

AREA EFFECTS AND THE STRUCTURE OF PERIPHERAL POPULATIONS OF CEPAEA NEMORALIS.

by

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INTRODUCTION.

Darwin's great contribution to biology was to emphasise the basic simplicity and unity of the processes determining the structure of natural populations. Application of his theories, combined with our modern knowledge of the mechanism of heredity (which is itself a major unifying concept of biology) has given rise to the sciences of evolutionary and population genetics. Perhaps the most remarkable contribution of these disciplines to our understanding of the mechanism of evolution has been the discovery of vast amounts of genetic variability within almost every species studied, and the elucidation of the forces maintaining such polymorphisms is the major task facing workers in these fields.

Man is among the most polymorphic of all species, displaying variation in, for example, skin- and hair- colour, blood-groups, haemoglobins, glucose-6-phosphate dehydrogenase, and in many other enzyme systems. An understanding of the mechanisms maintaining these polymorphisms would be of tremendous social value in such fields as racial genetics and eugenics, and could also be of great medical significance in the study of congenital abnormalities and the numerous known associations between such polymorphisms and susceptibility to various diseases.



Unfortunately, Homo sapiens is far from being the ideal material for the study of genes in populations. It is very difficult to collect large amounts of data from human subjects, and almost impossible to ensure that the samples so collected are completely random. Man's life-cycle is protracted, so that the formal genetics of human polymorphisms rests at the moment almost entirely on pedigree studies, which are, of course, useless in the case of the recently-discovered biochemical polymorphisms.

The polymorphic snail Cepaea nemoralis has several advantages which make it almost uniquely suitable for the study of population genetics. It has a clear-cut polymorphism for shell colour (which may be pink, yellow or brown) and banding (0 - 5 bands), which is very easy to score, and whose formal genetics is well known. The animals are relatively immobile, and are thus easy to collect and to mark for field experiments, and, in suitable habitats, Cepaea is often very abundant.

Populations of this species are now being studied intensively, and have revealed a very interesting pattern of microgeographic variation, which is analogous to patterns found in many other species, including man.

Local Genetic Variability in Populations.

As well as many examples of large-scale geographical variation in gene-frequency found in many species, some animals and plants show remarkable local fluctuations in the frequency

of particular genes. These phenomena may be grouped under the general heading of "area effects", a term first used by Cain and Currey (4) to describe local variation in Cepaea. Some restricted regions of unusually high gene-frequency are obviously due to local selective forces - for example, Agrostis tenuis plants growing on Welsh lead mines show a far higher lead-tolerance than do adjacent populations growing on normal soil, and also differ from them in several other genetic characters. Area-effects which cannot be related to obvious local selection are less easily explicable, and have received much attention.

Epling & Dobzhansky (14), for example, studied the small annual plant Linanthus parryae in the Mojave Desert, and found that one type - the blue-flowered morph - occurred only in three separate "variable areas" in the midst of the far more common white-flowered type. Similarly, Da Cunha & Dobzhansky (12) have shown that chromosomal polymorphism in Drosophila willistonii in South America is usually proportional to the number of ecological niches utilised by each local population, but that in the Bahia district, chromosomal polymorphism is greatly restricted, with charactersitic frequencies of particular inversions, in spite of considerable environmental diversity. Very similar cases in Drosophila spp. on Caribbean islands, in the Great Basin of the Western United States, and on Brazilian islands have also been described (13).

The most remarkable examples of area effects are found in the land Mollusca. Cain & Currey (4) found great heterogeneity of phenotype



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 FIGURE 1. Proportions of five-banded shells and non-five-banded shells (00000 and 00300) in *C. nemoralis* on the Marlborough Downs. Proportions for five-bandeds in each sample black. A, non-five-banded area; B, Barbury area (transitional); C, five-banded area; D, southern intermediate area. The dotted line encloses colonies with a high proportion of spread-bandeds.

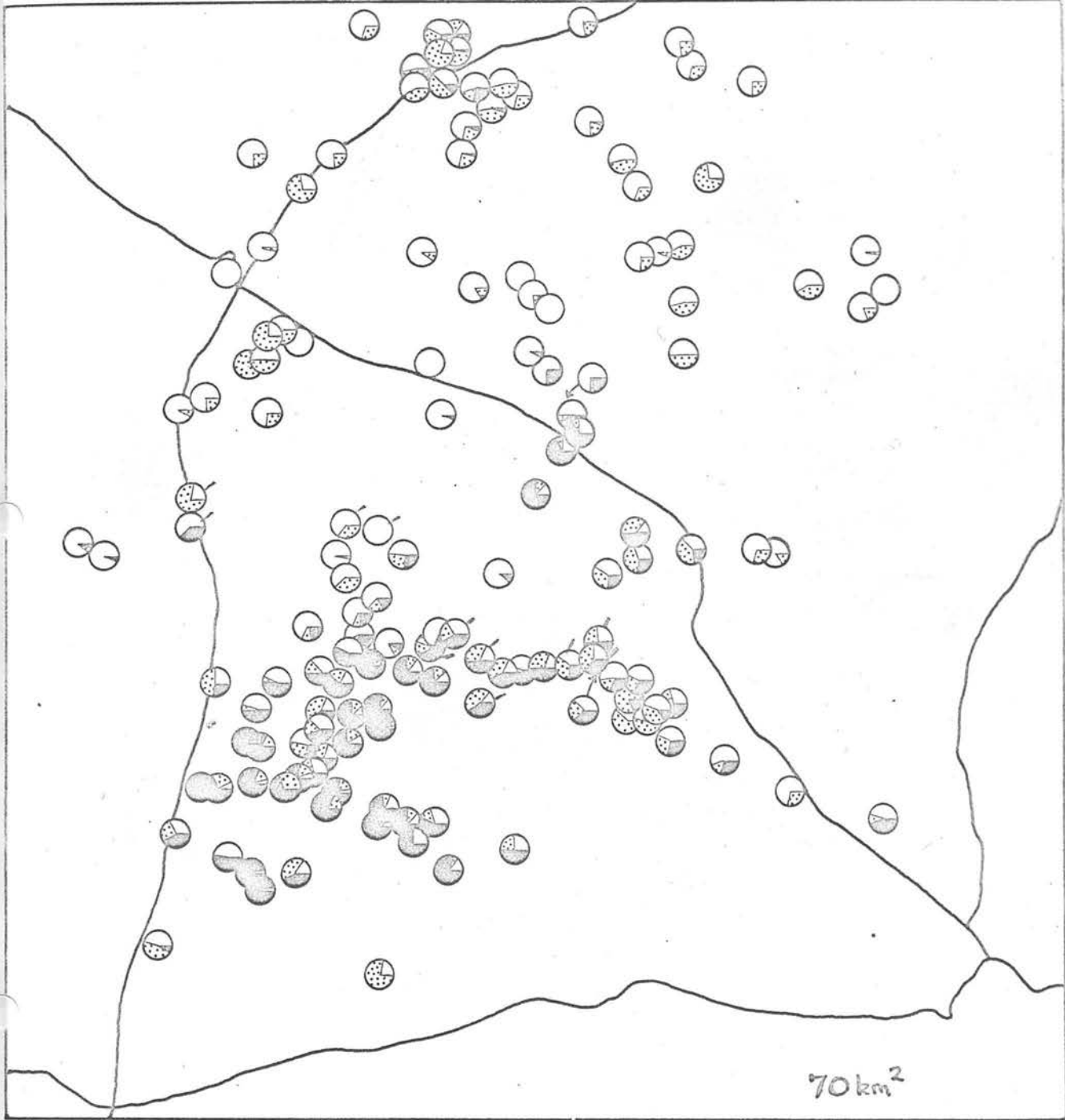


FIGURE 2. Proportions of yellow, pink and brown shells in *C. nemoralis* on the Marlborough Downs.
 Browns, black; pinks, stippled; yellows, white.

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distribution in C. nemoralis on the Marlborough Downs. In spite of the ecological variability of this high chalk plateau, large areas are characterized by an overwhelming preponderance of one colour or banding morph while adjacent, apparently similar areas have an equally excessive proportion of a different phenotype (figs. 1 & 2). In the non-5-banded area, for example, there were only eleven 5-banded shells out of 5767 collected, while the cline between the Yellow and the Brown areas in one locality shows a change in gene-frequency of 70% over a distance of only 130 metres without any apparent environmental discontinuity. Similar area effects in C. nemoralis have now been found in over twenty regions of Britain, France, and Spain, and also occur in the related species C. hortensis as well as in other molluscs such as Partula spp on Moorea in the Society Islands (10), and Bulimulus spp (11) in Puerto Rico.

Area-effects, in the widest sense, are also found in human populations. Because of man's great mobility, the local regions of high gene frequency are usually fairly large. Blood-groups, for example, often show striking variations between adjacent populations - the Blackfoot Indians of Western Canada, for instance, have a much higher frequency of group A than do neighbouring tribes, while the Basques have an equally excessive frequency of one Rh variant over neighbouring societies. Many such examples have been described; some, no doubt, are due to recent population movements, but the wide occurrence of such phenomena in human populations suggests that they may have something in common with area effects in other animals.

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EXPLANATIONS OF AREA-EFFECTS.

Early workers attempted to interpret area-effects as instances of simple genetic drift, whereby the gene frequencies in for example, the Linanthus "variable areas" were determined by random processes in small populations. This explanation has now been rejected for various reasons even by its original protagonists.

