur independently of each other. It is unlikely therefore, that the presence of this particular C group inversion is associated with an overall reduction in chromosome number.

It is clear that chromosomal architecture in Nucella lapillus has immense potential for variation. The results from the present investigation suggest that although some environmental selective agents may be strong enough to produce similarities in chromosome number between different regions, the distribution of chromosomal rearrangements may differ considerably between populations.

The situation, therefore, remains tantalizingly incomplete.

In view of the results from this study it is unlikely that chromosomal analysis of the type described in the present investigation, alone, will be sufficient to elucidate the obviously complex interactions that occur in populations of Nucella.

It will be necessary to combine several lines of enquiry to determine, for example, the relative fitness of different chromosomal types or the relationship between chromosome structure and shell morphology, in order to further our understanding of variation in Nucella lapillus.

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APPENDIX A

APPENDIX A

The co-efficients of variation for chromosome pairs one to three from populations of Cepaea nemoralis from the western Berkshire Downs.

Pop	Pair 1		Pair 2		Pair 3 *	
	Length	R value	Length	R value	Length	R value
A1	6.687	8.636	6.701	9.869	11.865	16.163
A2	7.675	7.688	6.843	7.869	11.999	18.359
B1	6.324	8.590	6.711	11.401	10.337	20.159
B2	5.983	7.122	6.919	9.169	10.805	17.124
C1	9.303	7.065	7.522	9.803	10.308	23.127
C2	7.211	3.212	8.889	9.425	9.577	15.785
C3	6.593	10.900	7.041	7.554	10.783	29.262
D1	7.234	9.392	8.284	8.941	11.686	1.5.398
D2	7.130	8.925	6.928	6.873	12.439	17.712
E	8.281	8.919	6.809	7.658	19.101	28.837

* Chromosome pairs possessing a secondary contriction

The co-efficients of variation of chromsomes from the human karyotype calculated from data presented in the Paris Conference on the standardization of Human Cytogenetics. (1971).

Chromosome pair	Length	R value	
1	5.130	2.411	
2	4.950	4.650	
3	4.612	3.316	
4	4.508	6.422	
5.	5.016	5.945	
6	4.475	4.264	
7	5.056	4.535	
8	5.294	5.277	
9	5.083	5.795	
10	4.815	7.223	
11	4.924	5.800	
12	4.549	7.755	
13	6.310	18.893	*
14	6.433	19.189	*
15	6.185	18.236	*
16	5.446	6.630	*
17	5.815	8.184	
18	5.597	9.841	
19	6.517	4.940	
20	6.445	5.558	
21	8,947	16.193	*
22	8.922	16.181	*
X	5.097	5.277	
Y	6.372	11.711	

The results of the intermediate G tests for the analysis of R values from populations of C. nemoralis from the western Berkshire Downs.

Populations

D_1 B_1 B_2 C_2	G = 24.544 > P > 0.995	ns
D_1 B_1 B_2 C_2 C_1	G = 31.052 0.995 > P > 0.9	ns
D_1 B_1 B_2 C_2 C_3	G = 29.974 0.995 > P > 0.9	ns
D_1 B_1 B_2 C_2 D	G = 32.394 0.095 > P > 0.9	ns
D_1 B_1 B_2 C_2 D_2 C_1 C_2	G = 41.168 0.995 > P > 0.9	ns
D_1 B_1 B_2 C_2 D_2 C_1 C_2 A_2 E	G = 97.818 P < 0.005	
A_1 A_2 E	G = 18.819 P > 0.995	ns
A_1 A_2 E D_2 C_1 C_3	G = 48.042 0.9 > P > 0.5	ns
A_1 A_2 E D_2 C_1 C_3 B_1 B_2 C_2	G = 89.879 P < 0.005	

Areas

A E	G = 7.694 P > 0.995 ns
A E C	G = 23.819 0.5 > P > 0.1 ns
A E C D	G = 35.848 0.1 > P > 0.05 ns
B C	G = 6.38 P > 0.995 ns
B C D	G = 10.168 0.995 > P > 0.975 ns
B C D E	G = 26.014 0.5 > P > 0.1 ns

The relative lengths(RL) and R values for the karyotypes used in the analysis of variation in chromsome structure in populations of C. nemoralis from the western Berkshire Downs.

POPULATION A1

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.88	8.42	.94	8.21	.80	9.24	.93	8.66	.96	9.13	.98	8.23
	.70	8.84	.87	8.00	.77	8.66	.86	8.98	.84	8.98	.98	8.58
Pair 2	.83	3.65	.86	3.22	.85	3.50	.79	3.38	.95	3.56	.69	3.52
	.82	3.05	.93	2.93	.94	3.65	.84	3.09	.75	3.34	.76	3.13
Pair 3	.30	2.98	.46	2.51	.35	2.73	.29	3.23	.36	2.32	.38	2.49
	.28	3.56	.38	2.80	.35	2.68	.28	3.02	.25	3.22	.28	2.97
	.73	2.66	.62	2.80	.74	2.70	.77	2.67	.66	2.41	.81	2.40
	.76	2.42	.55	2.76	.90	2.36	.78	2.44	.66	2.56	.75	2.50
	.92	2.07	.83	2.05	.61	2.40	.80	2.30	.90	2.16	.82	2.08
	.87	2.25	.88	2.24	.69	2.45	.81	2.11	.78	1.99	.84	2.36
	.48	2.54	.47	2.58	.48	2.32	.42	2.53	.38	2.36	.35	2.21
	.44	2.57	.42	2.37	.51	1.80	.38	2.40	.40	2.52	.45	2.56
	.75	1.35	.94	1.97	.62	1.43	.59	1.67	.83	1.82	.83	2.29
	.64	1.74	.60	1.61	.66	1.66	.53	2.17	.37	1.48	.57	1.42
	.69	1.97	.79	2.05	1	2.13	.77	1.48	.88	2.09	.56	2.19
	.67	1.66	.52	1.58	.91	1.60	.47	1.67	.44	1.61	.61	1.86
	.86	1.46	.77	1.82	.90	1.91	.78	2.05	.73	1.67	.96	1.96
	.81	1.65	.57	2.14	.73	1.62	.43	1.83	.57	1.57	.78	1.65
	.61	2.00	.86	.167	58	1.58	.57	1.64	.78	1.56	.80	2.16
	.68	1.81	.38	1.76	.43	1.73	.47	1.72	.62	1.77	.58	1.95
	.78	2.09	.64	1.54	.74	1.63	.97	2.29	.73	1.88	.65	1.60
	.88	1.87	.83	1.66	.94	1.77	.75	1.77	.55	1.48	.91	2.28
	.83	1.69	.47	1.73	.33	1.46	.77	1.75	.66	1.76	.66	2.12
	1	2.10	.69	1.69	.51	1.51	.45	1.88	.88	2.01	.68	1.53
	.38	1.75	.66	1.74	.60	2.16	.62	1.69	.54	1.77	.93	1.89
	.53	1.92	.62	1.65	.90	1.67	.80	1.57	.59	1.77	.59	1.57
	.56	1.85	.63	1.79	.58	1.60	.82	1.50	.83	2.05	.89	1.79
	.85	1.84	.45	1.53	.44	1.63	.86	1.67	.77	1.76	.54	1.72
	.78	1.85	1	1.64	1	1.62	.59	1.42	.69	1.61	.61	2.01
	.50	1.43	.82	1.82	.67	1.40	.64	1.72	.54	1.42	.46	1.73
	.81	1.62	.55	1.84	.63	1.97	.77	1.85	.51	1.52	.81	1.97
	.65	1.91	.45	1.76	.64	1.70	1	1.95	.67	1.62	.62	1.95
	.49	1.77	.73	2.16	.95	1.85	.79	1.61	.86	1.81	.98	1.68
	.57	1.40	.50	1.83	.55	1.63	.70	1.62	.65	1.62	.91	1.90
	.72	1.56	.72	2.06	.95	1.84	.46	1.42	.53	1.53	.74	1.69
	.50	1.73	.85	1.83	.70	1.85	.47	1.67	.46	1.42	.81	1.66
	.61	1.45	.85	1.92	.77	1.66	.69	1.73	.86	1.85	.79	1.75
	.60	1.43	.72	1,63	.66	1.66	.57	1.59	.63	1.83	.47	1.69
	.66	2.03	.62	1.65	.60	1.60	.42	1.54	.85	2.11	.62	1.87
	.50	1.49	.80	1.96	.55	1.82	.53	1.58	1	1.62	.82	1.72
	.55	1.51	.68	1.54	.64	1.85	.88	1.70	.71	1.53	.54	1.55
	.79	1.61	.51	1.89	.68	1.97	.80	1.70	.82	1.79	.55	1.99
	.73	1.71	.61	1.89	.88	1.80	.67	1.72	.39	1.77	.40	1.54
	.62	1.51	.79	1.97	.76	2.18	.83	1.83	.92	2.06	.88	1.99

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.92	8.03	.76	8.74	.97	8.26	.98	8.45	.87	8.09	.91	8.14
	.85	7.45	.85	8.85	.97	8,26	.84	6.71	.94	8.72	.78	8.07
Pair 2	.64	3.28	.79	2.78	.96	3.47	.82	3.67	.98	3.05	.80	3.31
	.71	3.69	.93	3.39	.78	3.40	.79	3.19	.88	3.16	.73	3.04
Pair 3	.35	2.83	.25	3.49	.34	2.78	.31	2.97	.45	2.25	.40	2.57
	.34	2.85	.32	2.74	.32	3.12	.36	2.79	.36	2.70	.36	2.25

POPULATION A1

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.88	8.42	.94	8.21	.80	9.24	.93	8.66	.96	9.13	.98	8.23
	.70	8.84	.87	8.00	.77	8.66	.86	8.98	.84	8.98	.98	8.58
Pair 2	.83	3.65	.86	3.22	.85	3.50	.79	3.38	.95	3.56	.69	3.52
	.82	3.05	.93	2.93	.94	3.65	.84	3.09	.75	3.34	.76	3.13
Pair 3	.30	2.98	.46	2.51	.35	2.73	.29	3.23	.36	2.32	.38	2.49
	.28	3.56	.38	2.80	.35	2.68	.28	3.02	.25	3.22	.28	2.97
	.73	2.66	.62	2.80	.74	2.70	.77	2.67	.66	2.41	.81	2.40
	.76	2.42	.55	2.76	.90	2.36	.78	2.44	.66	2.56	.75	2.50
	.92	2.07	.83	2.05	.61	2.40	.80	2.30	.90	2.16	.82	2.08
	.87	2.25	.88	2.24	.69	2.45	.81	2.11	.78	1.99	.84	2.36
	.48	2.54	.47	2.58	.48	2.32	.42	2.53	.38	2.36	.35	2.21
	.44	2.57	.42	2.37	.51	1.80	.38	2.40	.40	2.52	.45	2.56
	.75	1.35	.94	1.97	.62	1.43	.59	1.67	.83	1.82	.83	2.29
	.64	1.74	.60	1.61	.66	1.66	.53	2.17	.37	1.48	.57	1.42
	.69	1.97	.79	2.05	1	2.13	.77	1.48	.88	2.09	.56	2.19
	.67	1.66	.52	1.58	.91	1.60	.47	1.67	.44	1.61	.61	1.86
	.86	1.46	.77	1.82	.90	1.91	.78	2.05	.73	1.67	.96	1.96
	.81	1.65	.57	2.14	.73	1.62	.43	1.83	.57	1.57	.78	1.65
	.61	2.00	.86	.167	58	1.58	.57	1.64	.78	1.56	.80	2.16
	.68	1.81	.38	1.76	.43	1.73	.47	1.72	.62	1.77	.58	1.95
	.78	2.09	.64	1.54	.74	1.63	.97	2.29	.73	1.88	.65	1.60
	.88	1.87	.83	1.66	.94	1.77	.75	1.77	.55	1.48	.91	2.28
	.83	1.69	.47	1.73	.33	1.46	.77	1.75	.66	1.76	.66	2.12
	1	2.10	.69	1.69	.51	1.51	.45	1.88	.88	2.01	.68	1.53
	.38	1.75	.66	1.74	.60	2.16	.62	1.69	.54	1.77	.93	1.89
	.53	1.92	.62	1.65	.90	1.67	.80	1.57	.59	1.77	.59	1.57
	.56	1.85	.63	1.79	.58	1.60	.82	1.50	.83	2.05	.89	1.79
	.85	1.84	.45	1.53	.44	1.63	.86	1.67	.77	1.76	.54	1.72
	.78	1.85	1	1.64	1	1.62	.59	1.42	.69	1.61	.61	2.01
	.50	1.43	.82	1.82	.67	1.40	.64	1.72	.54	1.42	.46	1.73
	.81	1.62	.55	1.84	.63	1.97	.77	1.85	.51	1.52	.81	1.97
	.65	1.91	.45	1.76	.64	1.70	1	1.95	.67	1.62	.62	1.95
	.49	1.77	.73	2.16	.95	1.85	.79	1.61	.86	1.81	.98	1.68
	.57	1.40	.50	1.83	.55	1.63	.70	1.62	.65	1.62	.91	1.90
	.72	1.56	.72	2.06	.95	1.84	.46	1.42	.53	1.53	.74	1.69
	.50	1.73	.85	1.83	.70	1.85	.47	1.67	.46	1.42	.81	1.66
	.61	1.45	.85	1.92	.77	1.66	.69	1.73	.86	1.85	.79	1.75
	.60	1.43	.72	1,63	.66	1.66	.57	1.59	.63	1.83	.47	1.69
	.66	2.03	.62	1.65	.60	1.60	.42	1.54	.85	2.11	.62	1.87
	.50	1.49	.80	1.96	.55	1.82	.53	1.58	1	1.62	.82	1.72
	.55	1.51	.68	1.54	.64	1.85	.88	1.70	.71	1.53	.54	1.55
	.79	1.61	.51	1.89	.68	1.97	.80	1.70	.82	1.79	.55	1.99
	.73	1.71	.61	1.89	.88	1.80	.67	1.72	.39	1.77	.40	1.54
	.62	1.51	.79	1.97	.76	2.18	.83	1.83	.92	2.06	.88	1.99

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.92	8.03	.76	8.74	.97	8.26	.98	8.45	.87	8.09	.91	8.14
	.85	7.45	.85	8.85	.97	8,26	.84	6.71	.94	8.72	.78	8.07
Pair 2	.64	3.28	.79	2.78	.96	3.47	.82	3.67	.98	3.05	.80	3.31
	.71	3.69	.93	3.39	.78	3.40	.79	3.19	.88	3.16	.73	3.04
Pair 3	.35	2.83	.25	3.49	.34	2.78	.31	2.97	.45	2.25	.40	2.57
	.34	2.85	.32	2.74	.32	3.12	.36	2.79	.36	2.70	.36	2.25

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.62	2.41	.86	2.61	.78	2.64	.93	3.12	.73	2.73	.60	2.61
	.66	2.62	.84	2.57	.71	2.48	.92	2.59	.58	2.67	.57	2.58
	.81	2.19	.66	2.28	.86	2.34	.76	2.38	.72	2.38	.67	2.33
	.92	2.22	.70	2.31	.99	2.19	.72	2.14	.78	2.36	.65	2.61
	.39	2.52	.42	2.32	.37	2.25	.55	2.32	.52	2.37	.44	2.32
	.49	2.15	.33	2.43	.50	2.15	.38	2.62	.58	2.23	.50	2.46
	.69	1.77	.61	1.69	.77	.181	.96	.176	.45	1.77	.57	1.65
	.54	1.59	.91	2.01	.55	1.65	.45	1.68	.83	1.94	.77	1.95
	.80	2.14	.87	1.72	.58	1.67	.50	1.63	.46	1.92	.71	1.76
	.69	1.57	.68	1.88	.97	2.41	.54	1.70	.61	1.73	.70	1.58
	.37	2.01	1	1.46	.91	1.94	.93	2.09	.43	1.64	.62	1.84
	.67	1.92	.47	1.59	.81	1.72	.62	1.95	.69	2.02	1	1.83
	.81	1.51	.63	2.24	.57	1.72	.60	1.64	.90	1.79	.51	1.79
	.46	1.60	1	1.53	.88	1.62	.87	1.62	.81	1.51	.72	1.88
	.93	1.90	.75	1.50	.73	2.01	.67	1.87	.90	1.76	.70	2.32
	.43	1.69	.44	1.62	.69	1.59	.92	1.98	.73	1.99	.81	1.64
	.53	1.78	.74	1.83	.62	1.53	.61	1.47	.80	1.64	.61	2.06
	.83	1.72	.70	2.25	.75	1.67	.79	1.60	.68	1.65	.83	2.00
	.62	1.58	.79	1.79	.65	1.49	.60	1.84	.90	1.95	.71	1.60
	1	1.95	.69	1.60	.88	1.84	.57	1.81	.93	1.69	.80	1.46
	.55	1.46	.81	1.38	.85	2.03	.73	1.84	.80	1.82	.68	1.75
	.50	1.45	.68	1.51	.83	1,95	,82	1.68	.89	2.23	.83	2.14
	.93	1.67	.58	1.70	.81	1.72	.61	1.84	.55	1.83	.78	1.68
	.92	1.85	.52	1.42	.52	1.74	.49	1.84	.74	1.88	.61	1.69
	.79	1.83	.63	1.90	.85	1.81	.52	1.51	.78	1.40	.78	2.49
	.59	1.85	.78	1.39	.72	1.99	.48	1.42	.45	1.66	.86	1.44
	.87	2.15	.67	1.93	.61	1.64	1	1.89	.67	1.61	.81	2.07
	.81	2.09	.51	1.92	.60	1.72	.78	1.82	.84	2.24	1	1.48
	.72	1.89	.45	2.00	.90	1.71	.64	1.56	.69	1.97	.82	1.64
	.53	1.72	.89	1.92	.61	1.44	.70	1.64	.57	1.67	.75	1.63
	.63	2.02	.85	1.32	.85	1.76	.87	1.75	.59	1.69	.52	1.84
	.80	1.87	.52	1.60	.72	186	.83	2.30	.70	1.55	.93	1.78
	.72	1.67	.36	1.85	.76	1.75	1	2.03	.56	1.49	.91	1.91
	.73	1.65	.73	1.64	.41	1.58	.53	1.87	.58	1.97	.72	1.57
	.47	1.95	.73	1.90	.70	1.95	.63	2,15	.54	1.61	.82	1.53
	.48	1.76	.76	1.90	.36	1.58	.77	1.95	.71	1.75	.61	1.82
	.96	2.33	.79	1.95	.38	1.68	.62	1.53	.61	1.68	.55	1.40
	.59	1.59	.84	1.68	.71	1.92	.76	1.60	.83	2.46	.57	1.81