Genetic drift occurring at the present time obviously cannot explain area-effects in Cepaea populations, which are very large. Cain and Currey suggest that microclimate is important in determining C. nemoralis colour areas on the Marlborough Downs.

They argue that as the range of C. hortensis extends further North than that of C. nemoralis, then the former species is the more resistant to cold. On the Marlborough Downs, C. hortensis predominates in the valleys, and C. nemoralis on the uplands. This is due to the valleys acting as frost hollows, so that on clear summer nights the temperature drops to a level which can be tolerated only by C. hortensis.

The Brown morph is, they claim, commoner in the North of C. nemoralis' range than in the South. On the Downs, Brown shells are found at the lower levels of C. nemoralis' distribution, where it is colder at night. The Brown area-effects/

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effects are therefore due to Brown morph's greater resistance to cold giving it a selective advantage in frost hollows. The other colour and the banding area-effects are due to similar, but undetermined selective forces.

This theory is open to many criticisms, several of which derive from the study of peripheral populations of C. nemoralis. These criticisms will therefore be discussed after the description of two such populations.

The other theory of area-effects - the "coadaptive" theory - emphasises selection by the genetic environment rather than by the ecological environment. The concept of the coadapted gene-complex was developed by Wright who showed, mainly on mathematical grounds, that, because most mutations act primarily to modify the effects of other genes, selection will tend to favour linkage of groups of genes. As different populations will be subject to slightly different selective forces, and will respond with different combinations of genes, each local population will evolve a uniquely coadapted gene-complex, which will be incompatible with that of other populations.

The gene arrays in each population are therefore mutually adjusted so that the selective value of each gene depends upon the genetic background into which it is placed. This integrated genotype is protected from the disadvantageous effects/

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effects of segregation upon groups of modifiers by the accumulation of chromosomal inversions which prevent disruption of modifier blocks by crossing-over.

Many studies of the breakdown of fitness in crosses between geographically disjunct populations of Drosophila and in experimental introduction of foreign chromosomes into Drosophila populations have shown that coadaptation is generally important in the genetic systems of Drosophila spp. Many of the remarkable attributes of mollusc area-effects are easily explicable if such areas consist of populations with differently coadapted gene-complexes. Their stability, their apparent independence of environment and the steep clines between adjacent areas can all be explained as the result of hybrid disadvantage between mutually incompatible populations preventing genetic exchange between each area-effect.

Direct evidence for coadaptive divergence between Cepaea area-effects is difficult to obtain, and no results on deviation from Mendelian ratios (which might be due to breakdown of mutually incompatible gene complexes) in inter-area crosses have yet been published. In Partula however, Clarke and Murray have analysed a cline between two area-effects (for high and low frequency of Purple-shelled snails) in detail, and their results suggest that coadaptation may play an important/

important part in maintaining area effects in this genus.

At the steepest part of the "purple" cline, there is a phenomenal increase in the number of banded shells. The expression of banding in this region is unusual, with many intermediates between banded and unbanded shells. As the environment in this region shows no obvious peculiarity, this great increase in banding and the abnormalities in its expression is probably due to the disturbance of the genetic environment produced by hybridisation of the two different coadapted gene-complexes making up the colour areas. This interpretation is strengthened by Clarke and Murray's discovery of concomitant changes in shell length and in the snails' breeding condition (measured by the uterine contents) ~~and~~ within the cline.

The origin of coadapted gene-complexes such as those found in the Partula and possibly in the Cepaea area-effects is also a matter of contention. Sewall Wright (19) has developed, on mathematical grounds, a three-phase system involving first the differentiation of gene-complexes by random processes ("genetic drift"), which is followed by local selection and development of selectively superior integrated gene-pools. The most successful coadapted gene-complexes diffuse through the population until they meet, and each such genecomplex gives rise to a uniquely integrated area/

area-effect. Goodhart (15) has put forward an analagous theory, which involves the random distribution of genes among small isolated founder populations of Cepaea which evolve their own coadapted gene-complex and spread until they meet.

Cain and Currey (5) have pointed out that the geography of the Marlborough area-effects is difficult to reconcile with Goodhart's theory of founder populations. It is also rather hard to see how such theories can explain the steep clines in banding frequencies within uniform colour areas, and vice-versa.

An ingenious compromise between the purely selective and the purely coadaptive theories has been developed by Clarke (9). He calculates that accumulation of genes modifying the effect of the major gene will tend to steepen any slight environmentally - induced morph-ratio cline for this major gene and may ultimately lead to a stepped cline. Such processes will lead to differentiation of an originally uniform population into a mosaic of separate coadapted gene-complexes - i.e., in the case of Cepaea and Partula, to area-effects. The step in the cline will, he predicts, occur preferentially at an environmental discontinuity although such a discontinuity/

discontinuity is not essential for the formation of a step. The Clarke hypothesis may therefore explain area-effects - such as those in Agrostis - whose boundaries can be related to an environmental discontinuity as well as the Cepaea areas, which are usually impossible to correlate with ecological factors.

A preliminary study by Arnold (2) in the Pyrenees has now revealed a stepped cline. Clarke's theory is particularly interesting as it predicts that accumulation of incompatible modifiers in each area-effect may go so far as to lead to reproductive isolation between the genecomplexes involved - in other words, it may lead to semi-sympatric semi-speciation.

Area-effects in Cepaea may therefore be of more than merely specialist interest. Investigation of Cepaea populations at the edges of their range, where climate^{ic} selective conditions are likely to be extreme, should illustrate the relative importance of selection by the ecological environment and by the genetic environment of the population. Such populations are also known to be of great evolutionary significance in species other than Cepaea.

PERIPHERAL POPULATIONS AND EVOLUTIONARY GENETICS

Peripheral populations are of considerable interest to evolutionary and to population genetics for several reasons. They often exist in the face of environmental stress which prevents the species from extending its range, and therefore demonstrate the effects of intense selective forces on population structure in a more convincing manner than do laboratory experiments, which depend on arbitrarily defined conditions of extreme selection. The reduced gene-flow into peripheral populations which is due to only one frontier being in contact with a source of new genetic variability, and the fact that such populations often become completely isolated by colonisation of a new area means that peripheral populations may be particularly favourable for reorganisations of the genetic structure of a community which may lead to separation.

Distinct forms and populations with an unusual genetic structure are known from the edges of the range of many species. Two types of theory attempt to explain the unique characters of many marginal populations.

The "relict" theory states that these ^{are} remnants of formerly widespread types which have been largely replaced by the evolution of a new form. New varieties and species arise from rapid evolution and interdemic exchange of genes occurring at/

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at the centre of the range. Marginal populations have no evolutionary significance as their small size and isolation gives rise to fragile and specialised gene complexes which are easily overwhelmed by expansion of the main body of the species.

There is some evidence for this theory. Small isolated island populations are often overwhelmed by the introduction of mainland forms - bird species living on islands are over fifty times as likely to become extinct as are continental species. (17) Peripheral forms of some animals are superficially similar to forms found today only as fossils in the centre of the range of the main species. In the Bank-Voles Cleithronomys, for example, large dark races with a complex tooth-pattern now live only on islands off the British coast, but are ^{widely} ~~wholly~~ distributed as fossils throughout the European range of the smaller ^p ~~single~~-toothed main race.

The alternative (and perhaps more widely accepted) theory of marginal forms ascribes to peripheral populations a major role in speciation. Because of their small size and reduced gene-flow such populations are particularly liable to random alterations in gene frequency resulting from genetic drift. The extreme conditions of the edges of the range will/

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will subject such novel gene-complexes to rapid selective change. Once these populations have passed the "genetic bottleneck" (Dobzhansky) due to the fragility of their largely homozygous gene-complexes and have attained some degree of heterozygosity, they can respond rapidly to selection so that a new form may evolve which may occasionally replace the original form but will usually develop into a separate race or species in its own region.

Mayr (17) has put forward a great deal of evidence for the importance of these processes in evolution. In the New Guinea Kingfisher (Tanysiptera galatea) for example, the whole of the mainland is occupied by one race while each offshore island has its own unique race. Similarly, the House Mouse on St. Kilda has evolved into a distinct form in its 300 years isolation from the mainland population (18), and a detailed genetic analysis of the allegedly "relict" characters of the island Cleithronomys populations shows that these are in fact simply a response of the island populations to local selective forces (18).

As well as their importance in speciation, some marginal populations also play a part in maintaining the evolutionary flexibility of the parent species. Populations of Drosophila robusta at the edges of their range show far less inversion polymorphism than do those at the centre, and therefore have a much/

much higher incidence of crossing-over than do central populations. (7). Inversion polymorphism in some central populations reduces crossing-over to such an extent that chromosomal arrangements become "frozen". Although this system of polymorphism allows exploitation of specialised ecological niches, it greatly restricts the release of latent genetic variability which produces new genomes upon which selection can act. Such populations are therefore highly specialised and relatively inflexible. Peripheral populations cannot afford the loss of unfit segregating homozygotes inherent in a genetic system based on inversion polymorphism and therefore adapt to environmental changes in an "opportunistic" fashion involving free recombination. This system allows a rapid response to selection. Central populations, however, cannot respond as rapidly to sudden environmental changes. The marginal population may then act as an "escape mechanism" for the more rigidly adapted central populations, as new gene-complexes produced by its rapid response to selection can diffuse inwards, and thus provide a reservoir of available genetic variability which allows the central population to maintain a highly adapted, but rigid, genetic system in safety.

Peripheral populations are thus known to be of great importance in the evolution of species other than C. nemoralis. Investigation of such populations in this species, which is playing/

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playing an increasingly important part in population genetics, should therefore be of considerable interest, particularly as the factors limiting the distribution of Cepaea are quoted as evidence for Cain and Currey's theory of the causes of area effects.

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FIG. 3. 1" O.S. MAP OF MONROSE
AREA, SHOWING PLACE-NAMES ETC.



NORTHERN PERIPHERAL POPULATIONS OF C. NEMORALIS IN SCOTLAND.

(i). The Area Investigated.

The most northerly populations of C. nemoralis in Britain are found in the Montrose area on the East coast and on Raasay on the West. We have studied the Montrose populations in detail.

(ii). Geology, Topography and Vegetation. (See fig. 3)

Much of the region consists of Old Red Sandstone, together with a 2-mile wide belt of Andesitic Lavas running across the area. The river valleys and the Montrose-St. Cyrus plain are marine alluvia. Sand-dunes run from Montrose to St. Cyrus, while North of St. Cyrus the coast consists mainly of basic lava cliffs.

The dunes (which were surveyed in detail) fall into two main regions. "Fixed Dune", with a 30 foot seaward ridge sloping gently into a golf-course or rough dank grass behind predominates South of the North Esk, while North of the river this is succeeded by Dune Pasture. Fixed Dune consists mainly of clumps of marram (Ammophila arenaria) with varying amounts of Restharrow (Ononis repeus) mosses, short grass and open sand, while Dune Pasture has a very varied vegetation including much Sand Sedge (Carex arenaria) and other grasses etc. forming a dense turf.

The/

The basic coastal cliffs have a rich and diverse vegetation, including Nettles (Urtica dioica), Bracken (Pteris agintium) and various grasses and Compositae. Much of the hinterland is arable farmland and this type of habitat reaches the sea between Milton Ness and Inverbervie. Samples in this region were collected mainly from mixed patches of Nettles, Umbels (mainly Torilis japonica), Thistles (Carduus sp), and various grasses, although some collections were made on short turf and from strands of Rose Bay Willow Herb (Epilobium augustifolium). There are few deciduous woods and dense hedgerows of the type described by Cain and Sheppard (6) for the South of England in this region, and those which were examined proved to be almost devoid of Cepaea.

(ii). Collection Localities.

Three levels of sampling intensity were employed (See Figs 4 + 5). On the five-mile dune from Montrose to St. Cyrus, samples were collected every 100 metres along the seaward face of the dune, and these were supplemented by occasional samples on the landward slope. From St. Cyrus to Inverbervie every apparently suitable habitat was examined, and any Cepaea present collected. The remainder of the area was surveyed by traversing almost every negotiable road by car and examining suitable localities.

(iii). Distribution of Phenotypes.

Figs. 6, 7 + 8 show that there are marked area-effects for Yellow/

- X = No Snails Collected.
- = *C. nemoralis* only
- + = *C. hortensis* only
- ⊙ = Both Species Present.

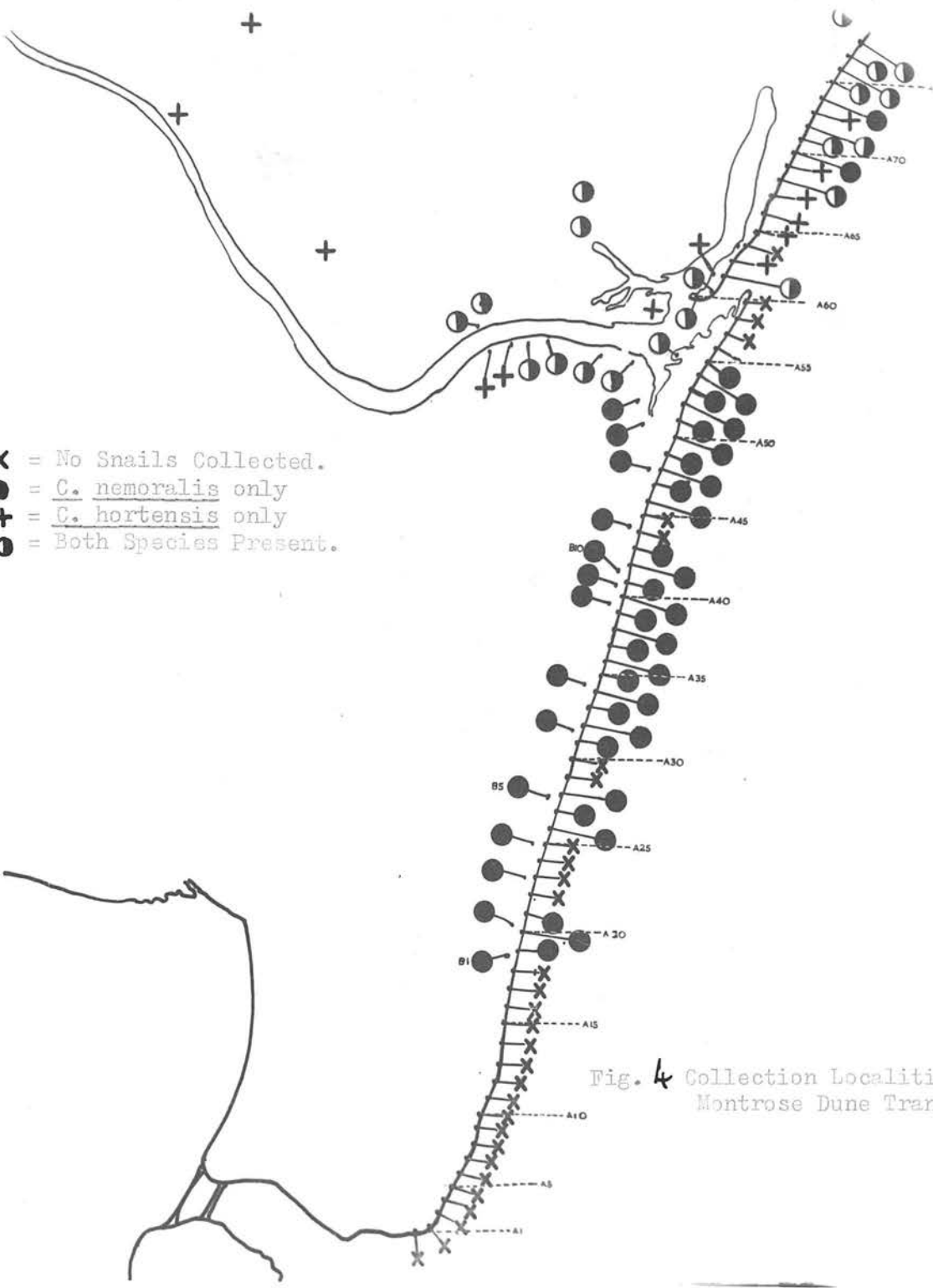


Fig. 4 Collection Localities in Montrose Dune Transect.

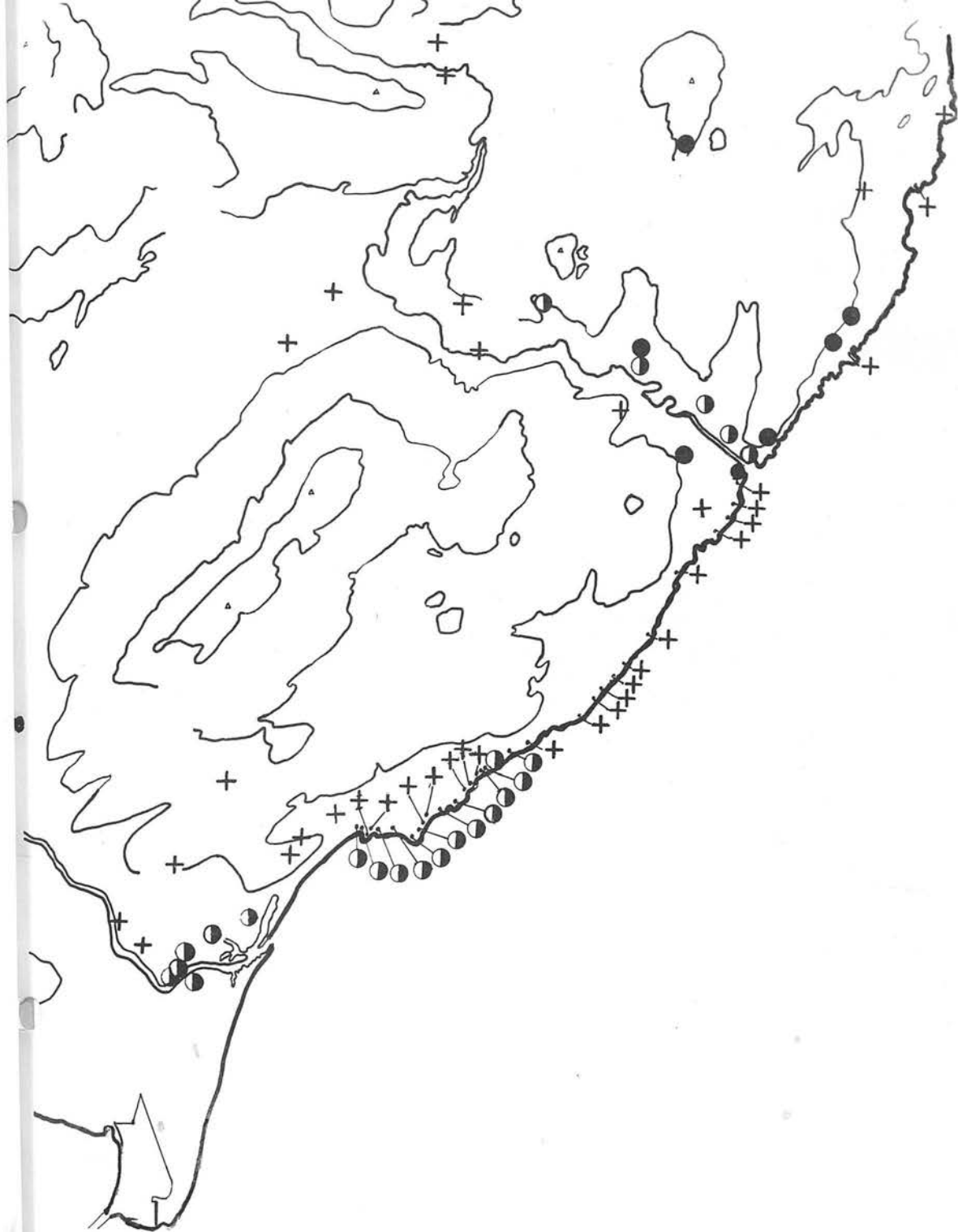


FIG. 5 Collection localities in Coastal and Inland Regions.