KARYOTYPE	13.		14.		15.		16.		17.	
	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.87	8.22	.85	8.90	.90	7.30	.80	7.43	.78	7.88
	.83	8.19	.85	8.19	.93	8.65	.76	7.98	.81	8.03
Pair 2	.94	3.16	.79	3.25	.82	3.51	.76	3.06	.83	3.11
	.89	3.20	.83	3.18	.84	3.34	.69	3.34	.83	3.42
Pair 3	.28	2.69	.31	2.55	.33	2.50	.29	2.56	.29	2.06
	.32	2.77	.43	2.73	.26	2.82	.33	.294	.40	2.61
	.67	2.72	.79	2.19	.54	2.44	.98	2.44	.98	2.43
	.65	2.31	.79	2.16	.61	2.31	.86	2.21	.72	2.62
	.79	2.20	.96	2.12	.82	2.24	.66	2.32	.90	2.40
	.74	2.13	.92	2.66	.79	2.05	.62	2.52	.82	2.41
	.45	2.53	.40	2.55	.53	2.40	.51	2.64	.45	2.78
	.48	2.60	.44	2.43	.46	2.38	.40	2.68	.41	2.58

KARYOTYPE	13.		14.		15.		16.		17.	
	R	RL	R	RL	R	RL	R	RL	R	RL
	.66	1.65	.84	1.91	.88	2.05	.90	1.98	.54	1.58
	.70	2.21	.54	1.47	.57	1.55	.73	2.01	.89	1.61
	.62	1.19	.92	2.11	.80	1.83	.58	1.98	.39	1.47
	.58	1.67	.67	1.97	1	2.16	.44	1.85	.70	1.49
	.74	2.18	.87	1.77	.43	1.57	.58	1.54	.73	1.49
	.78	1.65	.50	1.70	.56	1.79	.54	1.52	.53	1.60
	.64	1.83	.60	1.59	.55	1.31	1	1.91	.53	1.48
	.72	1.62	.61	1.91	.86	1.93	.71	2.13	.61	1.55
	.78	1.54	.72	1.83	.46	1.79	.93	1.50	.65	2.35
	.62	1.91	.95	1.53	.47	1.45	.51	1.83	.59	1.73
	.71	1.46	.72	1.96	.56	1.78	.69	1.70	.58	2.16
	.52	1.43	.86	1.86	.65	1.88	.80	1.70	.76	1.45
	.73	1.95	1	1.51	.90	1.82	.81	1.77	.77	1.83
	.39	1.53	.93	2.04	.82	1.57	.68	1.69	1	2.37
	.60	1.75	.60	1.74	.62	2.08	.82	2.01	.81	1.77
	1	1.50	.51	1.55	.62	2.09	.72	1.64	.93	1.71
	.71	1.61	.51	1.74	.52	1.76	.87	1.76	.52	1.52
	1	1.79	1	2.20	.62	1.59	.77	1.71	.66	1.93
	.68	1.68	.49	1.64	,71	2,03	,60	1,87	,84	2,08
	.42	1.84	.84	2.13	1	1.84	.87	1.79	.73	2.00
	.63	1.52	.77	1.83	.66	1.90	.73	1.94	.65	1.76
	.93	1.98	.82	2.25	.85	1.78	.74	1.88	.52	1.69
	.66	2.29	.56	1.54	.81	2.17	.78	2.29	.65	1.49
	.83	1.79	.78	1.90	.69	1.46	.85	1.82	.63	1.91
	.60	1.59	.45	1.62	.75	2.00	.76	1.79	.48	1.65
	.90	1.82	.48	1.71	.63	1.74	.56	1.46	.85	2.05
	.78	1.99	.93	1.43	.73	1.65	.72	1.76	.50	1.71
	.46	1.98	.76	1.74	.72	1.93	.67	1.96	.70	1.81
	.75	1,93	.34	2,01	,59	1,62	,93	1,75	,64	2,03
	.89	1,84	.54	1.28	.61	1.73	1	1.81	.89	1.81
	.62	1.53	.80	1.59	.86	1.75	.66	1.66	.91	1.82
	.79	2.05	.74	1.82	.83	2.15	.48	1.49	.48	1.51

POPULATION A2

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1.	.82	7.92	.81	9.31	.95	7.25	.86	8.58	.78	8.55	.84	7.83
	.75	8.16	.91	8.53	.88	8.37	.95	7.97	.83	7.35	.87	8.60
Pair 2.	.88	3.20	.81	3.36	.81	3.52	1	3.20	.83	3.45	.88	2.95
	.77	3.42	.93	3.58	.95	3.07	.95	2.89	.85	3.61	.99	2.76
Pair 3.	.37	2.89	.31	2.74	.37	2.55	.31	2.44	.44	2.15	.38	2.60
	.38	2.97	.43	2.48	.42	2.44	.39	2.70	.32	2.46	.38	2.60
	.76	1.68	.78	1.76	.52	2.21	.72	1.68	.86	1.82	.83	1.86
	.77	2.87	.76	2.24	.65	2.62	.73	2.25	.79	2.43	.81	2.52
	.77	2.66	.88	2.42	.49	2.05	.77	2.58	.69	2.61	.87	2.17
	.96	2.43	.72	2.63	.72	2.45	.78	2.03	.79	2.24	.76	2.38
	.90	2.35	.74	2.68	.55	2.64	.66	2.11	.56	2.46	.41	2.29
	.41	2.59	.55	2.41	.44	1.94	.38	2.52	.44	2.34	.52	2.49
	.46	2.46	.36	2.29	.57	2.04	.49	2.42	.45	2.55	.52	2.27
	1	2.19	.41	1.45	.76	1.67	.57	2.01	.72	1.63	.63	2.07
	.47	1.69	.43	1.74	.82	2.01	.70	1.98	.83	1.82	.71	1.86
	.79	1.64	.66	1.55	.68	1.58	.75	1.77	.69	1.62	.77	1.90

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.56	1.83	.61	1.62	.64	1.77	.91	1.91	.99	1.55	.78	1.95
	1	1.92	.47	2.15	.68	1.58	.55	1.83	.64	1.67	.88	2.04
	.72	1.83	.76	1.70	.36	1.93	.94	2.14	.96	2.07	.48	1.90
	.82	1.65	.71	1.78	1	1.71	.49	1.54	.83	1.84	.48	2.02
	.93	1.87	.59	1.72	.47	1.71	.61	1.74	.59	1.57	.69	1.52
	.79	1.94	.55	1.79	.46	1.93	.78	2.09	.48	1.67	.63	1.86
	.87	1.54	.53	1.54	.44	1.86	.91	1.91	.67	1.75	.52	1.62
	.60	1.60	1	1.91	.77	2.06	.52	1.70	.73	2.05	.79	1.67
	.88	1.97	.85	1.77	.55	1.91	.59	1.68	.79	1.84	.54	1.76
	.69	1.58	.64	1.52	.71	1.55	.74	1.48	.52	1.72	.85	1.71
	.84	1.84	.73	2.19	.90	1.69	.78	1.71	.82	1.79	.83	1.86
	.57	1,64	.66	1.94	.63	1.66	.77	1.68	.60	1.72	.80	1.62
	.93	1.62	1	1.86	.72	1.65	.45	1.73	.99	1.92	.74	1.93
	1	1.69	.56	1.60	.53	1.65	.45	1.98	.53	1.68	.90	2.17
	.68	1.72	.71	1.69	.78	1.80	.65	1.48	.65	1.75	.69	1.91
	.87	1.98	.78	1.72	.54	1.48	.87	1.59	.72	1.79	.75	1.85
	.67	1.67	.67	1.44	1	1.40	.83	1.61	.74	1.96	.49	2.02
	.74	1.78	.56	1.58	.86	1.92	.72	1.79	.62	1.98	.66	1.84
	.54	1.86	.61	1.76	.77	1.92	.83	1.85	.47	1.76	.75	1.56
	.94	1.76	.80	1.66	.70	1.80	.81	1.89	.82	1.63	.51	1.45
	.62	1.68	.62	2.26	.82	1.94	.58	1.90	.58	1.69	.56	1.90
	.84	1.70	.73	1.69	.69	1.80	.48	1.97	.68	1.44	.55	2.21
	.74	1.76	.58	1.53	.68	2.37	.55	1.79	.69	2.10	.57	1.69
	.52	1.71	.66	1.76	.21	2.41	.48	1.77	.47	2.09	.74	1.76
	.53	1.62	.89	1.72	.61	1.77	.69	1.81	.75	2.03	.65	1.92
	.68	1.64	.74	1.63	.87	1.83	.79	1.83	.72	2.16	.60	1.62
	.59	1.59	.44	1.41	.83	2.06	.74	1.90	.80	1.94	.58	1.49
	.81	1.68	.74	1.71	.86	2.21	.73	2.07	.58	1.66	.73	1.80

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1.	.82	8.76	.94	8.10	.78	9.45	.82	7.92	.95	7.74	.88	8.22
	.85	8.07	.85	9.52	.80	8.96	.75	8.16	.93	9.15	.74	7.81
Pair 2.	.82	3.09	.78	3.30	.97	3.02	.88	3.20	.83	3.14	.83	3.30
	.89	3.52	.78	2.96	.80	3.14	.77	3.42	.87	3.16	.90	3.21
Pair 3.	.47	2.45	.46	2.29	.40	3.20	.37	2.89	.29	2.93	.35	2.80
	.37	2.54	.45	2.60	.27	3.27	.38	2.97	.46	2.78	.21	3.91
	.78	2.46	.85	2.39	.88	2.77	.77	2.87	.95	2.56	.95	2.51
	.84	2.52	.78	2.68	.90	2.88	.77	2.66	.72	2.75	.81	2.68
	.90	2.33	.76	2.61	.72	2.30	.96	2.43	.75	2.31	.71	2.37
	.76	2.37	.69	2.50	.85	2.22	.90	2.36	.82	2.37	.80	2.20
	.46	2.29	.59	2.28	.39	2.53	.41	2.59	.40	2.28	.52	2.25
	.53	2.49	.53	2.20	.33	2.46	.46	2.46	.48	2.49	.34	2.14
	1	2.10	.82	1.97	.94	1.92	.76	1.68	.75	1.99	.63	1.72
	.60	1.57	.59	1.99	.51	1.89	1	2.19	.68	1.68	.70	1.78
	.66	1.67	.65	1.90	.59	1.90	.47	1.69	.77	1.70	.61	1.63
	.63	1.58	.68	1.84	.61	1.61	.79	1.64	.92	.145	.53	1.89
	.72	1.65	.51	1.93	.60	1.60	.56	1.83	.74	1.80	.75	1.79
	.86	1.61	.80	1.84	.53	1.62	1	1.92	.69	.159	.52	1.67
	.77	1.70	.72	1.76	.64	.176	.72	.183	.61	1.55	.90	1.62
	.89	1.70	.74	1.86	.66	1.95	.82	1.65	.45	1.81	.88	1.99
	.84	1.65	.91	1.66	.90	1.70	.93	1.87	.79	1.66	.67	1.56

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.73	1.77	.82	1.79	.56	1.37	.79	1.94	.52	1.98	.63	1.80
	.49	1.71	.70	1.56	.72	1.33	.87	1.54	.77	2.16	.61	1.70
	1	2.12	.47	1.56	.76	1.93	.60	1.60	.62	2.00	.61	1.79
	.78	1.55	.74	1.75	.76	1.48	.88	1.97	.66	1.79	.78	1.74
	.82	1.71	.51	1.58	.55	2.06	.69	1.58	.60	1.80	.67	1.67
	.62	1.85	.81	1.71	.61	1.60	.84	1.84	.94	2.29	.80	1.63
	.56	1.64	.80	1.64	.54	1.56	.57	1.64	.85	1.51	.51	1.97
	.80	1.61	.75	1.48	.79	1.66	.93	1.62	.71	1.45	.64	1.58
	.70	1.77	.64	1.48	.65	1.81	1	1.69	.89	1.58	.48	2.07
	.70	1.75	.77	1.69	1	1.65	.68	1.72	.78	1.88	.84	1.64
	.57	1.59	.62	1.79	.84	1.79	.87	1.98	.63	1.75	.67	1.52
	.51	2.00	.60	1.63	.77	1.79	.67	1.67	1	1.98	.71	1.51
	.66	2.02	.55	1.87	.67	1.61	.74	1.78	.91	1.90	.67	1.73
	.63	1.78	.53	1.77	.65	1.76	.54	1.85	.71	1.43	.48	1.73
	.86	1.95	.86	1.62	.70	1.38	.94	1.76	.88	1.60	.77	2.07
	1	1.61	.78	1.75	.70	1.45	.62	1.68	.66	1.91	.83	1.81
	.71	1.78	.76	1.87	1	1.58	.84	1.70	.83	1.78	.76	1.84
	.75	1.90	.79	1.98	.59	1.77	.74	1.76	.93	1.59	.80	1.71
	.72	1.93	.92	1.75	.55	1.62	.52	1.71	.83	1.54	.75	1.85
	.67	2.04	.92	1.83	.50	1.69	.53	1.62	.89	1.37	.52	1.96
	.70	1.69	.67	1.71	.73	1.34	.68	1.64	.68	1.58	.65	1.85
	.73	1.96	.58	1.95	.66	1.55	.59	1.59	.39	1.93	.90	1.93
	.83	1.75	.52	1.85	.87	1.74	.81	1.68	1	2.18	.83	1.93

POPULATION B1

KARYOTYPE	13.		1.		2.		3.		4.		5.	
Pair 1.	R	RL	R	RL	R	RL	R	RL	R	RL		RL
	.85	7.18	.86	8.88	.85	8.51	.93	7.89	.77	8.39	.87	7.67
	.97	8.61	.70	8.07	.95	8.96	.92	7.92	.92	8.45	.85	8.22
Pair 2.	.96	3.13	.98	3.38	.91	3.06	.72	3.06	.95	3.15	.83	3.07
	.76	3.47	.90	3.54	.97	2.81	.83	3.20	.70	3.16	.91	3.25
Pair 3.	.34	3.42	.35	2.71	.39	2.39	.47	2.64	.40	2.55	.57	2.13
	.30	3.06	.39	2.83	.40	2.89	.37	2.49	.52	2.47	.36	1.98
	.76	2.61	.72	2.49	.88	2.49	.80	2.65	.80	2.28	.79	2.76
	.76	2.32	.81	2.56	.78	2.66	.88	3.26	.94	2.58	.77	3.05
	.85	2.38	.92	2.01	.68	2.37	.94	2.21	.92	2.26	.87	2.30
	.86	2.38	.92	2.22	.76	2.10	.83	2.40	.78	2.41	.69	2.32
	.46	2.28	.54	2.41	.55	2.32	.49	2.46	.39	2.22	.49	2.37
	.53	2.00	.44	2.66	.50	2.40	.55	2.75	.42	1.88	.54	2.44
	.73	1.64	.88	1.99	.70	1.93	.57	1.58	.71	1.81	.63	2.17
	1	2.27	.70	1.84	.63	1.76	.62	1.69	1	1.97	.72	1.93
	.85	2.42	.69	1.66	.97	1.87	.73	1.56	.76	1.53	1	1.91
	.62	1.77	.95	1.79	.67	1.74	.90	2.01	.61	2.02	.78	1.57
	.77	1.79	.80	2.01	.72	2.12	.85	1.68	.55	1.50	.74	1.91
	.70	2.26	.71	1.64	.81	1.63	.76	1.63	.83	1.64	.75	2.20
	.68	2.01	.68	1.89	.66	1.69	.70	1.84	.81	1.65	.71	1.96
	.85	1.92	.71	1.73	.88	1.62	.88	1.88	.64	1.87	.94	1.80
	.60	1.80	.76	1.79	.72	1.92	.66	1.80	.50	1.96	.74	1.57
	.68	1.67	.81	1.83	1	1.84	.74	2.13	.80	2.01	.75	1.68
	.84	1.87	.55	1.53	.89	2.09	.77	1.98	.95	2.18	.75	2.08
	.73	1.49	.79	1.44	.81	1.55	.88	2.10	.94	1.79	.78	1.74
	.72	1.48	.69	1.77	.72	1.77	.61	1.53	.83	1.72	.84	1.54
	.51	1.51	.83	1.74	.90	1.84	.76	1.74	.89	1.93	.75	1.86
	.65	1.50	.61	2.10	.77	1.98	.74	1.63	.77	1.69	.86	1.82