Fig. 8. Frequency of Unbarbed Shells
in samples of more than 10 C. nemoralis
from the Montrose Dune Transect.

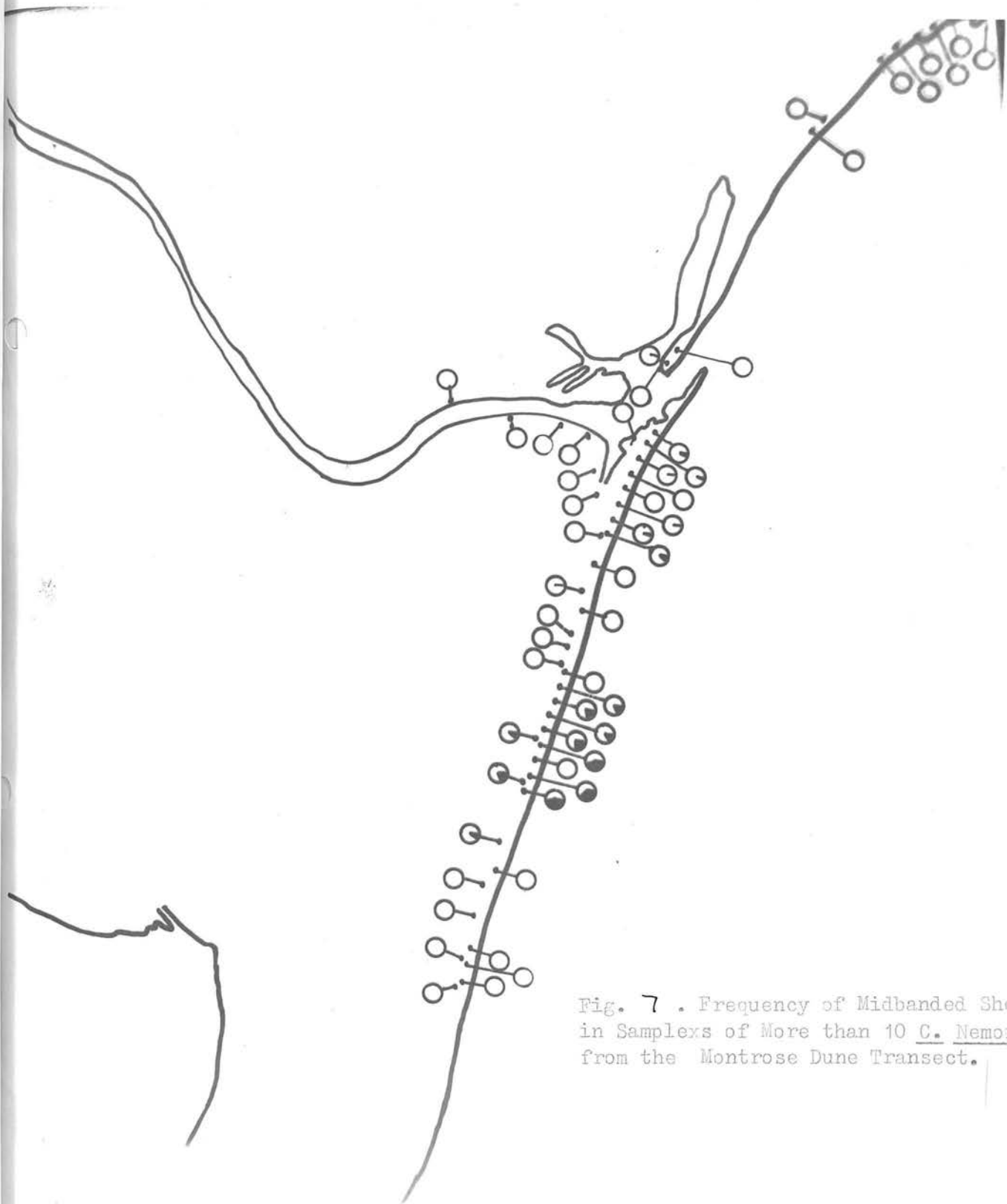


Fig. 7 . Frequency of Midbanded Shells
in Samplexs of More than 10 C. Nemoralis
from the Montrose Dune Transect.

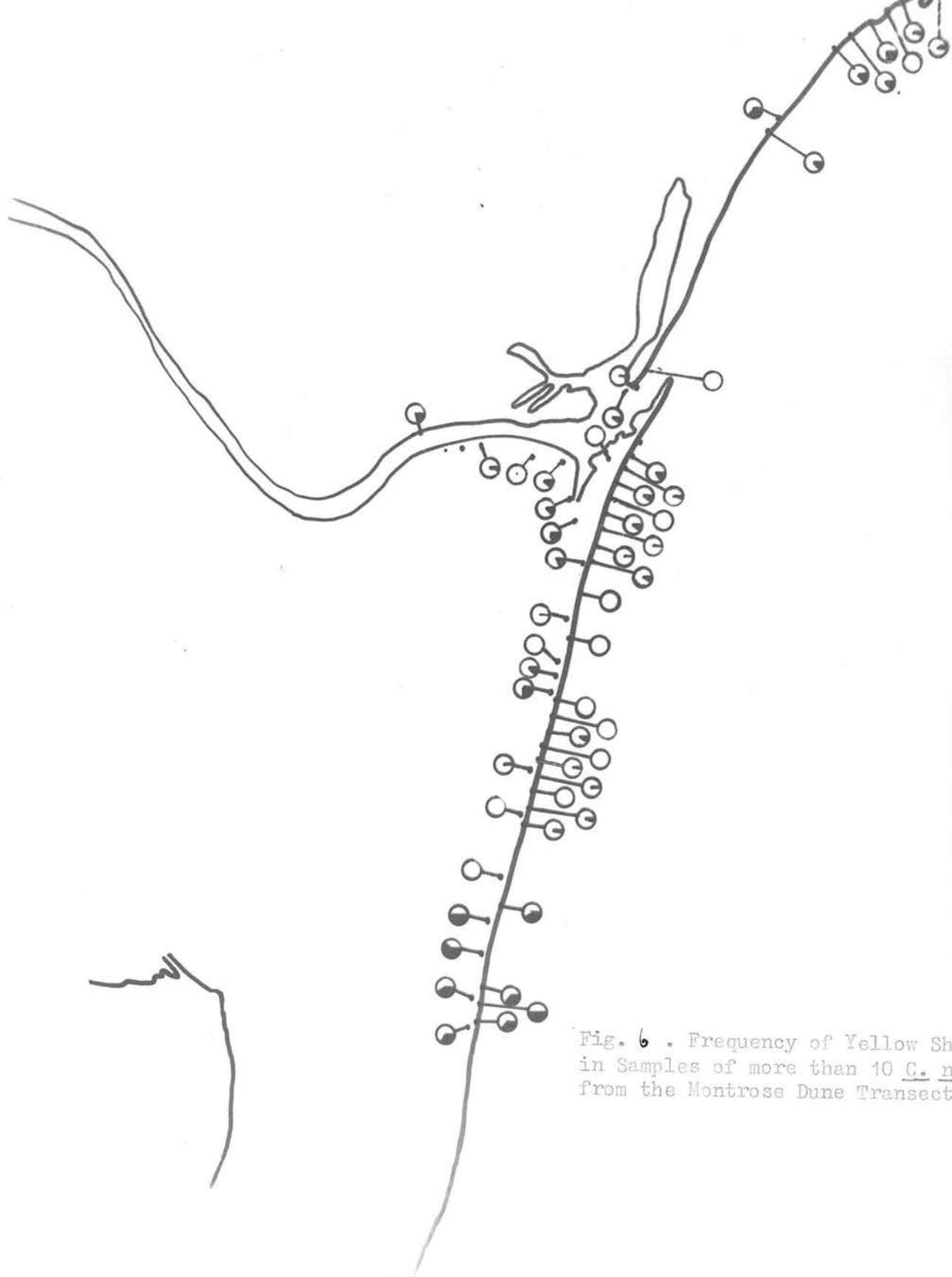


Fig. 6 . Frequency of Yellow Shells
in Samples of more than 10 G. nemoralis
from the Montrose Dune Transect.

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Yellow, Mid-banded and Unbanded in the dune transect. The rate of change of gene-frequency is often rapid - for example the frequency of Unbanded falls from 85% in sample A21 to 0% in sample B5 over a distance of only 200 metres, - although the area-effects themselves are generally not as marked as those described by Cain and Currey.

The remainder of the region also shows area-effects for colour and for banding (See Figs. 9+10). The Unbanded phenotype is rare along the coast, but reaches a frequency of thirty to forty per cent in the Bervie Valley region. Yellow shells, also, are far more common here than along the coast.

(iv). Variation in Gene Frequency with Habitat.

Fig. 11 illustrates the variation in phenotype frequency with habitat found by Cain and Sheppard (6) in the Oxford region. There is a marked relation between phenotype frequency and habitat, woodlands having a lower frequency of Yellow and higher frequency of effectively unbanded (00000 plus 00300) shells than do hedgerows, rough herbage and grasslands. This is, they have shown, due to differential predation against the less cryptic morphs by thrushes.

Fig. 12 is a similar scatter-diagram for our samples from the Montrose area. Cepaea occurs in fewer types of habitat in this area than around Oxford, and C. nemoralis does not occur/

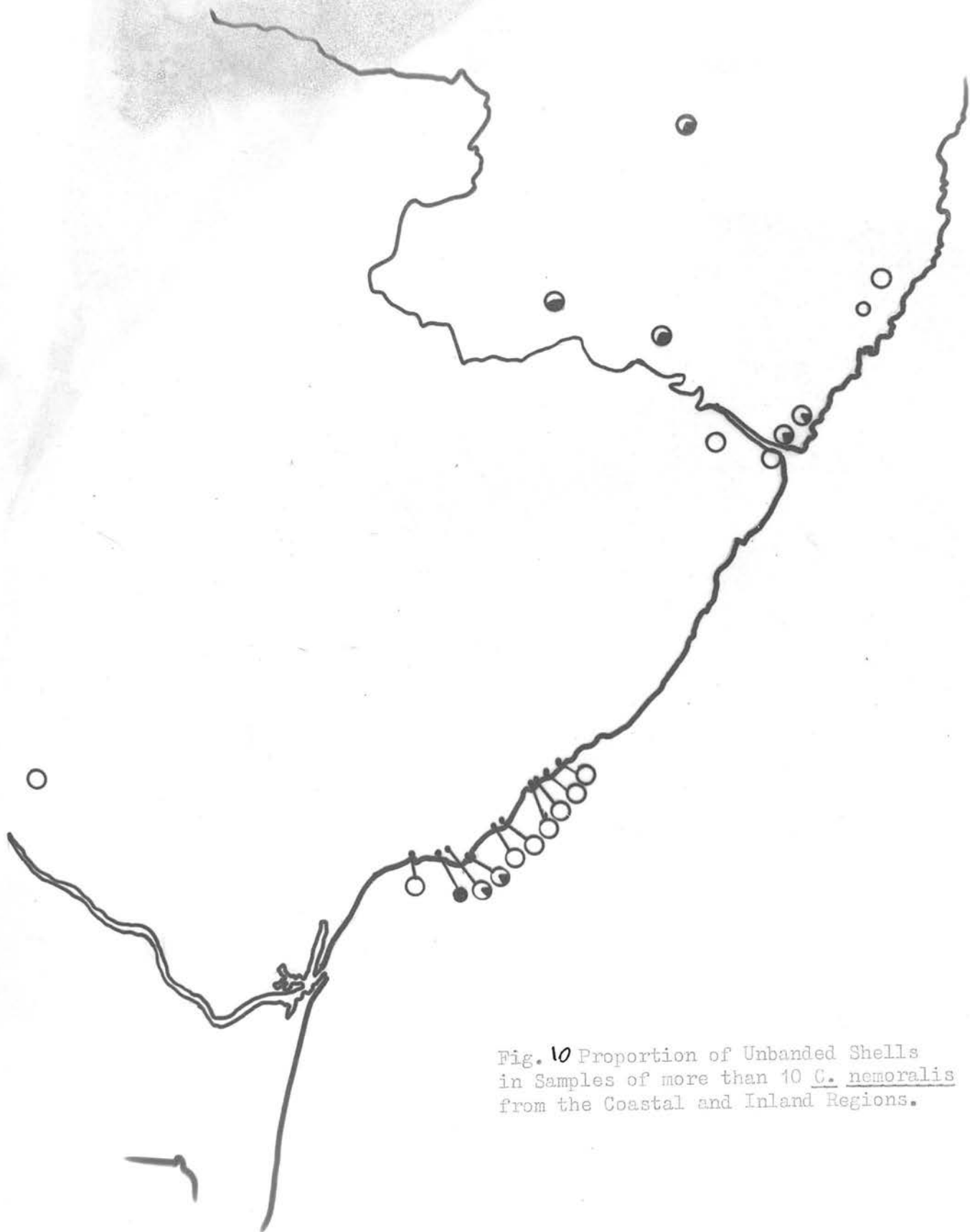


Fig. 10 Proportion of Unbanded Shells
in Samples of more than 10 *C. nemoralis*
from the Coastal and Inland Regions.

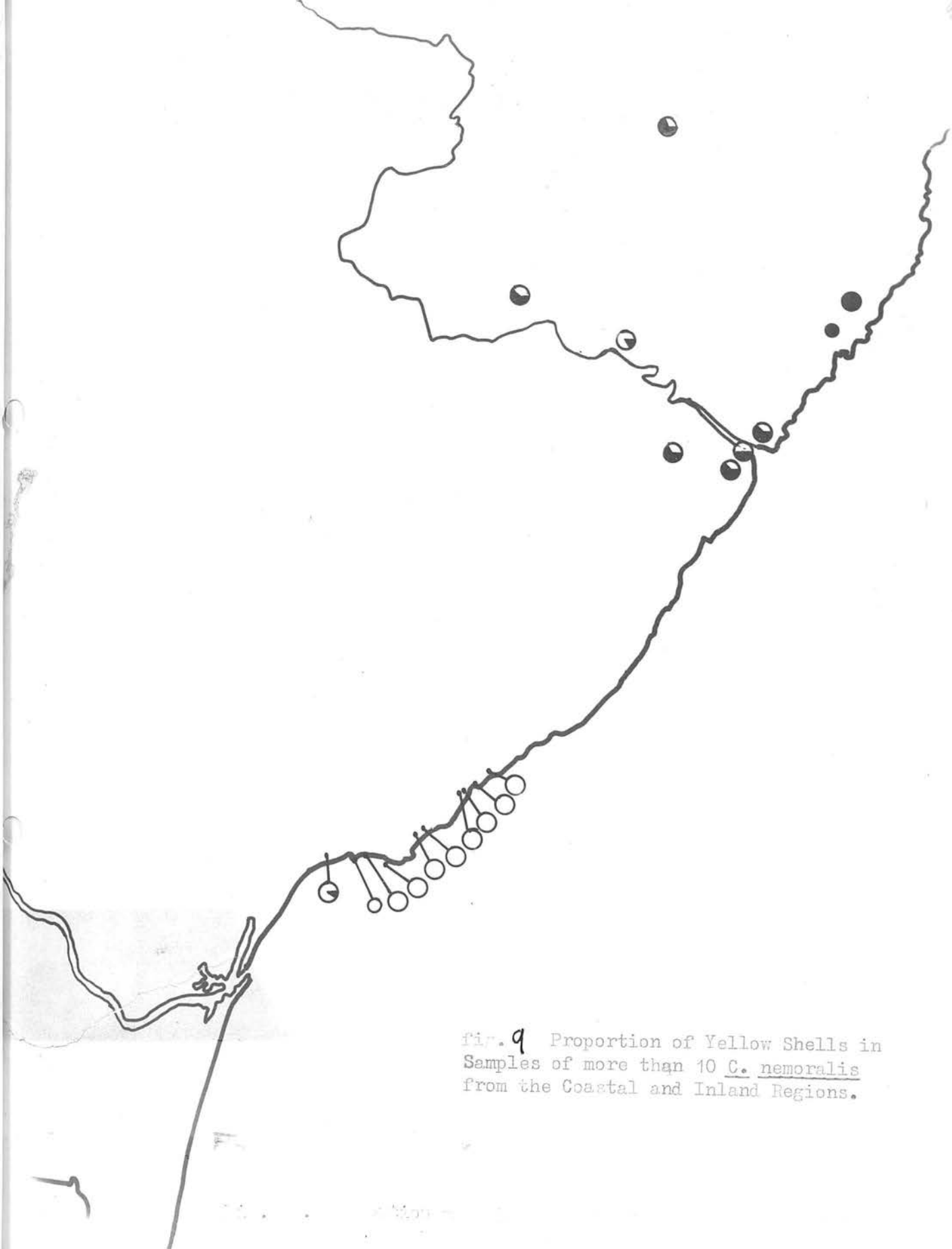
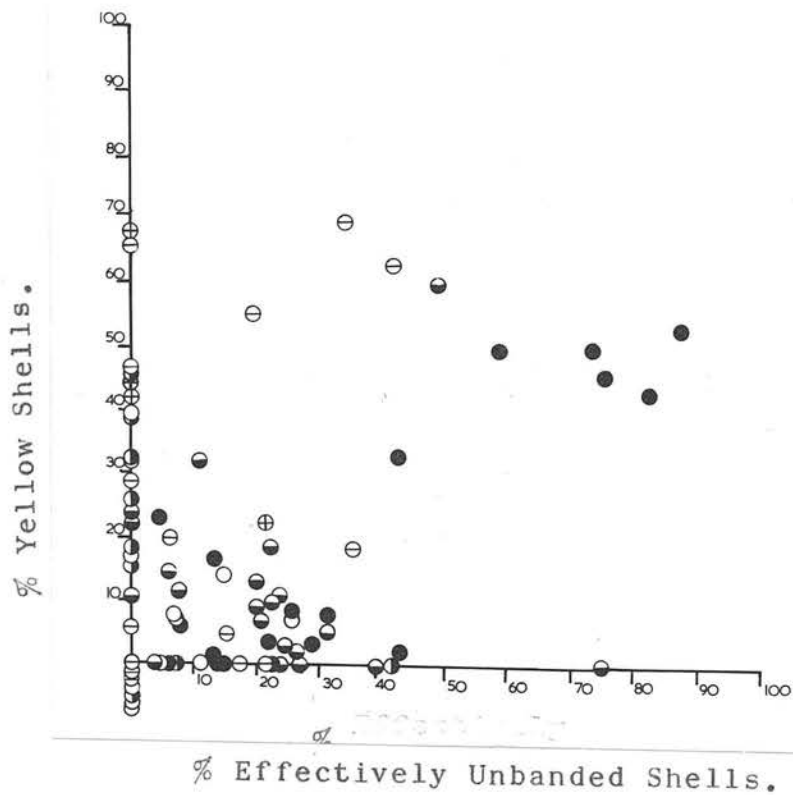