KARYOTYPE13.		1.		2.		3.		4.		5.	
R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
.81	1.65	.64	1.58	.73	1.34	.76	2.33	.65	1.61	.62	1.91
.69	1.91	.79	1.96	.92	1.54	.67	1.92	.89	1.92	.90	1.69
.61	1.83	.91	1.58	.57	1.74	.79	1.94	.71	1.75	.50	1.87
.93	1.51	.74	1.54	.77	1.65	.77	1.56	.80	1.53	.63	2.18
.77	1.98	.60	1.67	.83	1.42	.84	1.90	.67	1.81	.73	1.84
.91	1.81	.89	1.97	1	2.03	.77	1.70	.65	1.87	.89	1.97
.73	1.71	.71	1.46	.65	1.83	.72	1.72	.82	1.79	.55	1.90
.59	1.84	.97	1.92	.91	2.05	.76	1.55	.72	1.89	.88	1.76
1	2.06	.64	1.61	.63	1.56	.53	1.65	.62	1.75	.46	1.64
.87	1.80	.69	1.57	.93	2.09	.88	.173	.80	1.53	.72	1.92
.56	1.87	.92	1.45	.68	1.76	.73	1.71	.87	1.95	.97	1.78
.67	1.48	.47	1.50	.64	1.39	.88	2.09	.58	1.61	.77	1.79
.73	1.71	.65	2.02	.72	1.72	.54	1.55	.69	1.62	.69	1.92
.63	1.61	.88	2.11	.94	1.68	.75	1.58	.71	1.67	.65	1.60
.74	1.61	.66	1.84	.47	1.63	.57	1.58	.50	1.54	.88	1.52
.74	1.67	.83	1.67	.70	1.66	.51	1.77	.84	2.04	.76	1.55
.49	1.51	.60	1.77	.66	2.41	.92	1.77	.66	1.73	.65	1.64

KARYOTYPE	6.		7.		8.		9.		10.		11.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.79	7.89	.99	7.86	.80	8.63	.82	8.39	.89	8.85	.83	7.52
	.88	8.20	.89	7.49	.85	7.96	.99	8.25	.92	8.27	.79	7.26
Pair 2.	.80	3.34	.79	3.33	.95	3.47	.82	3.82	.86	3.11	.61	3.35
	.89	3.67	.81	3.33	.89	3.06	.84	3.29	.70	3.26	.72	3.41
Pair 3.	.40	2.85	.38	2.71	.35	2.31	.42	2.67	.36	2.69	.44	2.74
	.33	2.86	.43	2.94	.40	2.87	.40	2.64	.33	2.58	.63	2.29
	.72	2.78	.86	2.83	.74	2.73	.82	2.64	.78	2.74	.74	2.48
	.68	2.64	.72	2.78	.74	2.74	.73	2.50	.77	2.58	.77	2.49
	.87	2.36	.83	2.23	.75	2.24	.75	2.24	.81	2.13	.77	2.27
	.72	2.18	.75	2.37	.81	2.21	.69	2.14	.75	2.22	.84	2.46
	.50	2.76	.55	2.45	.45	2.68	.53	2.14	.42	2.42	.48	2.55
	.47	2.57	.56	2.41	.52	2.31	.49	2.31	.41	2.39	.51	2.40
	.64	1.77	.78	1.93	.53	1.52	.68	2.02	.64	1.93	.74	1.95
	.58	2.02	.59	1.55	.68	2.08	.95	2.00	.94	1.78	.79	2.06
	.58	1.58	.69	1.86	.85	1.83	.70	1.55	.58	1.63	.95	1.93
	.54	1.65	.69	1.64	.62	1.48	.84	1.74	.34	1.82	.89	1.75
	.85	1.55	.82	1.69	.56	1.76	.67	1.84	.67	1.64	.83	1.58
	.81	1.77	.77	1.88	.76	1.59	.62	2.17	.38	1.78	.78	1.68
	.75	1.69	.78	1.65	.82	1.84	.86	2.24	.38	1.65	.52	1.89
	.94	2.12	.83	1.66	.94	1.90	.63	1.52	.79	1.67	.83	1.83
	.80	1.81	.81	1.65	.91	2.08	.82	1.66	.74	1.67	.76	1.71
	.88	1.58	.79	1.85	.83	1.87	.75	1.86	.75	1.98	.75	2.19
	.63	1.73	.76	2.24	.50	1.62	.58	1.62	.64	2.07	.84	2.01
	.81	1.92	.76	1.75	.65	1.69	.37	1.66	.57	1.65	.84	1.89
	.70	1.53	.51	1.51	.83	1.55	.77	1.72	.57	1.76	.97	1.82
	.91	1.92	.65	1.62	.87	1.86	.59	1.71	.84	1.79	.80	1.60
	.72	1.64	.87	1.83	.57	1.73	.75	1.66	.78	1.84	.78	1.60
	.92	1.84	1	1.79	.83	1.61	.56	1.62	.80	2.04	.63	1.63
	.74	1.80	.88	1.94	.98	1.58	.94	1.95	.54	1.86	.58	1.78
	.67	2.02	.71	1.60	.60	1.69	.85	1.73	.93	1.22	.94	1.83
	.42	1.75	.72	1.64	.90	1.78	.50	1.58	.81	1.97	.61	1.78
	.58	1.62	.93	1.71	.84	1.91	.56	2.05	.90	1.69	.83	1.78
	.85	1.76	.69	1.81	.67	2.03	.55	1.58	.64	1.61	.84	1.98

KARYOTYPE	13.		1.		2.		3.		4.		5.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.81	1.65	.64	1.58	.73	1.34	.76	2.33	.65	1.61	.62	1.91
	.69	1.91	.79	1.96	.92	1.54	.67	1.92	.89	1.92	.90	1.69
	.61	1.83	.91	1.58	.57	1.74	.79	1.94	.71	1.75	.50	1.87
	.93	1.51	.74	1.54	.77	1.65	.77	1.56	.80	1.53	.63	2.18
	.77	1.98	.60	1.67	.83	1.42	.84	1.90	.67	1.81	.73	1.84
	.91	1.81	.89	1.97	1	2.03	.77	1.70	.65	1.87	.89	1.97
	.73	1.71	.71	1.46	.65	1.83	.72	1.72	.82	1.79	.55	1.90
	.59	1.84	.97	1.92	.91	2.05	.76	1.55	.72	1.89	.88	1.76
	1	2.06	.64	1.61	.63	1.56	.53	1.65	.62	1.75	.46	1.64
	.87	1.80	.69	1.57	.93	2.09	.88	.173	.80	1.53	.72	1.92
	.56	1.87	.92	1.45	.68	1.76	.73	1.71	.87	1.95	.97	1.78
	.67	1.48	.47	1.50	.64	1.39	.88	2.09	.58	1.61	.77	1.79
	.73	1.71	.65	2.02	.72	1.72	.54	1.55	.69	1.62	.69	1.92
	.63	1.61	.88	2.11	.94	1.68	.75	1.58	.71	1.67	.65	1.60
	.74	1.61	.66	1.84	.47	1.63	.57	1.58	.50	1.54	.88	1.52
	.74	1.67	.83	1.67	.70	1.66	.51	1.77	.84	2.04	.76	1.55
	.49	1.51	.60	1.77	.66	2.41	.92	1.77	.66	1.73	.65	1.64

KARYOTYPE	6.		7.		8.		9.		10.		11.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.79	7.89	.99	7.86	.80	8.63	.82	8.39	.89	8.85	.83	7.52
	.88	8.20	.89	7.49	.85	7.96	.99	8.25	.92	8.27	.79	7.26
Pair 2.	.80	3.34	.79	3.33	.95	3.47	.82	3.82	.86	3.11	.61	3.35
	.89	3.67	.81	3.33	.89	3.06	.84	3.29	.70	3.26	.72	3.41
Pair 3.	.40	2.85	.38	2.71	.35	2.31	.42	2.67	.36	2.69	.44	2.74
	.33	2.86	.43	2.94	.40	2.87	.40	2.64	.33	2.58	.63	2.29
	.72	2.78	.86	2.83	.74	2.73	.82	2.64	.78	2.74	.74	2.48
	.68	2.64	.72	2.78	.74	2.74	.73	2.50	.77	2.58	.77	2.49
	.87	2.36	.83	2.23	.75	2.24	.75	2.24	.81	2.13	.77	2.27
	.72	2.18	.75	2.37	.81	2.21	.69	2.14	.75	2.22	.84	2.46
	.50	2.76	.55	2.45	.45	2.68	.53	2.14	.42	2.42	.48	2.55
	.47	2.57	.56	2.41	.52	2.31	.49	2.31	.41	2.39	.51	2.40
	.64	1.77	.78	1.93	.53	1.52	.68	2.02	.64	1.93	.74	1.95
	.58	2.02	.59	1.55	.68	2.08	.95	2.00	.94	1.78	.79	2.06
	.58	1.58	.69	1.86	.85	1.83	.70	1.55	.58	1.63	.95	1.93
	.54	1.65	.69	1.64	.62	1.48	.84	1.74	.34	1.82	.89	1.75
	.85	1.55	.82	1.69	.56	1.76	.67	1.84	.67	1.64	.83	1.58
	.81	1.77	.77	1.88	.76	1.59	.62	2.17	.38	1.78	.78	1.68
	.75	1.69	.78	1.65	.82	1.84	.86	2.24	.38	1.65	.52	1.89
	.94	2.12	.83	1.66	.94	1.90	.63	1.52	.79	1.67	.83	1.83
	.80	1.81	.81	1.65	.91	2.08	.82	1.66	.74	1.67	.76	1.71
	.88	1.58	.79	1.85	.83	1.87	.75	1.86	.75	1.98	.75	2.19
	.63	1.73	.76	2.24	.50	1.62	.58	1.62	.64	2.07	.84	2.01
	.81	1.92	.76	1.75	.65	1.69	.37	1.66	.57	1.65	.84	1.89
	.70	1.53	.51	1.51	.83	1.55	.77	1.72	.57	1.76	.97	1.82
	.91	1.92	.65	1.62	.87	1.86	.59	1.71	.84	1.79	.80	1.60
	.72	1.64	.87	1.83	.57	1.73	.75	1.66	.78	1.84	.78	1.60
	.92	1.84	1	1.79	.83	1.61	.56	1.62	.80	2.04	.63	1.63
	.74	1.80	.88	1.94	.98	1.58	.94	1.95	.54	1.86	.58	1.78
	.67	2.02	.71	1.60	.60	1.69	.85	1.73	.93	1.22	.94	1.83
	.42	1.75	.72	1.64	.90	1.78	.50	1.58	.81	1.97	.61	1.78
	.58	1.62	.93	1.71	.84	1.91	.56	2.05	.90	1.69	.83	1.78
	.85	1.76	.69	1.81	.67	2.03	.55	1.58	.64	1.61	.84	1.98

KARYOTYPE	6.		7.		8.		9.		10.		11.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.78	1.85	.63	1.53	.86	1.78	.45	1.96	.83	1.83	.57	1.93
	.98	1.46	.70	1.73	.86	1.80	.54	1.67	.39	1.76	.71	1.77
	1	1.83	.68	1.98	.65	2.17	.97	1.99	.63	1.46	.97	1.82
	.90	1.93	.66	1.73	.73	1.59	.96	1.62	.80	1.99	.84	1.81
	.59	1.55	.76	1.89	.76	1.70	.76	1.80	.53	1.83	.84	1.98
	1	1.68	.87	1.71	.65	1.88	.64	1.72	.53	1.67	.94	2.01
	.82	1.58	.75	1.85	.89	1.94	.81	1.55	.82	1.58	.80	1.78
	.87	1.56	.58	1.91	.86	1.86	.86	1.96	.83	2.21	.89	1.72
	.69	1.72	.83	1.84	.78	1.64	.71	1.60	.87	1.63	.67	1.72
	.68	1.65	.83	1.90	.80	1.60	.79	1.73	.78	1.85	.92	1.98
	.77	1.78	.70	2.12	.60	1.62	.80	1.66	.64	1.89	.57	1.68

KARYOTYPE Pair 1	12. R	RL	13. R	RL	14. R	RL	15. R	RL	16. R	RL	17. R	RL
	.77	7.68	.81	9.06	.98	7.55	.74	8.72	.84	8.67	.84	8.67
	.76	8.95	.87	7.07	.98	8.23	.92	8.68	.88	8.59	.92	8.26
Pair 2	.83	3.43	.80	3.08	.68	3.65	.71	3.66	.88	3.01	.64	3.41
	.78	3.53	.86	3.26	.89	3.67	.77	3.21	.87	3.24	.67	3.42
Pair 3	.45	2.62	.32	3.06	.50	2.53	.43	2.67	.36	2.55	.24	3.25
	.37	2.71	.29	2.97	.40	2.95	.37	2.68	.37	2.43	.59	3.20
	.61	2.88	.78	2.62	.60	2.81	.70	2.75	.65	2.54	.58	2.55
	.71	2.70	.78	2.58	.66	2.82	.60	2.45	.86	2.80	.76	2.78
	.90	2.46	.82	2.31	.84	2.37	.69	3.15	.77	2.32	.70	2.18
	.62	2.41	.80	2.29	.79	2.33	.93	2.71	.78	2.43	.58	2.22
	.53	2.11	.44	2.62	.48	2.18	.37	2.73	.46	2.57	.46	2.39
	.70	1.51	.48	2.70	.54	2.67	.43	2.67	.47	2.41	.42	2.19
	.81	2.15	.73	1.99	.65	1.49	.39	1.58	.80	1.73	.80	1.88
	.64	1.63	.89	2.08	.60	1.60	.71	1.67	.75	1.56	.77	1.77
	.71	2.09	.83	1.78	.74	1.52	.92	1.54	.77	1.46	.83	1.89
	.57	1.51	.51	1.61	.86	2.22	.71	1.91	.78	1.72	.67	1.49
	.87	1.92	.80	1.82	.97	1.72	.64	1.55	.82	1.79	.63	1.71
	.76	1.56	.85	1.57	.68	1.65	.73	1.59	.52	1.57	.76	1.97
	.89	2.01	.68	1.96	.78	1.59	.52	1.70	.54	1.79	.94	1.87
	.57	1.90	.86	1.85	.86	1.46	.62	1.47	.63	1.67	.57	1.73
	.76	1.94	.72	1.74	.73	1.45	.97	1.72	.78	1.75	.55	1.63
	.71	2.12	.88	1.47	.78	1.61	.95	1.76	.83	1.92	.83	1.74
	.63	1.72	.88	1.74	.90	1.77	.69	1.72	.92	1.99	.46	1.62
	.64	1.73	.79	1.47	.76	1.76	.91	1.88	.92	1.73	.91	1.91
	1	1.66	.57	1.52	.70	1.60	.92	1.98	.68	1.79	.85	2.05
	.56	1.77	.85	1.50	.88	1.82	.81	1.89	.99	1.26	.64	1.78
	.86	2.23	.94	1.51	.87	1.64	.52	1.61	.78	1.98	.65	2.05
	.88	2.05	.74	1.76	.55	1.48	.62	1.46	.72	1.45	.62	1.81
	.70	1.70	.93	1.01	.66	1.63	.53	1.61	.58	1.66	.88	1.72
	.86	2.03	.78	1.93	.74	1.94	.75	1.65	.82	2.19	.66	1.58
	.52	1.55	.90	1.91	.64	1.50	.76	1.67	.63	2.19	.85	1.56
	.85	1.53	.42	1.65	.63	1.90	.95	1.91	.42	1.62	.53	1.67
	.45	1.41	.70	1.60	.69	1.96	.83	1.62	.77	1.87	.99	1.58
	.59	1.78	.95	1.89	.79	1.71	.53	1.39	.73	1.93	.55	1.77
	.83	1.66	.65	1.80	.43	1.88	.84	1.75	.89	2.05	.63	2.18
	.89	1.42	.84	1.98	.30	2.25	.72	1.88	.78	1.54	.81	1.70
	.85	1.52	.86	1.91	.66	1.68	.64	2.17	.92	1.61	.76	1.47
	.76	1.62	.54	1.77	.74	2.06	.92	2.17	.92	1.60	.60	1.66
	.68	1.89	.70	1.83	.73	1.85	.84	1.81	.45	1.64	.71	1.55
	.64	1.88	.52	1.74	.92	2.01	.56	1.90	.83	1.61	.61	1.65

KARYOTYPE	12.		13.		14.		15.		16.		17.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.83	1.72	.71	1.82	.66	1.71	.79	1.52	.79	1.87	.79	1.62
	.89	1.82	.57	1.81	.59	1.86	.69	1.70	.54	1.72	.73	1.48
	.77	1.52	.61	1.32	.58	1.64	.75	1.64	.96	1.82	.86	1.60
	.87	1.65	.56	2.14	1	2.08	.75	1.75	.88	2.12	.66	1.66