fig. 9 Proportion of Yellow Shells in
Samples of more than 10 *C. nemoralis*
from the Coastal and Inland Regions.

FIGURE 100.

Scatter Diagram showing relation between % Yellow Shells, % "Effectively Unbanded" (00000 + 00300) Shells and Habitat for C. NEMORALIS in the Montrose Region.



- Short Turf
- ⊖ Nettle Stands
- ⊙ Long Grass
- ⊕ Open Mixed Vegetation

- ⊗ Dense Mixed Vegetation
- ⊖ Dune Pasture Edge
- ⊖ Sparse Dune
- Rich Dune

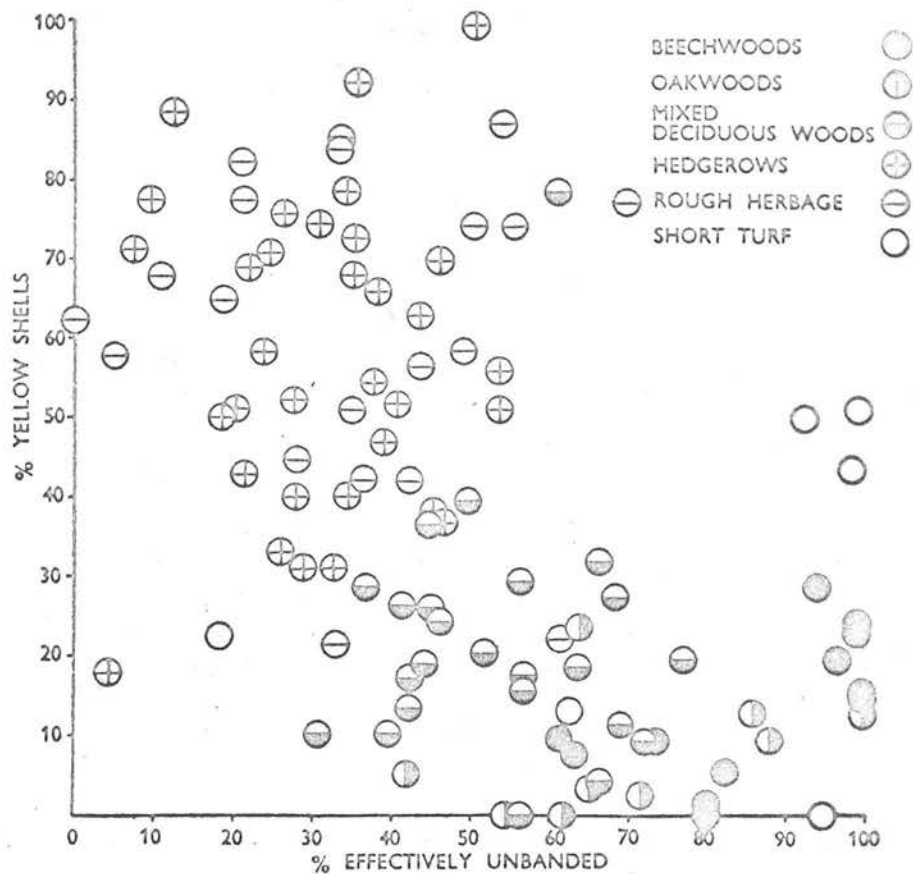


FIG. 2.—*C. nemoralis*. A scatter-diagram showing the relation between percentage of yellow shells, percentage of "effectively unbanded" shells, and the nature of the habitat (after Cain and Sheppard, 1954).

11.
FIGURE ~~11~~ 11a.

Open Field
 Open Field
 Open Field
 Open Field

Open Field
 Open Field
 Open Field
 Open Field

occur in woods. We have therefore had to adopt a habitat classification different from that of Cain and Sheppard (See fig. 12). From this diagram it is obvious that there is no marked association of colour or banding frequencies with habitat in the Montrose district. Each non-dune zone of high or low frequency of a particular gene contains a variety of habitats - for example, both the regions of low Yellow North of St. Cyrus and that of high Yellow in the Bervie Valley include samples found in nettles, in long and in short grass and in both open and dense mixed vegetation. For these regions of high and low frequency of the Yellow gene, therefore, ecologically similar, but geographically disjunct samples show considerable differences in gene frequency while ecologically dis-similar, but geographically conjunct samples have close similarities in the frequency of the Yellow gene. The same is true for the distribution of the Unbanded gene in relation to habitat and to position.

The geographical variations of gene-frequency in C. nemoralis in the Montrose region therefore represent a situation where "throughout an area large compared with the panmictic population of Cepaea, one colour or banding variety is predominant throughout without regard to habitat" - in/

in other words they are area effects as defined by Cain
and Currey.



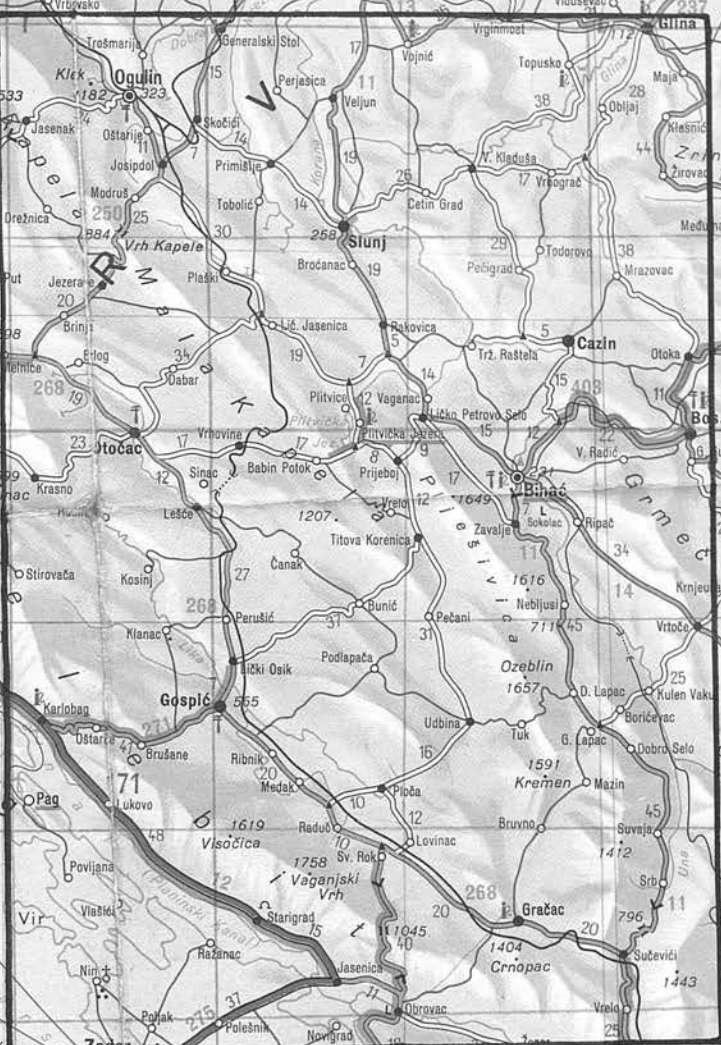
SOUTHERN PERIPHERAL POPULATIONS IN YUGOSLAVIA.

We have worked on these in the coastal region of Croatia (see fig. 13), where 12 Edinburgh University students spent two months collecting 20,000 specimens of C. nemoralis (and the related species C. vindobonensis) during the Summer of 1966.

i) Topography, Geology, and Vegetation.

The survey covered 3000 sq. miles of the Velebit Mountains and their hinterland in Croatia. Most of the region is a limestone massif which has been extensively fractured and folded. It displays very marked karstic features - most of the water circulation is underground, and this leads to large sterile rocky areas on the surface. On the slopes of the mountains, the surface is pitted by hundreds of depressions - "dolines" - formed by solution of the limestone surface by rainwater. These develop into zvekara (or "swallow holes") which open at their bases into spilja, the systems of caverns which seam the karstic mountains.

Large enclosed basins - the polja - form major relief features in the area. The floors of these polja are very level, and the mountain walls rise in steep scarps around them. Some polja flood during the winter as the water rises in the cavern systems below, and the receding waters leave a layer of silt, so that the polja are the only cultivable surfaces in the karst. Within the larger polja, the underground rivers reach the surface, only to disappear once more into the caverns after having traversed the polje.



AREA COVERED
IN SURVEY.
(SEE LARGE R MAP)



SCALE
(MILES)

FIG. 13

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Climate, soil, and biotic factors vary very considerably over the region studied, and this is reflected in a great diversity of vegetation. The offshore islands and the slopes of the Velebit mountains which overlook the sea are made up of almost bare karst surface with a few shrubs, together with sheltered areas which have a Mediterranean ecology. Over the crest of the five thousand foot Velebit mountains, there is a sudden change of vegetation, first to dense beech forest, then, in some places, to turf-covered doline regions and finally to the cultivated floor of the polje. The ribs of limestone between the polja show a return to bare karst with a few stunted beech trees and shrubs.

Collection localities

Cepaea was found only in the polja and on the passes separating them. Within the polja they are largely confined to roadside hedges, ditches and lush road verges. A few samples were collected in beech scrub and one or two in beechwood proper. C. vindobonensis was widely distributed, but C. nemoralis tended to be very colonial, although where this species did occur, it was often very dense.

Most of the region was surveyed by traversing as many roads as possible and examining apparently suitable localities. This general survey was supplemented by a transect of 106 paired samples 200 metres apart across a polje where Cepaea was dense, in the centre of the region.

Distribution of Phenotype Frequencies.

i) Colour.

In contrast with any other population of C. nemoralis previously

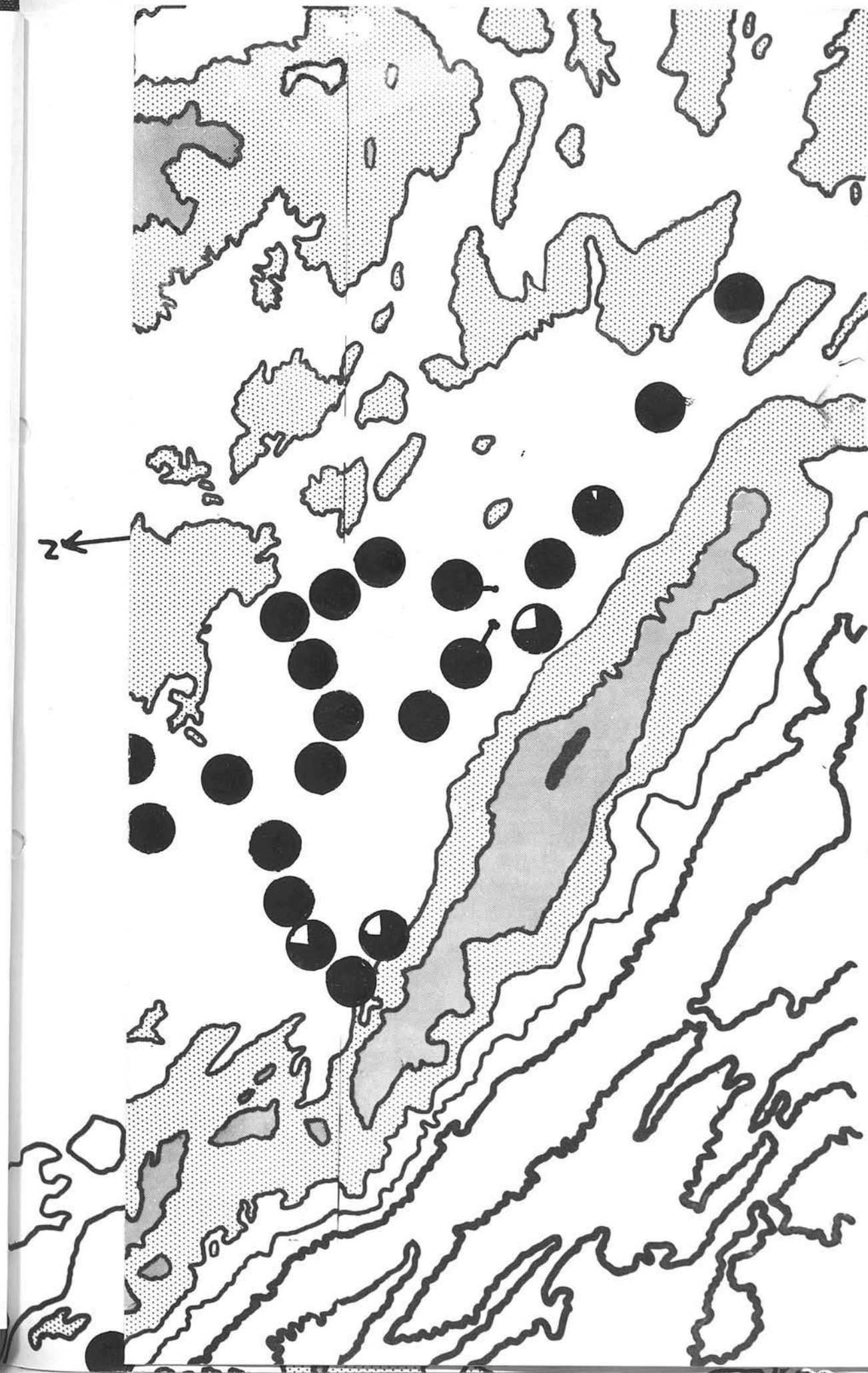
described, there is an overwhelming preponderance of one colour morph - Yellow - over the whole of the three thousand square miles studied. Fig. 14. shows that the general frequency of Yellow is over 95%. The frequency of this gene within the transect is also very high.

ii) ~~manns~~. **BANDING**

In contrast to the gross disturbances in the relative frequency of the colour genes, at the Southern limit, no one banding morph is preponderant in this region. Mid-banded, for example (fig. 15) is not at an unusually high or low frequency in Yugoslavia, and, in spite of the large distance between samples caused mainly by the patchy distribution of C. nemoralis, shows a tendency to be grouped into area effects. This tendency is also noticeable within the transect, where the frequency of 00300 may rise from 0 - 60% within two hundred metres. The frequency of unbanded shells is relatively low in the Southern half of the study area, although there is an area-effect for Unbanded (which may reach a frequency of 25%) in the Northern portion.

The distribution of the modifiers of the expression of the banding genes is interesting. One of these ("Dotted Bands"), which causes flecking of the bands on the shell, is at a relatively high frequency throughout, and is also aggregated into marked area-effects (fig. 16.) which are particularly noticeable in the transect. Other modifiers - for example "Fused Bands" - are present, but are generally at a fairly low frequency .

The overall impression gained from this study of a population of



FREQUENCY OF YELLOW IN YUGOSLAVIA.

FIG.



FIG. 14 . FREQUENCY OF
YELLOW IN YUGOSLAVIA.