POPULATION B2

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.90	7.63	.92	8.13	.76	8.09	.85	9.11	.78	7.90	.86	8.36
	.81	7.46	.79	7.97	.78	7.68	.70	8.58	.88	8.84	.87	8.12
Pair 2	.94	3.48	.84	3.43	.97	3.26	.92	3.16	.78	3.51	.90	3.48
	.96	3.04	.81	3.17	1	3.29	.84	3.25	.97	3.34	.87	3.74
Pair 3	.39	2.63	.44	2.66	.54	2.38	.32	2.51	.29	2,74	.38	2.52
	.41	2.63	.41	2.55	.49	2.09	.31	2.83	.39	2.70	.31	3.04
	.83	2.66	.90	2.78	.77	2.44	.89	2.51	.81	2.63	.77	2.68
	.84	2.37	.74	2.48	.91	2.62	.83	2.90	.73	2.55	.83	2.23
	.91	2.34	.80	2.21	.82	2.10	.79	2.35	.80	2.17	.68	2.38
	.78	2.55	.90	2.39	.80	2.31	.81	2.22	.65	1.97	.82	2.20
	.38	2.28	.44	2.65	.51	2.29	.49	2.33	.51	2.34	.38	2.32
	.51	2.38	.52	2.39	.59	2.46	.46	2.37	.37	2.56	.51	2.36
	.49	1.73	.73	1.86	.73	1.71	.55	1.53	.68	2.04	.77	1.94
	.58	1.67	.71	1.75	.73	2.05	.65	1.74	.71	1.50	.62	1.85
	.83	1.87	.81	1.83	.92	1.81	.70	1.60	.71	1.47	.75	1.78
	.56	1.76	.74	1.81	.85	1.59	.73	1.81	.84	1.57	.56	1.63
	.68	1,88	,52	1,63	,75	1,70	,57	1,67	,80	1,63	,84	1,76
	.55	1.91	.68	1.65	.79	1.75	.61	1.67	.75	1.81	.66	1.69
	.79	1.72	.49	1.72	.66	1.82	.95	1.50	.57	1.70	.61	1.85
	.88	2.04	.77	1.71	.78	1.78	.86	1.59	.83	1.60	.77	1.74
	.66	1.85	,53	1,97	,46	1,77	,61	1.84	.74	1.76	.78	1.88
	.60	2.13	.79	1.90	.62	1.79	.57	1.71	.58	2.05	.80	1.76
	.77	1.91	.81	2.15	.83	1.97	.61	1.61	.85	2.03	.79	1.86
	.50	1.84	.87	1.71	.59	1.72	.89	1.73	.53	1.51	.79	1.84
	.75	1.75	.73	1.97	.55	1.52	.68	1.64	.85	1.99	.62	2.07
	.86	1.94	.72	1.65	.44	1.72	.81	1.67	.69	1.80	.64	1.47
	.75	1.94	.68	1.74	.67	1.90	1	2.07	.93	1.90	.64	1.66
	.77	1.74	.78	1.79	.64	1.69	.84	1.75	.45	1.58	.72	2.04
	.84	1.81	.83	2.10	.86	2.04	.73	2.03	.86	1.92	.53	1.58
	.84	1.51	.76	1.80	.68	1.74	.59	1.68	.92	2.01	.44	2.18
	.81	1.62	.72	1.80	.68	1.74	.59	1.68	.92	2.01	.44	2.18
	.68	1.80	.67	1.62	.85	2.05	.74	1.44	.88	1.70	.88	1.65
	.71	1.91	.88	1.95	.86	1.62	.72	1.85	.70	1.88	.84	1.55
	.74	1.54	.62	1.65	.71	1.98	.69	1.48	.68	1.65	.76	2.02
	.97	2,07	,67	1,74	,76	1,85	,63	1,64	,63	1,82	,68	1,77
	.91	1.83	.73	1.55	.63	1.87	.88	2.01	.71	1.74	.75	1.77
	.67	2.00	.87	1.84	.68	2.08	.77	1.81	.76	1.58	.68	1.88
	.88	1.76	.73	2.05	.59	1.56	.80	1.76	.56	1.76	.69	1.56
	.75	1,53	.74	1.72	.80	2.20	.83	1.65	.74	2.04	.68	1.48
	.70	1.72	.92	1.90	.63	1.61	.68	1.81	.71	1.73	.66	1.79
	.68	1.75	.74	1.62	.66	2.10	.86	1.66	.58	1.83	.82	1.48
	1	1.91	.66	1.59	.64	1.86	.73	1.93	.80	2.05	.61	1.88
	.77	1.94	.79	1.79	.52	2.04	.88	1.62	.68	1.50	.87	1.44
	.81	1.97	.83	1.71	.70	1.61	.79	1.81	.85	1.66	.68	1.69

POPULATION B2

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.81	8.67	.94	7.89	.85	8.19	.90	7.99	.87	7.05	.78	7.94
	.86	8.73	.85	8.05	.81	8.96	.80	8.00	.83	8.45	.91	7.61
Pair 2	.74	3.44	.79	3.37	.95	3.05	.72	3.49	.82	3.42	.85	3.19
	.91	2.93	.82	3.48	.70	3.14	.97	3.36	.84	2.23	.93	3.13
Pair 3	.36	2.66	.32	2.58	.38	2.36	.41	2.82	.39	2.72	.52	2.40
	.37	2.98	.30	2.55	.34	2.64	.34	3.00	.42	2.57	.42	2.43
	.69	2.71	.54	2.52	.79	2.66	.77	2.49	.81	2.15	.86	2.79
	.75	2.39	.62	2.50	.75	2.54	.77	2.33	.87	2.34	.79	2.36
	.81	2.17	.88	2.45	.95	2.30	.71	2.25	.71	2.72	.80	2.15
	.64	2.30	.65	2.56	.75	2.30	.80	2.30	.78	2.59	.87	2.47
	.62	2.32	.37	2.46	.51	2.16	.45	2.35	.55	2.46	.48	2.35
	.51	2.59	.31	2.43	.56	2.04	.38	2.22	.62	2.58	.53	2.58
	.55	1.90	.72	1.64	.70	1.58	.72	1.76	.59	1.48	.52	1.82
	.74	1.80	.71	1.86	.80	1.79	.46	1.54	.85	1.67	.92	1.99
	.68	1.96	.74	1.70	.53	1.43	.94	1.95	.48	1.60	.84	2.04
	.63	1.85	.74	1.91	.94	1.55	.66	1.68	.65	1.65	.73	1.69
	.90	1.96	.61	1.63	.70	1.68	.55	1.65	.92	2.07	.74	1.68
	.61	1.82	.75	1.64	.85	1.69	.60	1.99	.68	1.84	.84	2.08
	.87	1.71	.67	1.58	.71	1.87	.63	1.65	.84	2.24	.51	1.84
	.81	1.74	.74	1.89	.56	1.59	.71	1.70	.54	1.58	.70	1.55
	.68	1.70	.70	1.74	.81	1.91	.55	1.57	.84	2.01	.80	2.07
	.72	1.85	.63	1.55	.80	1.61	.58	1.45	.74	1.72	.76	1.66
	.73	1.56	.50	1.67	.99	1.98	.74	1.51	.71	1.93	.67	2.33
	.76	1.57	.58	1.74	.71	1.77	.79	1.79	.71	1.74	.86	1.70
	.68	1.52	.81	1.83	.54	1.70	.85	1.83	.90	1.62	.75	2.15
	.75	1.65	.83	1.93	.67	1.54	.63	1.61	1	2.03	.77	1.73
	.73	1.73	.59	1.48	.63	1.71	.64	1.48	.82	1.94	.63	1.83
	.76	1.56	.91	2.12	.57	1.97	.66	1.60	.81	1.56	.77	1.72
	.68	1.67	.65	2.00	.69	1.52	.79	1.56	.77	1.77	.50	1.99
	.72	1.81	.85	1.63	.68	1.82	.89	2.07	.66	2.04	.61	1.92
	.63	1.74	.51	1.75	.85	1.89	.81	1.61	.74	1.88	.76	2.05
	.75	2.02	.77	1.63	.78	1.66	.81	2.04	.73	1.77	.95	1.92
	.71	1.82	.37	1.82	.87	1.92	.82	2.14	.55	1.84	.77	1.91
	.53	1.44	.58	2.06	.77	1.76	.52	1.58	.82	1.62	.81	1.67
	.71	1.80	.66	1.87	.70	1.83	.64	1.89	.68	1.68	.73	1.68
	.69	1.89	.77	1.96	.90	1.92	.90	2.04	.90	1.63	.70	1.68
	.57	1.75	.47	1.48	.58	1.70	.67	2.17	.56	1.74	.73	1.78
	.95	1.84	.75	1.75	.80	2.03	.87	1.76	.75	1.92	.67	1.84
	.84	1.98	.69	1.96	.78	1.84	.54	2.01	.66	1.75	.71	1.47
	.57	1.47	.70	1.37	.82	2.08	.82	1.90	.85	2.03	.88	1.45
	.68	1.93	.73	1.67	.76	2.11	.64	2.07	.78	1.48	.66	1.91
	.75	1.96	.97	2.03	.66	1.88	.82	2.11	.77	1.74	.91	1.95
	.82	1.60	.91	1.60	.95	1.91	.76	1.54	.92	2.25	.62	1.72
	.71	1.62	.56	1.93	.73	1.94	.43	1.96	.66	1.68	.67	1.56

POPULATION C1

KARYOTYPE	13.		14.		15.		1.		2.		3.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.84	9.22	.86	8.29	.87	7.93	.90	7.62	.87	8.70	.73	7.58
	.89	8.20	.79	8.33	.99	8.18	.77	7.25	.84	7.99	.88	7.40
Pair 2	.95	3.09	.95	3.59	.85	3.17	.82	3.37	.87	3.33	.81	3.26
	.87	2.97	.92	3.83	.94	3.40	.88	3.32	.84	3.30	.79	2.98
Pair 3	.50	2.91	.35	2.65	.41	2.06	.48	2.58	.43	2.46	.48	2.93
	.42	2.74	.37	2.44	.31	2.62	.41	2.76	.45	2.76	.51	2.51

KARYOTYPE	13.		14.		15.		1.		2.		3.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.85	2.50	.55	2.70	.73	2.73	.61	2.78	.87	2.39	.81	2.35
	.92	2.41	.72	2.83	.78	2.55	.71	2.35	.91	2.39	.75	2.29
	.72	2.38	.72	2.26	.62	2.63	.68	2.14	.91	2.41	.82	2.18
	.78	2.36	.62	2.13	.63	2.51	.94	2.18	.90	2.51	.84	2.40
	.54	2.18	.53	2.12	.45	2.35	.49	2.56	.46	2.35	.47	2.64
	.47	2.23	.47	2.06	.37	2.45	.61	2.43	.55	2.36	.60	2.23
	.68	2.19	.69	1.58	.57	2.02	.87	2.03	.39	1.74	.84	1.72
	.66	1.85	.86	1.90	.85	1.85	.73	1.91	.83	1.68	.84	2.08
	.61	1.65	.69	1.64	.84	1.86	.89	1.83	.67	1.82	.75	2.07
	.85	1.88	.75	1.89	.91	1.84	.53	1.61	.87	1.88	.83	1.69
	.63	1.83	.69	1.33	.91	1.70	.77	1.76	.68	1.89	.88	1.97
	.67	1.86	.90	1.59	.88	1.57	.73	1.88	.64	1.84	.65	1.71
	.71	1.64	.55	1.46	.62	1.38	.59	1.69	.79	1.64	.58	1.73
	.58	1.58	.99	1.81	.48	1.85	.90	1.75	.56	1.54	.71	1.88
	.64	2.07	.73	1.86	.88	1.71	.78	1.93	.72	1.76	.83	1.65
	.64	2.06	.60	1.83	.74	1.46	.80	1.89	.91	1.79	.71	2.01
	.86	1.68	.74	1.71	.89	1.67	.88	2.23	.85	1.75	.60	1.93
	.74	1.64	.92	2.09	.68	1.73	.91	1.98	.81	1.96	.86	2.15
	.88	1.60	.78	1.88	.60	1.95	.50	1.62	.82	1.88	.75	2.19
	.67	1.84	.63	1.60	.81	1.98	.76	1.54	.75	1.61	.76	1.63
	.66	1.57	.58	1.76	.47	1.45	.72	1.73	.79	1.69	.74	1.51
	.80	1.54	.70	1.79	.51	1.68	.71	1.42	.75	1.84	.59	1.92
	.80	1.94	.67	1.41	.55	1.57	.64	1.68	.74	1.86	.90	2.07
	.92	1.77	.55	1.70	.56	1.64	.69	1.64	.61	1.95	.76	1.82
	.50	2.22	.61	1.52	.60	1.98	.86	1.77	.66	1.57	.47	1.95
	.87	1.72	.57	1.80	.69	1.89	.74	1.91	.57	1.64	.92	2.13
	.65	1.66	.78	2.11	.77	1.80	.59	1.73	.87	1.96	.89	1.80
	.77	1.64	.65	1.82	.66	2.01	.72	1.73	.73	2.10	.60	1.71
	.76	1.62	.75	1.92	.38	1.79	.97	1.75	.77	1.75	.66	1.54
	.85	1.68	.44	1.65	.42	1.57	.73	1.92	.91	1.75	.75	2.08
	.58	1.45	.86	2.02	.54	1.83	.67	1.82	.70	1.84	.89	1.89
	.84	1.79	.50	1.97	.42	2.22	.91	1.93	.87	1.77	.82	1.77
	.79	1.66	.67	1.52	.57	1.62	.91	1.94	.64	1.58	.95	1.89
	.88	1.66	.71	1.52	.51	1.98	.54	1.96	.72	1.95	.73	1.68
	.90	2.19	.65	2.24	.60	1.96	.85	2.20	.55	1.75	.82	1.71
	.64	1.69	.84	1.70	.88	1.98	.61	1.64	.77	1.63	.75	1.68
	.57	1.74	.50	2.23	.69	1.69	.89	1.93	.83	1.73	.79	1.63
	.65	1.71	.69	1.73	.86	2.25	.90	2.07	.84	1.72	.48	1.74

KARYOTYPE	4.		5.		6.		7.		8.		9.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.84	7.34	.86	8.30	.81	9.77	.83	7.08	.87	7.24	.87	8.02
	.86	8.21	.81	9.16	.89	7.55	.84	7.01	.88	8.59	.93	7.65
Pair 2	.91	3.58	.97	2.94	.97	3.25	.91	3.16	.86	3.06	.86	3.22
	.86	2.92	.86	3.17	.87	3.15	.84	3.12	.76	3.45	.69	3.73
Pair 3	.43	2.79	.38	2.77	.29	2.94	.38	2.75	.28	2.61	.32	2.86
	.37	2.98	.49	2.54	.35	2.53	.44	2.68	.39	2.50	.33	3.09
	.81	2.24	.84	2.20	.81	2.31	.88	2.28	.92	2.33	.88	2.27
	.80	2.33	.59	2.40	.90	2.16	.71	2.78	.89	2.71	.81	2.36
	.75	2.43	.83	2.17	.82	2.20	.86	2.34	.69	2.25	.74	2.37
	.83	2.10	.87	2.35	.68	2.40	.68	2.64	.76	2.13	.77	2.35
	.54	2.61	.50	2.14	.49	2.35	.51	2.42	.41	2.97	.44	2.59
	.64	2.29	.43	2.32	.45	2.46	.48	2.37	.45	2.66	.43	2.38
	.66	1.83	.80	1.64	.81	1.74	.73	1.87	.68	1.95	.82	2.06
	.85	1.84	.47	1.75	.66	2.01	.57	1.99	.78	2.11	.81	1.66
	.49	1.71	.70	1.96	.61	1.74	.63	1.71	.67	1.70	.32	1.74

POPULATION C1

KARYOTYPE	4.		5.		6.		7.		8.		9.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.95	2.10	.82	1.99	.59	1.99	.70	1.62	.68	2.09	.80	1.78
	.78	1.83	1	1.97	.94	1.58	.59	1.83	.92	1.83	.86	1.72
	.68	1.90	.60	1.48	.72	2.30	.55	1.46	.62	1.68	.75	1.71
	1	1.78	.64	1.72	.52	1.92	.58	2.04	.53	1.59	.53	1.67
	.64	1.69	.80	2.04	.79	2.02	.62	1.69	.91	1.67	.80	1.67
	.79	1.73	.63	1.53	.49	1.94	.54	1.69	.72	1.57	.53	1.97
	.57	1.79	.90	1.97	.69	1.79	.85	1.99	.46	1.47	.91	1.69
	.93	2.04	.89	1.84	1	1.98	.78	2.09	.84	1.94	.85	1.83
	.85	1.97	.56	1.77	.87	1.17	.95	1.81	.84	1.68	.70	1.44
	.78	1.70	.76	1.61	.78	1.83	.65	1.82	.79	1.77	.65	1.63
	.74	1.64	.95	1.86	.77	1.83	.92	1.90	.94	1.59	.81	1.65
	.74	1.75	.78	1.80	.76	1.92	.88	2.00	.56	1.55	.70	2.07
	.71	1.66	.73	1.74	.66	1.56	.71	2.27	.93	1.65	.78	1.67
	.75	1.63	.90	2.12	.72	1.81	.82	1.94	.72	2.62	1	2.18
	.64	1.81	.74	1.75	.88	1.64	.77	1.89	.82	1.79	.41	1.92
	.84	1.81	.67	1.62	.72	1.50	.89	1.84	.49	1.74	.59	1.68
	.69	1.87	.78	1.64	.56	1.30	.43	1.52	.66	1.65	.65	1.78
	.66	1.73	.70	1.79	.71	1.69	.66	2.06	.67	1.86	.60	1.64
	.85	1.63	.82	2.16	.66	1.56	.97	1.87	.45	1.79	.69	1.96
	.83	1.95	.92	1.74	.66	1.48	1	1.93	.75	1.67	.74	1.65
	.81	1.66	.91	1.61	.74	1.76	.80	1.99	.64	1.29	.70	1.56
	.54	1.86	.72	1.61	.56	1.68	.77	1.91	.87	1.63	.58	1.89
	.79	1.67	.76	1.86	.41	2.15	.85	2.01	.44	1.62	.40	1.83
	.94	1.99	.67	1.75	.57	1.78	.80	1.98	.67	2.04	.76	1.44
	.92	2.09	.65	2.15	.81	1.46	.54	1.72	.58	2.16	.90	1.97
	.84	1.87	.85	1.78	.74	1.86	.56	1.62	.78	1.97	.85	2.06
	.54	1.51	.56	1.87	.74	1.99	.69	1.66	.61	1.45	.81	1.51
	.80	2.02	.78	1.71	.82	1.68	.71	1.67	.50	1.88	.93	2.13
	.69	1.91	.51	1.53	.89	2.09	.97	1.81	.89	1.89	.74	1.84

KARYOTYPE	10.		11.		12.		13.		14.		15.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.90	8.53	.91	7.98	.96	10.18	.95	8.88	.86	8.15	.92	9.02
	.85	8.42	.85	8.71	.78	8.10	.90	7.81	.87	8.30	.9	9. 2
Pair 2	.85	3.34	.94	3.51	.82	3.07	.87	3.05	.78	3.31	.75	3.28
	.79	3.21	.86	2.95	.69	3.22	.88	.22	.	3.3	.62	3.77
Pair 3	.33	2.47	.27	2.77	.39	2.61	.43	2.57	.22	3.50	.34	2.62
	.33	3.03	.38	2.44	.47	2.28	.39	2.70	.26	3.19	.49	2.55
	.85	2.44	.87	2.43	.73	2.16	.88	2.66	.63	2.63	.72	2.40
	.86	2.50	.70	2.60	.89	2.17	.70	2.51	.89	2.73	.59	2.54
	.74	2.14	.96	2.33	.63	2.28	.63	2.44	.92	2.25	.94	2.52
	.68	2.45	.76	2.16	.55	2.69	.64	2.36	.83	2.18	.90	2.17
	.51	2.61	.55	2.40	.48	2.69	.43	2.68	.41	2.52	.42	2.34
	.50	2.31	.47	2.52	.59	2.48	.54	2.24	.38	2.58	.36	2.64
	.66	1.65	.69	1.44	.74	1.70	.54	1.58	.60	1.70	.64	1.79
	.48	2.08	.54	1.55	.72	1.77	.72	1.75	.77	1.52	.52	1.69
	.67	1.60	.76	1.55	.78	2.02	.59	1.64	.91	2.05	.73	1.74
	.73	1.82	.47	1.72	.73	1.69	.66	1.60	.70	1.41	.63	1.49
	.84	1.73	.64	1.79	.57	1.76	.79	1.76	.96	1.21	.71	1.56
	.57	1.45	.60	1.60	.74	1.90	.68	1.83	.79	1.69	.57	1.49
	.55	1.56	.72	2.05	.87	1.85	.87	1.87	.94	1.99	.54	1.58
	.55	1.68	.69	2.01	.65	1.79	.88	1.78	.53	1.71	.64	1.57
	.84	1.56	.77	1.57	.69	1.73	.77	1.96	.54	2.12	.70	1.54
	.86	1.60	.69	1.74	.73	1.67	.47	2.13	.44	2.15	.89	2.23
	.56	1.69	.59	1.84	1	1.92	.77	1.67	1	1.93	.83	1.86

KARYOTYPE	10.		11.		12.		13.		14.		15.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.86	1.81	.67	1.58	.62	1.85	.70	1.50	.60	1.47	.73	1.81
	.40	1.63	.66	1.44	.65	1.69	.84	1.38	.85	1.89	.55	1.55
	.79	1.94	.42	1.69	.48	1.61	.71	1.89	.64	1.61	.87	1.80
	.76	1.67	.76	2.14	.72	1.95	.67	1.86	.70	1.63	.75	2.02
	.65	1.67	.58	1.76	.73	1.62	.57	1.47	.80	1.42	.75	1.50
	.84	1.80	.84	2.11	.77	1.62	.78	1.99	.58	1.55	.47	1.64
	.69	2.02	.65	1.76	.57	1.75	.65	1.56	.87	1.72	.75	1.61
	.81	1.85	.55	1.62	.69	1.57	.70	1.68	.89	1.21	.69	1.83
	.55	1.90	.59	2.15	.77	1.65	.91	2.18	.72	1.88	.61	1.47
	.70	1.68	.80	1.88	.67	1.46	.67	1.84	.55	1.87	.68	1.95
	.54	1.66	.63	1.73	.75	1.41	.90	2.11	.67	1.68	.58	1.41
	.74	1.60	.67	1.80	.68	1.98	.56	1.71	.80	1.75	.61	1.39
	.65	1.80	.86	1.81	.68	1.81	.79	1.61	.76	1.64	.60	1.83
	.71	1.67	.87	1.53	.75	1.68	.78	2.04	.71	1.60	.77	1.94
	.80	2.03	.62	2.11	.65	1.61	.70	1.80	.64	1.76	.79	1.93
	.85	1.69	1	1.91	.56	1.64	.80	1.71	.43	1.70	.77	1.73
	.74	2.11	.73	2.04	.87	1.85	.68	2.01	.73	1.73	.81	1.88
	.73	1.73	.82	1.78	.75	2.03	.64	1.67	.44	1.78	.86	1.79
	.48	1.81	.63	1.97	.69	1.89	.72	1.60	.55	1.53	.46	1.75
	.77	1.93	.56	1.74	.76	1.68	.68	1.72	.71	1.66	.56	1.90
	.43	1.68	.59	1.63	.75	1.79	.88	1.53	.47	1.69	.35	1.57

POPULATION C2

KARYOTYPE	16.		1.		2.		3.		4.		5.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.89	7.79	.88	9.32	.98	9.21	.83	7.54	.74	8.50	.85	8.64
	.67	8.37	.80	8.23	.77	8.28	.71	7.94	.91	8.73	.96	8.31
Pair 2	.94	3.68	.82	3.35	.71	3.61	.94	3.08	.91	2.98	.89	3.19
	.86	3.94	.86	3.47	.95	3.88	.74	2.90	.85	3.00	.87	3.01
Pair 3	.27	3.23	.39	2.72	.42	2.28	.39	2.43	.49	2.59	.43	2.45
	.67	2.21	.42	2.68	.40	2.58	.44	2.73	.44	2.67	.29	2.33
	.75	2.38	.82	2.66	.80	2.31	.93	2.13	.58	2.97	.59	2.55
	.78	2.27	.83	2.56	.86	2.18	.81	1.97	.78	2.80	.85	2.56
	.71	2.24	.78	2.12	.82	2.40	.51	2.46	.62	2.03	.76	2.29
	.90	2.30	.85	3.02	.79	2.70	.69	2.37	.75	2.28	.72	2.32
	.57	2.22	.43	2.61	.45	2.48	.52	2.33	.61	2.50	.43	2.27
	.43	2.80	.47	2.32	.43	2.29	.47	2.45	.35	2.47	.36	2.43
	.71	1.66	.64	2.05	.67	1.60	.59	2.17	.78	1.59	.60	1.96
	.87	1.84	.64	1.91	.66	1.55	.87	1.68	.81	1.66	.67	1.93
	.60	1.77	.75	1.77	.60	1.45	.78	1.79	.65	1.86	.43	1.55
	.43	1.46	.98	1.77	.55	1.32	.53	1.77	.67	1.69	.87	1.70
	.79	1.61	.76	1.61	.75	1.97	.67	1.66	.80	1.57	.89	2.15
	.70	1.39	.83	1.75	.61	2.02	.45	1.55	.63	1.77	.67	1.49
	.63	2.01	.72	1.73	.75	1.75	.68	1.77	.69	1.75	.72	1.43
	.77	2.03	.88	1.74	.49	1.73	.54	1.75	.77	1.78	.60	1.79
	.88	1.95	.77	1.85	.95	1.60	.64	1.78	1	1.86	.55	2.02
	.87	1.77	.55	1.68	.80	2.17	.86	2.11	.79	1.53	.66	1.63
	.83	1.65	.56	1.67	.70	1.68	.59	2.08	.77	1.78	.91	1.47
	.58	1.46	.62	1.47	.91	1.57	.65	1.84	.78	2.18	.88	1.91
	.71	1.54	.73	2.04	.66	1.52	.90	2.19	.73	1.64	.97	1.43
	.88	1.56	.47	1.58	.73	1.90	.78	1.76	.61	1.51	.79	1.63
	.63	1.80	.87	1.93	.54	1.65	.50	1.93	.82	1.78	.86	1.80
	.53	1.99	.92	1.72	.98	1.70	.85	1.87	.67	1.67	.92	2.49
	.59	1.95	.71	1.94	.74	1.62	.86	2.08	.87	1.92	.77	1.89
	.68	1.62	.73	1.51	.56	1.49	.56	1.53	.79	1.81	.59	1.68
	.78	1.71	.73	1.49	.76	1.73	.62	1.51	.78	1.52	.73	2.17

POPULATION C2

KARYOTYPE	16.		1.		2.		3.		4.		5.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.60	1.99	.68	1.78	.51	2.15	.95	1.75	.80	1.79	.87	1.78
	.56	1.58	.84	2.05	.74	1.71	1	2.28	.79	1.74	.65	1.48
	.56	1.94	.61	1.70	.45	1.45	.95	1.98	.84	1.54	.85	1.71
	.68	1.78	.77	1.50	.68	1.78	.83	2.05	.59	1.67	.98	2.05
	.73	1.69	.69	1.73	.82	1.85	.85	1.94	1	1.61	.67	1.53
	.92	1.61	.69	1.80	.60	1.90	.88	1.98	.96	2.05	.79	1.95
	.55	2.01	.63	1.55	.46	1.62	.83	2.16	.83	1.90	.80	1.67
	.67	1.74	.73	1.56	.68	1.70	.81	1.63	.65	1.81	.71	1.39
	.60	1.82	.44	1.79	.76	2.06	.65	1.75	.94	2.12	.85	2.02
	.45	1.87	.69	1.73	.34	2.03	.72	1.66	.53	1.77	.69	1.66
	.83	2.06	.94	1.88	.73	1.83	.67	1.90	.56	1.69	.41	1.04
	.52	1.84	.61	1.53	.75	1.48	.73	1.83	.84	1.76	.69	1.56
	.62	1.67	.56	1.99	.56	1.99	.54	1.73	.91	1.92	.63	1.66

POPULATION C3

KARYOTYPE	6.		7.		8.		9.		1.		2.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.92	9.24	.89	8.85	.84	7.38	.79	7.51	.88	8.31	.97	7.97
	.90	8.06	.87	8.74	.94	7.68	.93	9.72	.83	7.98	.68	8.61
Pair 2	.92	3.13	.76	3.59	.93	3.03	.71	3.68	.85	3.55	.64	3.23
	.93	3.34	.78	3.61	.81	3.49	.84	3.10	.76	3.57	.82	3.75
Pair 3	.33	2.51	.54	2.70	.44	2.61	.32	2.67	.37	2.52	.30	3.32
	.35	2.86	.35	3.13	.36	3.32	.35	2.80	.42	2.70	.41	2.58
	.80	2.39	.78	2.67	.97	2.23	.67	2.73	.77	2.38	.86	2.69
	.75	2.37	.78	2.63	1	2.17	.78	2.39	.74	2.18	.82	2.64
	.40	2.83	.43	2.17	.53	2.48	.39	2.54	.36	2.72	.38	2.63
	.38	2.36	.37	2.12	.58	2.43	.38	2.33	.64	2.25	.30	2.53
	.69	1.87	.91	1.54	.62	1.94	.60	1.55	.72	1.85	.66	1.86
	.87	1.64	.59	1.55	.65	1.93	.78	1.61	.80	1.67	.79	1.46
	.60	1.68	.64	1.88	.82	1.74	.50	1.48	.74	1.71	.84	2.00
	.85	1.64	.63	1.84	.67	1.78	.64	1.51	.79	1.75	.47	1.88
	.92	2.04	.73	1.51	.81	1.71	.77	1.82	.72	1.78	.88	1.93
	.62	1.49	.83	1.89	.76	1.75	.96	1.79	.70	2.25	.68	1.94
	.53	1.86	.80	1.34	.76	1.72	.66	1.68	.88	1.98	.73	1.92
	.88	1.81	.91	1.83	.91	1.80	.76	1.69	.66	1.62	1	1.74
	.94	2.14	.64	1.68	.80	1.70	.66	1.60	.69	1.60	.81	1.66
	.44	1.87	.66	1.61	.83	1.62	.59	1.60	.45	1.68	.50	1.95
	.68	1.84	.73	1.70	.70	2.06	.89	1.84	.78	2.02	.64	1.57
	.67	1.70	.70	1.61	.59	1.97	.74	2.07	.92	1.66	.71	1.79
	.73	1.54	.49	1.93	.90	1.86	.75	1.54	.77	1.86	.72	1.66
	.72	1.79	.64	1.65	.90	1.93	.74	1.70	.65	1.67	.71	1.40
	.82	1.97	.62	1.82	.69	1.78	.81	1.83	.56	2.06	.97	1.95
	.58	1.53	.82	1.62	.66	1.72	.71	1.79	.57	1.85	.77	1.38
	.84	1.76	.86	2.00	.83	1.70	.94	1.83	.79	1.84	.94	1.97
	.64	1.70	.66	1.60	.81	1.91	.64	1.86	.77	1.97	.81	1.29
	.68	2.09	.37	2.17	.94	1.99	.52	1.57	.63	1.71	.55	1.67
	.86	1.77	.73	1.66	.90	1.67	.61	1.42	.74	1.76	.50	1.74
	.64	1.53	.50	1.62	.73	1.77	.72	1.66	.71	1.85	.59	1.42
	.87	1.80	.62	1.58	.77	1.76	.83	2.50	.83	2.55	.66	1.60
	.78	1.59	.81	1.91	.83	1.57	.73	1.82	.76	1.58	.57	1.63
	.73	1.40	.75	2.09	.89	.54	1.52	1.52	.74	1.83	.39	1.65

KARYOTYPE	6.		7.		8.		9.		1.		2.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.89	1.91	.76	1.71	.68	1.87	.72	1.77	.85	1.74	.68	1.80
	.51	1.70	.61	1.45	.66	1.87	.79	1.66	.69	1.55	.76	1.80
	.93	1.47	.77	1.42	.59	1.92	.44	1.50	.75	1.76	.94	2.04
	.71	1.72	.56	1.40	.82	1.84	.81	2.13	.89	1.62	.44	1.69
	.94	1.81	.86	1.92	.69	1.76	.57	1.87	.84	2.13	.70	1.72
	.60	1.81	.72	1.83	.78	1.86	.67	2.14	.80	1.88	.65	2.07
	.51	1.75	.53	1.67	.87	1.96	.70	1.65	.56	1 50	.50	1.44
	.81	1. 2	.56	1.96	.85	1.86	.81	1.81	.73	1.66	.75	1.44

KARYOTYPE	3.		4.		5.		6.		7.	
Pair 1	.73	7.37	.82	8.89	.82	8.18	.89	8.62	.66	8.65
	.98	7.12	.82	7.69	.78	8.19	.86	8.30	.71	7.75
Pair 2	.81	3.27	.74	3.33	.84	3.27	.82	3.80	.74	3.83
	.79	3.26	.90	3.12	.81	3.19	.77	3.60	.78	3.31
Pair 3	.58	3.67	.41	2.80	.45	2.41	.22	3.38	.34	2.57
	.41	3.10	.65	2.60	.41	3.09	.33	2.95	.36	2.78
	.71	2.58	.80	2.44	.73	2.53	.87	2.54	.79	2.50
	.70	2.67	.70	2.45	.88	2.43	.77	2.50	.79	2.21
	.49	2.32	.43	2.28	.46	2.60	.47	2.53	.44	2.45
	.49	2.27	.54	2.27	.45	2.57	.41	2.45	.43	2.20
	.81	1.81	.70	1.65	.75	1.85	.65	1.96	.62	2.00
	.73	1.92	.92	2.05	.69	1.54	.52	1.63	.52	1.82
	.78	2.06	.60	1.79	.63	1.58	.49	1.48	.51	1.87
	.58	1.66	.72	1.74	.76	2.09	.92	1.70	.70	1.64
	.72	1.72	.75	1.95	.77	1.86	.65	2.07	.52	1.44
	.78	1.82	.50	1.93	.53	1.66	.38	1.66	.75	1.92
	.65	1.84	.66	1.71	.84	1.69	.65	2.16	.63	1.60
	.89	1.91	.61	1.89	.59	1.78	. 1	1.66	.53	1.44
	.64	1.59	1	1.87	.84	2.09	.75	2.06	.57	1.53
	.78	1.77	.68	1.60	.75	1.83	.74	1.46	.69	1.76
	.78	2.01	.48	1.55	92	2.03	.55	1.80	.76	2.15
	.72	1.94	.79	1.88	.68	1.57	.71	1.64	.58	1.90
	.67	2.06	.81	2.02	.99	1.86	.57	1.56	.66	1.92
	.60	2.12	.79	1.77	.82	1.57	.92	1.85	.74	2.05
	.89	1.97	.82	1.84	.70	2.08	.63	1.14	.38	1.51
	.83	1.83	.82	1.84	.57	1.76	.54	1.67	.78	1.93
	.77	1.81	.93	1.76	.61	1.75	.51	1.67	.90	1.79
	.97	2.00	.82	1.74	.78	1.89	.59	1.55	.69	1.63
	.89	1.94	.58	1.61	.38	1.83	.71	1.59	.60	1.73
	.85	1.72	.68	2.05	.96	1.79	.94	1.63	.61	1.53
	.86	1.96	.50	1.82	.67	1.87	.73	1.30	.87	1.93
	.80	1.54	.73	1.98	.94	1.87	.85	1.78	.84	1.84
	.95	1.61	.91	1.67	.52	1.50	.84	1.83	.63	1.81
	.83	1.72	.67	1.68	.88	1.91	1	1.82	.83	1.68
	.84	1.74	.66	1.56	.79	1.66	.69	1.82	.87	1.56
	.81	1.62	.53	1.92	.75	1.98	.87	1.78	.75	1.67
	.78	1.74	.77	1.86	.78	1.60	.72	1.58	.76	1.85
	.60	1.65	.79	1.71	.57	1.51	.87	1.44	.45	1.77
	.64	2.10	.75	1.71	.76	1.91	.69	1.68	.82	1.69
	.56	1.66	.77	1.91	.74	1.44	.76	1.55	1	2.07
	.53	1.98	.70	1.59	.67	1.82	.84	1.78	.53	1.61
	1	1.65	.70	1.84	.72	1.84	.96	2.09	.84	2.07

POPULATION D1

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.84	8.32	.97	8.56	.81	7.18	.85	8.66	.84	7.13	.84	8.56
	.92	8.99	.74	8.23	.89	9.00	.82	8.13	.98	8.31	.99	8.60
Pair 2	.72	3.39	.79	3.41	.84	3.60	.77	3.68	.94	2.97	.88	3.33
	.90	3.52	.95	3.41	.87	3.07	.93	3.25	.75	3.23	.83	2.73
Pair 3	.45	2.41	.41	2.50	.44	2.08	.54	2.41	.32	2.85	.49	2.16
	.41	2.31	.43	2.76	.46	2.48	.48	2.71	.35	2.90	.41	2.93
	.79	2.62	.83	2-68	.78	2.60	.86	2.37	.94	2.41	.96	2.39
	.72	2.45	.85	2.45	.69	2.64	.94	2.33	.67	2.42	.68	2.74
	.71	1.82	.82	2.20	.82	2.34	.74	2.22	.71	2.32	.71	2.49
	.90	2.39	.81	2.37	.71	2.16	.75	2.55	.80	2.22	.67	2.55
	.53	2.67	.56	2.35	.55	2.39	.47	2.35	.95	2.14	.55	2.05
	.44	2.42	.47	2.09	.52	2.32	.43	2.70	.95	2.14	.55	2.05
	.64	1.80	.81	1.79	.60	1.66	.93	1.85	.73	2.61	.72	1.74
	.71	1.84	1	1.68	.55	2.24	.88	1.73	.54	2.38	.30	1.62
	.86	1.66	.81	1.55	.72	1.65	.81	1.66	.64	1.76	1	1.45
	.88	1.63	.91	1.71	.65	1.81	.68	1.90	.60	2.02.	.84	2.08
	.64	1.76	.76	1.85	.84	1.55	.67	1.63	.75	1.73	.62	1.63
	.45	1.68	.63	1.84	.99	1.78	.96	1.71	.71	1.60	.71	1.68
	.66	1.97	.62	1.64	.84	1.77	.63	1.81	.56	1.56	.53	1.20
	.55	1.78	.81	1.89	1	1.79	.70	1.92	.75	1.62	.63	1.31
	.81	1.63	.71	1.61	.66	1.59	.78	1.61	.71	1.48	.81	1.79
	.75	1.63	.64	1.62	.76	1.72	.69	1.78	.72	1.76	.61	1.71
	.69	1.70	.62	1.83	.96	1.52	.85	1.65	.51	1.76	.88	1.84
	.73	1.79	.72	1.83	.85	1.94	.65	1.63	.55	1.61	.93	1.87
	.64	1.74	.70	2.00	.70	2.01	.53	1.53	.78	1.85	.63	1.84
	.83	1.94	.67	2.16	.69	1.53	.71	1.70	.64	1.82	.84	2.15
	.40	1.74	.84	1.86	.79	1.73	.71	2.10	.31	2.06	.60	1.75
	.63	1.70	.59	1.80	.85	1.70	.68	1.79	.74	1.85	.92	2.23
	.89	1.82	.90	1.9-	.54	1.68	.84	1.63	.89	2.02	1	1.66
	.62	1.65	.78	1.77	.68	1.61	1	1.72	.80	1.55	.67	1.84
	.65	1.67	.55	1.93	.73	1.98	.60	1.79	.84	1.89	.79	1.94
	.55	1.68	.71	1.82	.86	1.82	.71	1.51	.60	1.88	.65	1.61
	.79	1.93	.88	1.61	.89	1.75	.83	1.10	.73	1.89	.49	1.80
	.84	1.79	.68	1.93	.77	1.88	.54	1.62	.64	1.58	.59	2.00
	.58	1.62	.70	1.56	.64	1.87	1	1.76	.71	1.85	.58	1.11
	.71	1.81	.94	1.99	.69	1.94	.50	1.76	.68	1.67	.77	1.70
	.63	1.56	.83	1.73	.52	1.63	.89	1.96	.81	1.93	.73	2.19
	.82	1.71	.57	1.58	.67	2.23	.61	1.79	.77	1.81	.68	1.52
	.77	2.00	.79	1.58	.82	1.83	.78	1.82	.69	1.94	.61	2.08
	.35	1.60	.86	2.00	.87	1.91	.82	1.80	.79	2.05	.68	1.95
	.83	1.75	.89	2.04	.89	1.84	.70	1.97	.53	1.94	.86	1.93
	.65	1.98	.54	1.59	.73	1.83	.79	1.79	.82	2.04	.62	1.96
	.61	1.74	.66	1.69	.89	1.48	.66	1.70	.82	1.77	.63	1.78
	.75	2.13	.55	1.69	.47	1.66	.62	2.05	.74	1.76	.83	1.78

POPULATION D2

KARYOTYPE	1.		2.1		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.91	9.02	.89	7.33	.83	8.78	.88	7.96	.99	7.90	.96	8.08
	.95	7.35	.89	3.17	.84	8.17	.95	8.11	.92	8.15	.93	8.00
Pair 2	.92	3.41	.91	3 .06	.78	3.68	.90	3.34	.81	4.06	.84	3.14
	.92	3.34	.86	3 .53	.83	3.36	.80	3.97	.80	3.38	.89	3.02

KARYOTYPE	1.		2.		3.		4.		5.		6.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 3	.36	2.59	.34	3.13	.25	2.96	.33	2.01	.33	2.79	.45	2.57
	.42	2.25	.47	2.33	.35	2.16	.42	2.06	.43	2.40	.37	2.97
	.88	2.46	.90	2.47	.82	2.89	.80	2.68	.79	2.50	.76	2.55
	.81	2.65	.76	2.57	.64	2.73	.76	3.57	.85	2.48	.68	2.74
	.59	2.46	.70	2.71	.90	2.76	.76	2.24	.73	2.27	.75	2.37
	.50	2.83	.60	2.71	.70	2.77	.78	2.16	.69	2.35	.68	2.38
	.38	2.70	.46	2.66	.50	2.37	.42	2.47	.43	2.46	.57	2.25
	.42	2.25	.49	2.12	.40	2.14	.39	2.74	.38	2.45	.56	2.60
	.73	2.01	.51	1.99	.84	1.66	.89	1.64	.80	1.92	.78	2.11
	.50	1.44	.81	1.74	.60	1.60	.57	1.43	.70	2.05	.88	1.91
	.42	1.63	.68	2.17	.71	1.44	.82	1.91	.79	1.83	.70	2.05
	.44	1.53	.86	2.24	.85	2.39	.93	1.89	.45	1.83	.96	1.87
	.43	1.79	.64	2.10	.58	1.68	.51	1.67	.72	1.81	.50	1.78
	.85	2.01	.83	1.67	.65	1.69	.79	2.21	.69	1.97	.46	1.55
	.62	1.68	.40	1.62	.62	1.89	.64	1.80	.48	1.56	.66	1.62
	.73	1.73	.64	2.29	.58	1.72	.65	1.54	.64	1.75	.62	1.61
	.43	1.73	.83	1.91	.76	2.02	.78	1.47	.88	1.88	.80	1.70
	.60	1.84	.69	1.59	.78	1.79	.63	1.69	.68	2.01	.79	1.58
	.56	1.55	.63	1.92	.64	1.45	.67	1.59	.82	1.57	.61	1.81
	.75	1.83	1	1.97	.50	1.73	.63	1.54	.64	1.70	.82	1.66
	.75	1.72	.56	1.65	.47	1.34	.91	1.83	.95	1.69	.69	1.55
	.64	1.78	.61	1.45	.50	1.77	.62	2.07	.74	1.62	.89	2.12
	.86	2.02	.69	1.77	.47	1.90	.95	2.16	.95	1.77	.77	1.69
	.86	2.07	.77	1.94	.64	1.72	.73	1.85	1	2.05	.82	1.73
	.71	1.63	.77	2.04	.80	1.55	.65	1 86	.84	1.86	.69	1.62
	.65	1.60	.73	1.94	.70	1.44	.81	2.04	.79	1.76	.42	1.80
	.67	1.77	.52	1.93	.51	1.50	.75	1.83	.70	1.82	.73	1.83
	.67	1.77	.52	1.93	.51	1.50	.75	1.83	.70	1.82	.73	1.83
	.61	2.03	.45	2.01	.76	1.85	.61	1.80	.89	1.93	.78	2.12
	.71	1.93	.60	1.47	.65	1.58	.49	1.90	.67	1.61	.63	1.81
	.61	1.60	.60	1.66	.75	1.95	.57	1.87	.67	1.51	.66	1.41
	.96	1.83	.55	1.38	.95	2.10	.79	1.83	.54	1.54	.78	1.58
	.59	1.56	.45	1.41	.74	1.73	.61	1.44	.60	2.00	.64	1.77
	.82	1.68	.91	1.77	.71	1.51	.91	1.86	.85	1.76	.69	1.42
	.90	1.76	.69	1.38	.81	1.67	.79	1.73	1	1.98	.84	2.16
	.65	1.61	.71	1.43	.62	1.85	.66	2.03	.75	1.56	.81	1.60
	.45	1.66	.61	1.50	.65	1.65	.72	1.55	.72	1.30	.68	1.94
	.72	1.87	.64	1.47	.59	1.51	.72	1.52	.70	1.86	.80	1.54
	.86	1.98	.75	1.71	.93	1.77	.63	1.58	.59	1.72	.90	1.88
	.78	1.77	.67	1.37	.66	1.57	.82	2.11	.88	1.89	.89	1.94
	.65	1.84	.83	1.50	.66	1.69	.68	1.55	.59	1.53	.91	2.35

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.91	8.72	.80	8.57	.78	7.96	.85	8.54	.81	8.40	.93	9.14
	.75	7.88	.99	8.90	.87	8.10	.91	9.55	.73	8.28	.87	9.37
Pair 2	.93	3.47	.80	2.99	.71	3.78	.89	3.37	.84	3.38	.80	3.49
	.81	3.27	.70	3.20	.83	3.44	.91	3.30	.77	3.14	.69	3.14
Pair 3	.42	2.99	.31	3.03	.47	2.51	.42	2 38	.30	3.28	.36	2.67
	.41	2.54	.36	3.03	.36	2.61	.34	2.36	.36	2.47	.27	2.30
	.73	2.79	.88	2.71	.93	2.10	.93	2.68	.80	3.08	.94	2.32
	.67	2.50	.92	2.20	.73	2.45	.94	2.67	.69	2.95	.83	2.47
	.66	2.34	.72	2.21	.79	2.33	.83	2.14	.84	2.18	.77	2.37
	.80	2.29	.85	2.20	.79	2.35	.83	2.37	.65	2.46	.82	2.32

KARYOTYPE	7.		8.		9.		10.		11.		12.	
	.48	2.34	.46	2.15	.50	2.67	.40	2.74	.39	2.59	.37	2.56
	.45	2.69	.47	2.53	.48	2.32	.35	2.57	.39	2.28	.43	2.25
	.78	1.88	.54	1.60	.77	1.87	.73	2.08	.54	1.40	.56	1.85
	.85	1.88	.60	1.74	.83	1.88	.76	1.72	.50	1.58	.94	1.86
	.69	1.64	.82	2.10	.62	1.90	.83	1.56	.83	2.07	.38	2.07
	.74	1.76	.44	1.91	.69	1.55	.67	1.57	.81	1.72	.66	1.62
	.82	1.76	.88	1.74	.73	1.99	.84	1.78	.68	1.76	.54	1.50
	.62	1.89	.68	1.66	.72	1.68	.83	1.21	.66	1.60	.68	1.84
	.59	1.92	.64	1.60	.68	1.52	.57	1.95	.92	2.10	.82	1.41
	.77	2.04	.42	1.72	.80	1.63	.88	1.98	.86	2.08	.92	1.91
	.58	1.87	.76	1.88	.73	1.55	.49	1.98	.60	1.43	.67	1.54
	.70	1.60	.64	1.63	.92	1.86	.68	1.37	.80	1.79	.70	1.80
	.75	1.62	.61	1.53	.99	1.83	.65	1.68	.59	1.61	.60	1.84
	.77	1.78	.78	1.46	.76	1.83	.81	1.92	.57	1.51	.44	1.72
	.68	1.71	.82	1.99	.72	2.01	.45	1.80	.58	1.50	.66	1.69
	.79	1.95	.90	1.98	.56	1.61	.66	1.76	.63	1.58	.76	1.66
	.96	1.70	.66	1.44	.76	1.91	.41	1.54	.61	2.09	.84	1.70
	.67	1.62	.71	1.86	.62	1.80	.81	1.96	.84	1.85	.37	1.46
	.80	1.67	.67	1.57	.69	1.80	.58	1.61	.58	1.80	.60	1.41
	.90	1.85	.74	1.86	.90	1.69	.72	1.65	.46	1.66	.51	1.49
	.92	1.83	.55	2.05	.57	1.75	1	1.73	.58	1.79	.30	1.29
	.52	1.82	.84	1.78	.51	1.58	.93	1.64	.60	1.81	1	1.74
	.66	1.50	.81	1.86	.76	2.08	.90	1.88	.62	1.51	.57	2.21
	.66	1.47	.76	1.89	.82	1.52	.51	1.46	.50	1.63	.73	2.03
	.74	1.49	.64	1.36	.86	2.15	.71	1.51	.70	1.57	.51	1.57
	.84	1.87	.81	1.70	.75	1.82	.91	1.67	.69	1.97	.88	1.65
	.53	1.57	.65	1.61	1	1.86	1	1.82	.55	1.78	.86	1.67
	.98	1.80	.70	1.78	.67	2.19	.80	1.54	.50	1.83	.64	1.85
	.84	1.64	.91	2.19	.72	1.63	.31	1.85	.49	1.64	.51	1.89
	.77	1.71	.88	1.75	.72	1.98	.73	1.70	.50	1.86	.86	1.46
	.76	2.00	.97	1.66	.56	1.76	.57	1.50	.54	1.90	.90	1.58
	.65	1.75	.73	1.62	.60	1.80	.82	2.02	1	1.67	.79	1.78
	.78	1.54	.78	1.59	.76	1.40	.77	1.76	.89	1.65	.74	1.82
	.74	1.82	.78	1.60	.62	1.61	.52	1.57	.57	2.25	.75	1.82

KARYOTYPE	13.		14.		15.		16.		17.		18.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.97	8.13	.93	8.33	.77	9.07	.83	8.96	.73	8.33	.74	7.39
	.92	8.92	.91	8.19	.87	8.12	.85	8.23	.89	8.32	.74	7.92
Pair 2	.94	3.33	.88	3.94	.94	3.48	.98	3.49	.81	3.35	.91	3.21
	.82	3.07	.67	4.03	.90	3.07	.87	3.35	.88	2.78	.98	3.55
Pair 3	.41	3.08	.42	1.95	.47	2.56	.43	2.14	.39	2.78	.30	2.83
	.42	2.59	.37	2.82	.40	2.71	.59	1.96	.43	2.34	.46	2.15
	.88	2.30	.88	2.53	.59	2.91	.53	2.58	.83	2.52	.85	2.82
	.77	2.39	.79	2.28	.79	2.40	.70	2.62	.89	2.32	.82	2.64
	.62	2.72	.65	2.12	.58	2.45	.86	2.41	.90	2.14	.86	2.25
	.55	2.31	.69	2.05	.65	2.77	.83	2.41	.64	2.42	.78	2.07
	.50	2.50	.56	2.39	.49	2.19	.57	2.16	.42	2.36	.44	2.27
	.50	2.57	.54	2.45	.51	2.15	.73	2.14	.52	3.45	.58	2.48
	.86	2.02	.55	1.71	.56	1.45	.70	1.71	.67	1.71	.82	1.72
	.93	1.81	.53	1.70	.72	1.58	.46	1.87	.62	2.41	.77	1.74
	.79	2.05	.92	1.64	.94	1.78	.55	1.70	.58	1.70	.61	1.51
	.69	1.83	.80	1.91	.88	2.04	.65	1.60	.81	1.87	.74	1.92
	.72	1.88	.55	1.63	.83	1.94	.80	1.76	.79	1.89	.69	1.58
	.94	2.17	.77	2.04	.85	1.81	.90	1.95	.59	1.69	.78	1.91
	.64	1.39	.97	1.86	.78	1.69	.79	1.76	.81	1.66	.62	1.77

KARYOTYPE	13.		14.		15.		16.		17.		18.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.77	2.07	.57	1.94	.46	1.77	.94	1.83	.88	1.89	.55	1.55
	.70	1.61	.82	1.56	.88	1.8	.76	1.76	.83	1.72	.79	2.10
	.76	1.57	.53	1.52	.73	2.10	.75	2.00	. 8	1.97	.79	2.07
	.89	1.48	.62	1.73	.77	1.87	.78	2.49	.86	1.88	.75	1.77
	.74	1.48	.84	1.82	.81	1.87	.79	1.56	.67	1. 9	1.	1.67
	.90	1.72	.90	1.76	.76	1.93	.70	1.84	.69	1.55	.56	1.91
	.55	1.52	.50	1.74	.94	1.78	.64	1.63	.84	1.76	.78	1.63
	.76	1.46	.63	1.79	.90	2.09	.72	1.74	.78	1.68	.66	1.83
	.48	1.83	.61	1.88	.78	1.76	1	1.97	.72	1.72	.85	1.80
	.94	1.53	.64	2.15	.68	2.10	.84	1.82	.85	1.81	.66	1.84
	.53	1.72	.78	1.89	.78	1.76	1	1.79	.61	1.92	.75	2.14
	.73	1.51	.69	1.60	.59	1.51	.56	1.53	.57	1.62	.92	1.91
	.79	1.42	.58	1.64	.58	1.68	.70	1.72	.68	1.61	.80	1.72
	.69	1.58	.69	1.47	.47	1.66	.83	1.92	1	1.95	.65	1.55
	.55	1.51	.59	1.35	.65	1.76	.89	1.90	.53	1.80	.74	1.95
	.73	1.66	.81	2.19	.73	1.36	.86	2.20	.69	1.87	.98	1.72
	.74	2.06	.75	1.74	.55	1.75	.62	1.70	.73	1.90	.64	1.51
	.70	1.48	.70	2.00	.72	2.10	.68	1.58	.60	1.66	.58	1.65
	.64	1.43	.76	2.07	.64	1.49	.68	1.64	.75	1.92	.82	2.01
	.77	1.6	.73	1.55	.58	1.79	.78	1.80	.85	1.04	.68	1.86
	.67	1.63	.77	1.62	1	1.49	.56	1.56	.73	1.64	.82	1.98
	.68	1.92	.69	1.75	.78	1.58	.55	1.70	.47	1.64	.80	1.95
	.73	1.95	.77	1.70	.72	1.53	.65	1.81	.83	1.68	.73	2.11
	.83	1.81	.99	1.57	.63	1.43	.51	1.62	.58	1.74	.74	2.10
	.80	2.16	.93	2.21	.59	1.57	.79	1.78	.77	2.06	.58	1.71

KARYOTYPE	19.		20.		21.		22.		23.		24.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.92	8.87	.79	7.77	.90	8.06	.92	8.34	.75	8.17	.85	8.77
	.83	8.66	.84	7.71	.78	8.36	.95	7.52	.78	8.01	.88	8.74
Pair 2	.82	3.19	.81	3.64	.89	2.96	.94	3.14	.95	3.51	.85	3.28
	.75	3.51	.81	3.58	.86	2.80	.80	3.01	.91	3.45	.77	3.31
Pair 3	.34	2.65	.31	2.52	.51	2.40	.42	2.54	.28	2.62	.36	2.54
	.45	2.44	.30	3.17	.47	2.46	.40	2.90	.35	2.93	.34	2.65
	.89	2.47	.71	2.48	.90	2.64	.81	2.64	.77	2.65	.72	2.42
	.86	2.74	.84	2.70	.80	2.59	.70	2.84	.91	2.50	.78	2.50
	.82	2.27	.76	2.16	.94	2.17	.72	2.07	.96	2.31	.85	2.27
	.79	2.27	.74	2.24	.84	2.33	.70	2.44	.78	2.13	.95	2.59
	.85	1.52	.79	1.98	.80	1.84	.73	1.61	1	1.76	.72	1.52
	.64	1.87	.60	1.69	.77	1.67	.71	1.66	.58	1.64	.80	1.61
	.52	2.53	.53	2.48	.55	2.56	.51	2.45	.47	2.45	.47	2.29
	.44	2.37	.65	2.58	.60	2.14	.53	2.27	.48	2.49	.40	2.37
	.81	1.47	.57	1.61	.76	1.49	.85	1.73	.77	1.64	.87	1.79
	.51	2.48	.58	1.77	.74	1.88	.77	1.37	.58	1.72	.60	1.63
	.58	1.82	.80	1.57	1	1.66	.78	1.54	.87	1.77	.92	1.88
	.92	1.80	.72	1.82	.81	1.74	.89	1.86	.90	1.64	.80	1.78
	.57	1.52	.76	2.07	1	2.18	.51	2.00	.88	2.06	.59	1.66
	.75	1.77	.85	1.94	.79	1.66	.65	1.74	.55	1.71	.66	1.87
	.68	1.89	.71	1.86	.59	1.74	.98	2.14	.92	1.75	.87	1.86
	.87	1.69	.49	1.92	.55	1.64	.73	1.84	.66	1.77	.53	1.63
	.84	1.77	.55	1.61	.73	1.63	.60	1.79	.74	1.64	.64	1.69
	.57	1.58	.77	2.41	.85	1.74	.68	1.82	.80	1.78	.71	1.63
	.90	1.53	.77	1.67	1	1.87	.70	2.01	.78	1.84	.71	1.85
	.66	1.58	.76	1.77	1	2.16	.58	1.60	.59	1.57	.80	1.97
	.68	1.84	.70	1.77	.63	1.67	.65	1.70	.87	2.11	.60	1.63
	.62	1.94	.71	1.89	.65	1.88	.51	1.64	.77	1.52	.80	1.77

KARYOTYPE	19.		20.		21.		22.		23.		24.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.63	1.73	.83	1.80	.80	2.28	1	2.09	.81	1.92	.81	1.68
	.75	1.94	.98	2.09	.63	1.98	.71	1.52	.65	1.62	.79	1.70
	1	1.91	.81	1.74	.66	2.03	.54	1.65	.71	1.86	.60	1.83
	1	1.47	.74	2.00	.89	1.97	.81	1.54	.55	1.77	.74	1.35
	.65	1.58	.54	1.58	.87	1.99	.84	1.84	.80	1.91	.70	1.55
	.74	1.77	1	1.60	.79	1.86	.69	1.84	.70	1.64	.70	1.97
	.77	1.61	.60	1.62	.69	1.62	.85	1.90	1	1.92	.88	1.93
	.50	2.38	.48	1.52	.74	1.97	.93	2.27	.77	1.81	.67	2.13
	.59	1.45	.73	1.88	.70	1.68	.69	1.68	.74	1.82	.72	1.75
	.74	1.69	.52	1.72	.75	1.69	.70	2.20	.67	1.61	.80	1.54
	.58	1.71	.56	1.48	.87	1.82	.69	1.71	.65	1.58	.57	1.82
	.71	1.59	.76	2.05	.72	1.69	.53	1.83	.75	1.81	.63	1.70
	.87	1.83	.53	1.73	.86	1.79	.63	1.76	.63	2.02	.74	1.95
	.73	1.77	.72	1.76	.90	1.60	.52	1.71	.95	1.61	.92	2.05
	.87	1.65	.63	1.52	.77	2.02	.79	2.03	.58	2.00	.55	1.41
	.79	1.70	.54	1.35	.87	1.86	.76	1.94	.56	1.74	.66	1.89

POPULATION E1

KARYOTYPE	25.		26.		27.		28.		29.		1.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.77	9.00	.74	6.98	.65	8.00	.85	8.00	.83	8.49	.98	6.90
	.82	8.77	.78	6.71	.91	7.96	.86	7.72	.73	7.92	.88	7.67
Pair 2	.89	2.69	.98	3.56	.90	3.51	.92	3.18	.90	3.43	.94	3.27
	.88	2.60	.97	4.19	.96	3.22	.90	3.35	.90	3.31	.84	3.18
Pair 3	.31	2.84	.33	2.90	.29	2.69	.42	2.92	.32	2.98	.32	2.61
	.34	2.37	.32	3.49	.28	3.06	.33	2.53	.35	2.76	.24	3.50
	.88	2.18	.95	2.74	.85	2.42	.70	2.78	.76	2.56	.70	2.51
	.70	2.54	.84	2.75	.72	2.49	.59	2.57	.88	2.50	.70	2.68
	.76	2.15	.90	2.62	.89	2.46	.76	2.18	.80	2.42	.74	2.16
	.69	2.26	.81	2.24	.90	2.51	.86	2.36	.73	2.55	.65	2.34
	.51	2.64	.58	2.22	.45	2.42	.36	2.68	.54	2.66	.40	2.84
	.51	2.71	.44	2.82	.74	1.87	.61	2.71	.58	2.58	.52	2.45
	.72	1.67	.87	1.79	.98	1.68	.86	1.89	.51	1.58	.79	2.11
	.55	1.76	.72	1.73	.86	2.01	.76	1.84	.76	1.88	.86	1.81
	.63	2.11	.69	2.17	.61	1.96	.60	1.64	.90	1.93	.67	1.40
	.53	1.60	.75	1.77	.85	1.99	.65	1.68	.73	2.02	.91	1.89
	.62	1.67	.69	1.78	.55	1.91	.71	1.60	.69	1.59	.96	1.73
	.55	1.53	1	1.68	.86	1.81	.57	1.85	.75	1.95	.90	1.56
	.68	1.60	.61	1.46	.88	2.36	.81	2.13	.94	2.07	.95	1.86
	.84	1.61	.76	1.45	.47	1.41	.74	1.90	1	1.67	.87	2.22
	.60	1.70	.57	1.67	.57	1.47	.76	2.29	.93	1.89	.68	1.93
	1	1.68	.86	1.83	.76	1.62	.78	1.72	.65	1.48	.76	1.72
	.92	1.75	.63	1.57	.76	1.65	.63	1.61	.64	1.85	.65	1.88
	.68	1.77	.84	1.77	.45	1.87	.53	1.47	.46	1.89	.68	1.66
	.59	1.89	.67	1.80	.68	1.73	.78	1.82	.53	1.70	.76	1.58
	.91	2.02	.88	1.95	.61	1.59	.73	1.65	.85	1.86	.66	1.82
	.46	1.56	1	1.88	.80	1.52	.80	1.99	.86	1.83	.69	1.61
	1	1.96	.67	1.63	.73	1.54	.73	1.80	.71	1.80	.40	2.00
	.67	2.01	.77	1.43	.64	1.84	.54	1.71	.96	1.70	.68	2.01
	.87	1.97	.62	1.67	.57	1.76	.82	1.55	.82	1.73	.93	2.00
	.92	1.90	.73	1.65	.67	1.96	.46	1.57	.99	1.90	.84	2.12
	.74	1.68	.79	1.61	.71	1.69	.43	1.62	.72	1.83	.73	1.54
	.71	1.89	.55	1.67	.76	1.42	.64	1.75	.65	1.46	.62	1.63
	.98	1.68	.83	1.76	.77	1.48	.47	1.72	.63	1.48	.82	1.80
	.93	1.54	.78	1.76	.94	2.06	.68	1.91	.70	1.68	.54	1.56
	.60	1.90	.55	1.83	.69	1.58	.69	1.70	.74	1.47	.66	1.61

KARYOTYPE	25.		26.		27.		28.		29.		1.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
	.82	2.06	.74	2.04	.52	1.50	.96	2.10	.74	1.63	.84	1.92
	.72	1.72	.82	2.02	.84	1.52	.76	1.80	.79	1.51	.70	1.84
	.86	1.78	.69	1.98	.86	1.96	.92	1.77	.92	2.03	.50	1.63
	.53	1.83	.79	1.93	.81	1.67	.48	1.91	.87	1.70	.62	1.71
	.73	1.80	.63	1.73	.75	2.00	.85	1.76	.61	1.45	.98	1.71
	.81	1.59	.74	2.12	.61	1.73	.77	1.72	.67	1.66	.53	1.60
	.56	1.88	.71	1.77	.78	2.58	.82	1.69	1	1.77	.85	1.90
	.56	1.77	.46	1.70	.44	2.46	.92	1.60	.77	1.68	.45	2.19

POPULATION E1

KARYOTYPE	2.		3.		4.		5.		6.		7.	
	R	RL	R	RL	R	RL	R	RL	R	RL	R	RL
Pair 1	.73	8.71	.78	8.51	.94	7.75	.75	8.41	.72	8.73	.83	10.14
	.87	8.06	.81	8.37	.83	8.27	.81	8.58	.83	8.37	.90	7.37
Pair 2	.83	3.76	.77	3.94	.85	3.40	.74	3.77	.83	3.19	.92	3.26
	.81	3.46	.72	3.68	.86	3.38	.71	3.41	.84	3.68	.81	3.28
Pair 3	.31	2.73	.32	2.77	2.9	2.64	.45	2.48	.23	2.77	.62	2.27
	.33	2.80	.44	2.71	.39	2.81	.48	2.42	.35	2.83	.36	2.56
	.78	2.81	.59	2.78	1	2.34	.84	2.40	.55	2.43	.84	2.21
	.80	2.58	.81	2.56	.80	2.23	.64	2.67	.72	2.54	.89	2.46
	.86	2.18	.50	2.34	.84	2.11	.87	2.22	.66	2.74	.91	1.99
	.90	2.47	.54	2.31	.56	2.82	.89	2.24	.66	2.12	.93	2.16
	.45	2.37	.33	2.51	.38	2.54	.46	2.42	.37	2.26	.42	2.42
	.42	2.60	.46	2.75	.40	2.26	.55	2.51	.38	2.64	.37	2.56
	1	1.94	.90	1.76	.93	1.56	.57	1.55	.64	1.73	.57	2.08
	.66	1.83	.63	1.67	.81	1.74	.53	1.60	.76	1.32	.92	1.94
	.78	1.57	.49	1.41	.84	1.56	.84	1.78	.81	1.56	.70	1.65
	.53	2.12	.75	1.52	.53	1.46	.80	2.00	.75	1.88	.88	1.90
	.79	1.85	.67	1.88	.55	1.92	.61	1.59	.58	1.92	.80	1.79
	.79	1.36	.45	1.62	.72	1.99	.90	2.04	.69	2.25	.73	1.77
	.70	1.58	.59	1.40	.68	1.97	.77	1.69	.70	1.54	.93	1.61
	.69	1.58	.51	2.10	.62	1.45	.87	1.81	.78	1.34	.74	1.64
	.57	1.84	.53	1.57	.63	1.76	.80	1.74	.67	1.63	.66	1.71
	.48	1.73	.75	1.65	.65	1.74	.62	1.92	.75	1.61	.62	1.73
	.72	1.61	.54	1.88	.70	1.95	.73	2.10	.60	1.78	.58	1.71
	.55	1.77	.73	1.77	.55	2.12	.83	2.01	.56	1.50	.86	1.57
	.67	1.93	.83	1.99	.55	2.09	.54	1.66	.43	1.87	.88	2.04
	.78	1.39	.62	1.46	.54	1.75	.69	1.42	.52	2.08	.50	1.90
	.56	1.64	.80	1.64	.84	2.09	.68	1.92	.46	2.10	.61	1.54
	.76	1.66	.79	1.62	.53	1.49	.77	1.82	.72	1.85	.68	1.74
	.74	1.66	1	2.15	.52	1.61	.67	1.55	.76	1.53	.81	1.61
	.55	1.96	.77	1.74	.64	1.52	.69	1.85	.73	2.04	.99	1.68
	.67	1.58	.51	1.66	.72	2.25	.64	2.17	.54	2.57	.65	1.91
	.38	1.52	.66	1.65	.65	1.92	.68	1.97	.87	1.78	.82	1.78
	.76	1.71	.64	1.68	.80	2.35	.76	1.77	.73	1.82	.59	1.53
	.57	1.92	.69	1.92	.83	1.74	.86	1.68	.60	1.55	.76	1.64
	.81	1.87	.72	1.92	.60	.54	.80	1.54	.79	1.36	.54	1.61
	.65	2.01	.52	1.68	.94	1.62	.60	1.46	.65	1.55	1	1.65
	.51	2.00	.69	1.42	.89	1.65	.69	1.49	.82	1.38	.65	1.67
	.67	1.85	1	1.95	.61	1.70	.94	1.95	1	1.50	.66	1.84
	.90	1.98	.78	1.41	.66	1.84	.84	1.80	.63	1.65	.74	1.65
	.60	1.45	.63	1.46	.71	1.95	.65	1.79	.54	1.55	.64	1.79
	.74	1.38	1	2.03	.65	1.40	.64	1.49	.82	1.48	.79	2.00
	.72	1.68	.65	1.47	.70	2.04	.76	1.65	.66	2.03	.79	2.48
	.70	1.58	.57	1.69	.67	1.88	.69	1.88	.67	1.98	.52	1.97
	.81	1.68	.77	1.91	.78	1.60	.70	1.53	.66	2.04	.65	2.01

KARYOTYPE	8.		9.		10.	
	R	RL	R	RL	R	RL
Pair 1	.99	9.33	.86	8.25	.77	7.82
	.79	8.42	.85	7.95	.82	8.09
Pair 2	.82	3.44	.94	3.52	.89	3.09
	.84	3.37	.81	3.81	.84	3.55
Pair 3	.36	2.80	.24	2.73	.56	2.71
	.34	2.58	.41	2.12	.51	2.70
	.64	2.62	.84	2.50	.86	2.80
	.74	2.62	.89	2.36	.80	2.56
	.86	2.41	.80	2.29	.73	2.43
	.83	2.29	.81	2.69	.86	2.40
	. 5	2.32	.32	2.47	.37	2.27
	.46	2. 0	.35	2.30	.59	2.15
	.79	2.06	.60	2.00	.58	1.65
	.63	2.02	.60	1.88	.63	1.49
	.75	1.52	.63	1.73	.56	1.56
	.64	1.79	.44	1.74	.96	1.55
	.61	2.06	.52	1.88	.98	1.97
	1	1.66	.57	1.62	.75	1.94
	.61	1.68	.64	1.89	.60	1.62
	1	1.59	.67	1.89	.87	1.50
	.87	1.51	.52	1.94	.74	1.70
	.59	1.77	.73	2.01	.85	1.73
	.70	1.84	.64	1.64	.55	1.77
	.78	1.78	.96	1.58	.75	1.72
	.56	1.70	.61	1.66	.61	1.82
	.72	2.29	.54	1.52	.76	2.10
	.80	1.58	.87	1.91	.68	1.80
	.71	1.62	.47	1.72	.80	2.21
	.67	2.09	.47	2.02	.57	1.63
	.91	1.69	.59	1.48	.38	1.63
	.80	1.94	.60	1.83	.57	1.79
	.71	1.51	.85	1.86	.78	1.91
	.73	1.92	.61	1.30	.76	2.21
	.80	1.75	.50	1.60	.79	1.68
	.51	1.45	.48	2.03	.61	1.97
	.72	1.42	.47	1.50	.71	1.91
	.94	1.52	.34	2.73	1	1.66
	.63	1.52	.58	1.46	.62	1.77
	.71	1.95	.73	2.22	.85	1.62
	.81	1.83	.91	1.73	.64	1.73
	.62	1.52	.83	2.10	1	1.98
	.41	1.68	.42	1.36	.96	2.28
	.73	1.41	.82	0.94	.69	1.60
	.57	1.90	.81	1.97	.68	1.60

APPENDIX B

The relative lengths (RL) and R values for the karyotypes measured for the photographic plates 1 to 27.

R Rottingdean, Sussex
CH Cuckmere Haven, Sussex.
IC Isle of Cumbrae,Firth of Clyde.
SB St. Brides Haven, Pembrokeshire.
CB Castlebeach Bay,Pembrokeshire.

6A and 7A are the data from 2n = 27 karyotypes from Rottingdean,Sussex.

Origin R Plate 1			Origin R Plate 2			Origin R Plate 3			Origin R Plate 4		
Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
A	6.72	.67	A	6.96	.80	A	6.29	.70	A	6.59	.91
	6.73	.70		6.49	.78		5.73	.85		6.20	.80
	5.60	.93		6.44	.97		5.24	.95		5.60	.67
	6.08	.74		5.67	.82		5.82	.89		6.29	.76
	5.51	.64		5.29	.67		4.66	.67		5.61	.62
	5.25	.64		5.40	.71		4.31	.58		5.80	.64
	5.18	.63		4.93	.68		4.60	.72		5.74	.68
	5.24	.68		5.29	.83		4.65	.69		5.12	.41
B	4.73	.41	B	4.34	.37	B	3.67	.42	B	4.66	.41
	4.79	.38		4.26	.46		3.31	.35		4.38	.43
	3.77	.45		3.55	.48		3.42	.40		3.45	.41
	3.83	.50		3.47	.56		4.12	.45		3.08	.55
C	3.73	.75	C	3.59	.96	C	2.91	.99	C	3.77	.70
	3.45	.75		3.43	.93		2.96	.82		4.02	.80
	3.27	.64		2.35	.16		2.60	.32		3.24	.29
	3.26	.59		5.23	.67		2.40	.29		3.44	.32
	3.01	.65		3.17	.68		2.89	.54		2.93	.53
	3.12	.53		3.02	.68		2.92	.49		2.94	.57
	2.80	.83		2.93	1		2.29	.83		2.59	.86
	2.72	.72		2.78	1		2.67	.75		2.60	.65
D	2.80	.32	D	2.66	.33	D	2.14	.30	D	2.61	.31
	2.29	.31		2.97	.45		2.09	.34		2.92	.44
E	1.93	1	E	2.13	1	E	1.65	1	E	1.84	.71
	1.98	1		1.98	.88		1.64	1		2.20	.78
	1.24	-		1.84	.74		1.16	.65		1.39	.68
	1.71	-		1.74	.79		1.06	-		0.86	-

Origin CH Plate 5			Origin R Plate 6			Origin R Plate 6A			Origin R Plate 7		
Group	RL	R	Group	RL	R	Group	RL	P	Group	RL	R
A	7.63	.78		6.35	.79		5.85	.66		6.83	.78
	7.74	.69		6.28	.93		6.44	.74		7.32	.86
	7.04	.99		5.67	.81		6.64	.80		5.66	.93
	6.26	.83		5.31	.74		6.76	.79		5.89	.90
	5.67	.66		6.65	.83		5.74	1		5.32	.83
	5.72	.66		5.05	.58		5.54	.83		5.41	.67
	4.49	.35		5.06	.64		5.53	.60		5.25	.97
	4.49	.37		5.17	.56		5.22	.55		5.09	.99

Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
B	3.60	.27	B	4.83	.41	B	4.96	.42	B	4.21	.34
	3.68	.37		3.97	.42		4.54	.33		4.18	.41
	3.89	.22		3.64	.37		3.59	.48		3.37	.37
	3.90	26		3.62	.50		3.39	.48		3.09	.43
C	3.83	.86	C	3.72	.66	C	3.76	.82	C	4.03	.87
	3.85	.76		3.76	.86		4.01	.91		4.25	.79
	3.25	.52		3.02	.82		2.98	.63		3.27	.59;
	3.46	.57		3.02	.57		2.97	.54		3.35	.61
	3.32	.53		2.79	.79		2.67	.74		3.41	.84
	3.22	.55		2.79	.75		2.58	.69		3.10	.74
	2.99	.68		3.18	.54		3.06	.51		2.18	.71
	2.86	.75		1.20	-		1.27	-		1.86	.48
D	2.82	.32		2.33	.64		1.51	.60		1.34	-
	2.76	.24	D	2.53	.31	D	2.92	.27		1.45	-
E	1.57	.93		2.38	.28		2.65	.26	D	2.60	.23
	1.52	.87	E	1.82	1	E	1.50	.88		2.19	.16
	1.02	.68		2.12	1		1.44	.87	E	1.92	.70
	1.06	.61		1.75	.50		1.27	.46		1.59	.62
				1.74	.62		1.07	.47		0.79	-
										0.91	-

Origin R
Plate 7A

Origin CH
Plate 8

Origin CH
Plate 9

Origin IC
Plate 11

Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
A	6.97	.68	A	6.52	.83	A	6.37	.92	A	6.50	.95
	6.91	.95		5.84	.88		6.65	.83		6.57	.85
	5.56	.57		5.53	.82		6.31	.87		5.67	.88
	6.01	.64		6.59	.66		6.01	.95		5.29	.88
	4.88	.67		5.73	.90		5.87	.66		4.68	.81
	4.81	.66		5.07	.90		5.82	.57		4.98	.81
	3.94	.69		5.36	.78		4.94	.79		6.58	.92
	4.27	.82		2.29	-		2.60	.27		3.65	.30
				2.50	.43		2.87	.32		3.40	.23
B	4.42	.34	B	3.28	.48	B	3.39	.41	B	4.98	.47
	4.25	.34		4.15	.45		3.62	.47		5.04	.39
	3.64	.34		4.19	.33		3.11	.56		3.53	.46
	3.63	.39		4.15	.35		3.20	.51		3.75	.38
C	3.43	.61		3.68	.84		4.36	.95		3.77	.51
	3.20	.58		4.07	.88		4.64	.96		3.67	.75
	2.79	.57	C	3.43	.56	C	3.91	.72	C	3.40	.58

Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
	2.83	.57		3.82	.56		3.95	.82		3.36	.54
	2.97	.71		3.41	.50		2.80	.70		2.46	.23
	3.20	.70		2.75	.26		3.22	.66		2.48	2.5
	3.12	.21		2.86	.56		2.34	.79		2.68	.69
	3.23	.29		2.60	.63		2.59	2.75			
	2.06	.14									
D	2.68	.25	D	2.22	.31	D	2.24	.42	D	2.11	.22
	2.47	.11		2.38	.29		2.41	.35		2.15	.25
E	1.75	1	E	2.05	1	E	1.80	.61	E	1.38	.56
	1.91	1		2.10	1		1.74	.75		1.24	.61
	1.06	.30		1.53	.73		1.60	.47		1.89	1
	1.26	.30		1.48	.51		1.51	.39		1.89	.84

Origin IC				Origin C				Origin CH				Origin SB	
Plate 12				Plate 13				Plate 14				Plate 15	
Group	RL	R	Group	RL	R	Group	PL	R	Group	RL	R		
A	6.82	.82	A	6.78	.78	A	7.05	.80	A	7.72	.68		
	6.53	.69		6.80	.68		6.87	.75		6.61	.79		
	6.89	.73		6.03	.95		6.40	.95		5.26	.67		
	6.50	.63		6.36	.98		6.59	.97		5.25	.77		
	4.47	.78		5.46	.56		5.69	.57		5.62	.58		
	4.77	.86		3.30	-		5.01	.73		4.79	.58		
	4.25	.42		2.81	.45		2.38	-		3.20	.24		
	3.77	.36		4.68	.71		2.38	-		3.61	.29		
	3.56	.43		2.05	.15		3.52	.27		1.97	.60		
	3.22	.27		2.02	.21		2.11	.29		3.05	.22		
B	3.89	.58	B	4.35	.40	B	4.59	.41	B	5.19	.38		
	3.27	.44		4.49	.42		4.66	.47		3.19	.33		
	3.18	.54		3.18	.38		3.07	.48		3.42	.28		
	3.22	.57		3.30	.54		3.06	.60		5.05	.62		
C	3.68	.73	C	3.52	.80	C	3.78	.78		1.37	-		
	3.75	.76		3.97	.91		4.06	.82	C	3.60	.63		
	3.60	.65		2.97	.65		3.18	.68		2.83	.40		
	3.62	.51		3.02	.70		3.14	.59		2.79	.27		
	3.31	.50		2.57	.27		3.31	.50		2.78	.19		
	3.24	.52		3.14	.39		2.24	.46		3.10	.74		
	2.28	.92		2.47	.93		2.59	.77		3.08	.70		
	2.33	.76		2.60	.74		2.42	.77		3.19	.76		
D	3.02	.27	D	2.36	.18	D	2.90	.47		3.01	.70		

Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
	3.12	.34		2.28	-		2.85	.35		3.19	.76
E	1.68	.66	E	1.85	1	E	1.89	1		3.01	.70
	1.80	.81		1.74	1		1.89	1		2.94	.22
	1.67	.73		1.01	-		1.12	-		2.69	.25
									E	1.77	.83
										1.78	.84
										1.31	.52
										1.26	.53

Origin SB Plate 19			Origin IC Plate 20			Origin CB Plate 23			Origin IC Plate 24		
Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
A	6.33	.79	A	6.18	.55	A	6.89	.73	A	6.98	.77
	6.19	.62		6.56	.53		6.02	.67		6.60	.94
	4.78	.58		4.75	.88		4.75	.79		6.37	.92
	4.76	.65		5.12	.80		4.85	.66		6.88	.91
	4.75	.73		2.58	-		2.56	.27		5.46	.70
	5.08	.53		2.97	.28		2.73	.33		5.14	.75
	5.67	.86		3.11	.20		3.15	.46		4.48	.76
	2.86	.25		3.11	.22		3.30	.57		2.74	.32
	3.11	.43		2.52	-		2.95	.38		2.87	.15
B	4.74	.39		2.45	-		2.97	.31	B	3.48	.28
	4.18	.37		2.45	.28		2.71	.46		3.36	.33
	3.51	.42		2.20	.33		2.88	.33		4.15	.40
	3.22	.46	B	5.19	.35	B	3.38	.51		3.31	.21
C	3.25	.79		5.14	.35		3.66	.35		1.09	-
	3.80	.96		3.96	.32		4.36	.45	C	2.86	.71
	3.09	.99		3.82	.27		2.75	.19		3.06	.66
	3.48	1	C	3.93	.26		1.36	-		3.53	.86
	3.04	.55		3.33	.37	C	3.41	.94		3.34	.78
	3.48	.70		3.44	.86		3.22	.75		2.78	.23
	2.49	-		3.52	.81		2.94	.68		2.42	.21
	2.30	-		2.68	.67		2.82	.68		1.67	.73
	2.31	.52		2.89	.79		4.04	.91		2.99	.40
	1.33	-		1.86	.56		4.07	.92	D	2.58	.16
D	2.60	.24		1.81	.66		1.45	.56		2.53	.24
	2.74	.37		1.22	-		1.63	.50	E	1.68	.54
E	2.23	1		1.39	-		1.46	-		1.38	.71
	1.88	.89	D	2.87	.29		1.23	-		0.89	-

Group	RL	R	Group	RL	R	Group	RL	R	Group	RL	R
	1.12	.42		2.74	.28	D	2.11	-		0.89	-
	1.57	.44	E	1.83	.95		2.35	-			
				1.67	.70	E	1.78	.83			
				1.15	.51		2.11	1			
				1.39	.51		1.98	.43			
							1.95	.40			

Origin R

Plate 27

Group	RL	R
A	7.26	.86
	7.24	.80
	6.26	.85
	5.80	.84
	6.09	.65
	5.42	.63
	5.46	.67
	5.23	.55
B	4.40	.51
	4.53	.41
	3.54	.35
	3.60	.41
C	3.89	.52
	4.11	.49
	3.06	.60
	3.04	.65
	3.19	.66
	2.87	.61
	2.61	.67
	2.62	.66
D	2.10	-
	2.23	-
E	1.75	.88
	1.75	1
	0.92	-
	0.92	-

The number of slides prepared for each sample and the origin of each metaphase analysed in the investigation of chromosomal polymorphism at Rottingdean, Sussex.

Sampling square area	Chromosome number	no.	Number of slides
1	26	2	5
	27	2	
2	26	3	5
	26	3	5
7	26	2	2
	26	1	2
	26	3	5
10	26	4	5
	26	2	5
	26	2	5
2 1	26	6	5
	26	3	3
2	26	3	5
	27	1	
4	26	5	5
	26	3	2
6	26	2	2
7	26	1	3
	26	2	5
	27	1	
8	26	1	2
9	26	2	2
10	26	1	2
5 1	26	2	5
2	26	5	5
3	28	1	2
4	26	1	2
	28	1	
	26	3	5
	27	1	
7 1	26	3	5
2	26	1	2
	27	1	
	26	4	2
3	26	3	2
	26	9	5
	27	1	
4	26	4	5
	26	7	5
	27	1	
6	26	1	
12 2	27	2	5
7	26	5	5
	27	1	
5	26	2	5
	26	2	2
8	26	1	2

Sampling square		Chromosome number	no.	Number of slides
13	1	26	2	2
	2	26	1	2
	3	27	1	2
	5	26	3	5
	6	26	1	2
		27	1	
		26	4	5
	8	26	3	5
		27	1	
		26	3	2
		26	4	2
	9	26	3	4
	10	26	3	2
		26	3	5
		26	3	2
15	1	26	2	2
	2	26	2	2
		26	6	5

The number of slides prepared for each sample and the origin of each metaphase analysed in the investigation of chromosomal polymorphism at Cuckmere Haven, Sussex.

Sampling square		Chromosome number	no.	Number of slides
1	2	26	5	3
		26	3	2
		28	1	
	4	26	5	2
		26	5	2
2	2	26	4	5
		27	2	
	3	26	4	5
	4	26	6	5
		30	1	
	5	26	2	2
		26	3	3
		27	1	
	7	26	1	5
		27	2	
		28	1	
		26	2	2
		26	3	2
	8	26	4	5
		27	2	
		28	1	
	9	26	4	5
	10	26	4	5
		27	2	

Sampling square		Chromosome number	no.	Number of slides
5	1	26	3	5
		27	2	
	2	26	6	5
		27	1	
		28	2	
6	3	26	3	5
		27	1	
	5	26	2	2
	6	26	3	2
		26	2	5
		27	1	
7	2	26	2	2
	3	26	1	2
	4	26	4	5
		27	2	
		28	1	
	8	26	2	5
		30	1	
8	1	26	2	5
		27	2	
	2	26	2	2
	7	26	3	5
		27	1	
		29	1	
		26	3	5
		28	1	
		30	1	

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END