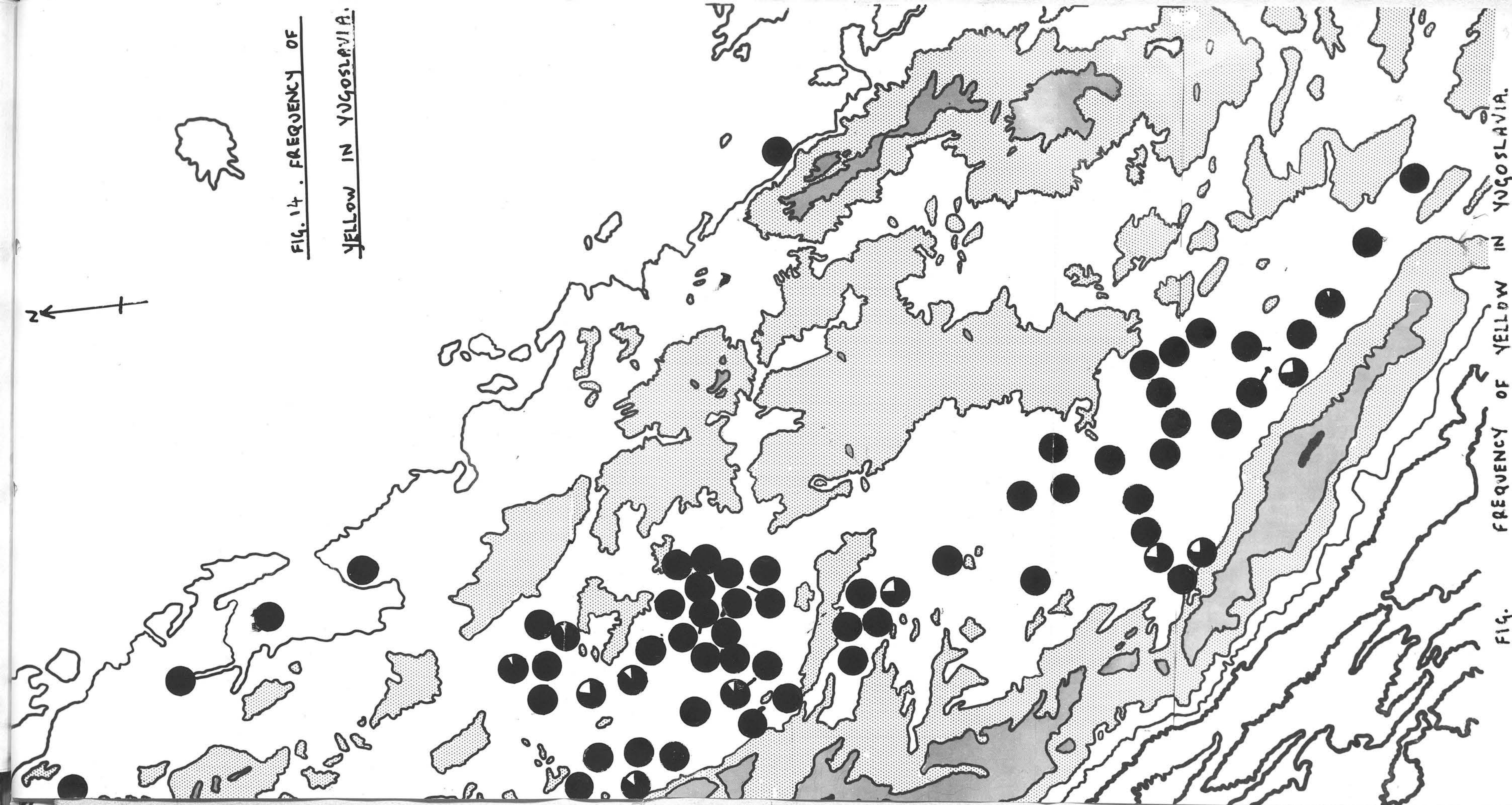
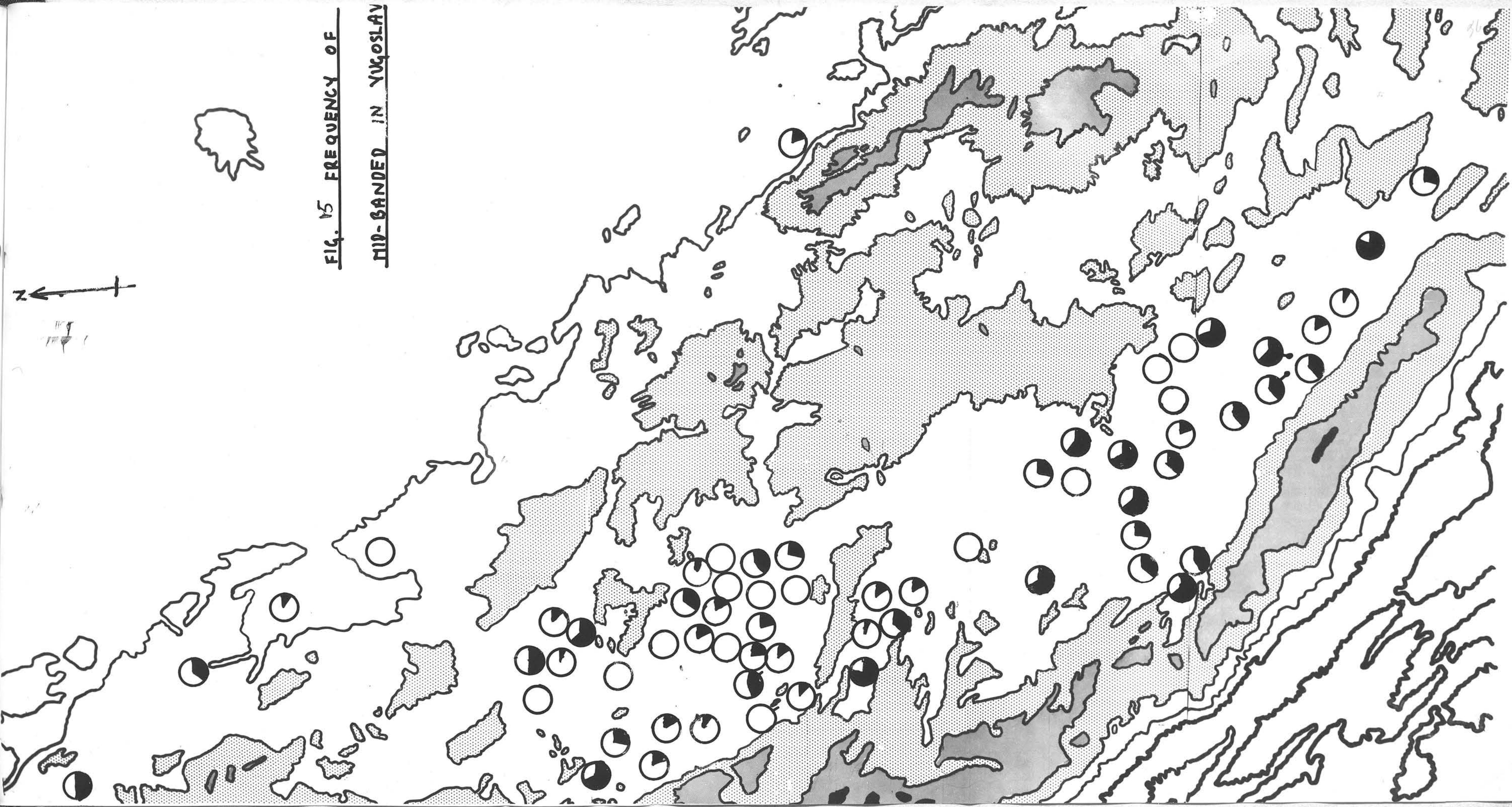


FIG. FREQUENCY OF YELLOW IN YUGOSLAVIA.



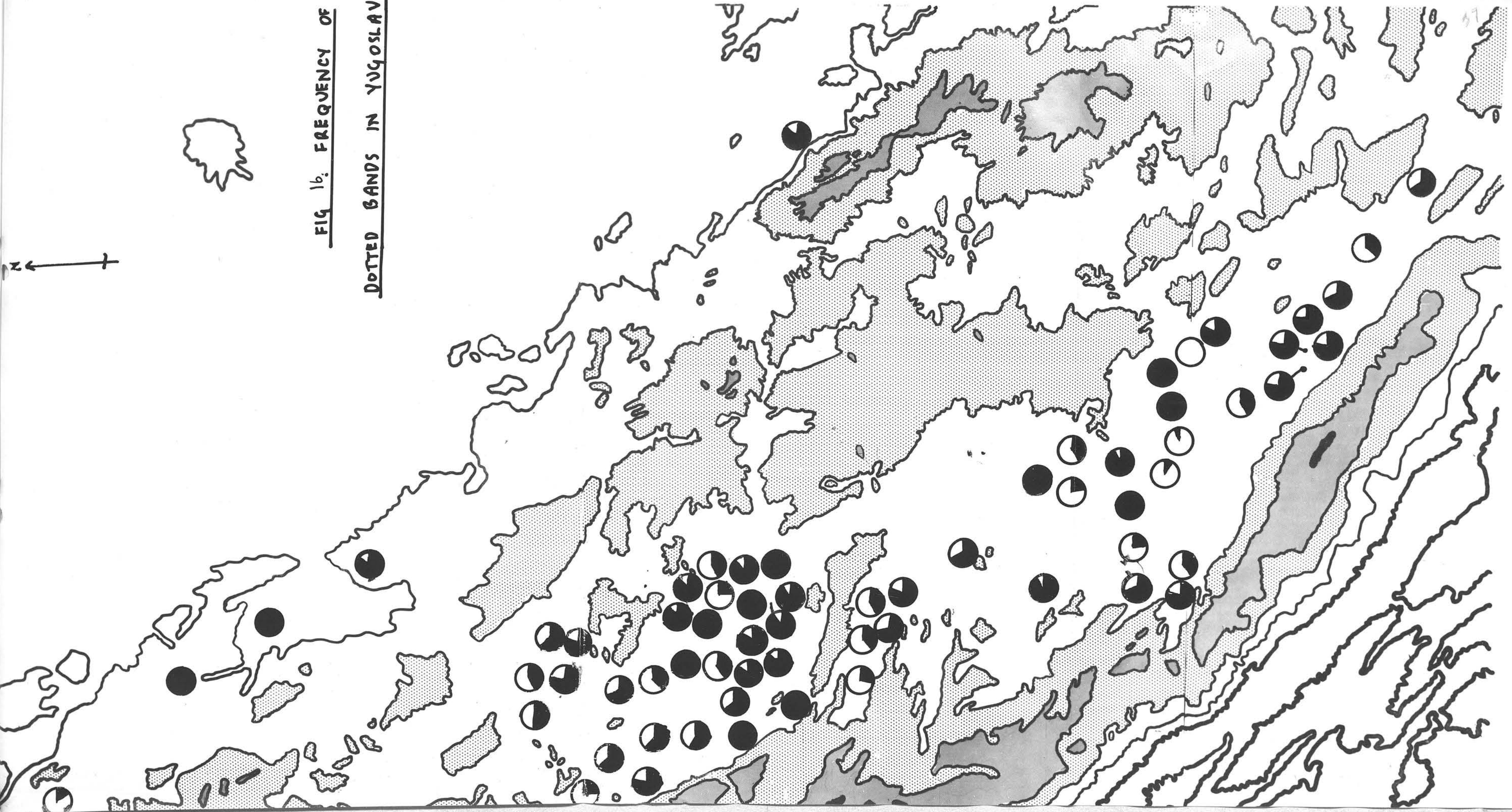
FIG. 15 FREQUENCY OF
MID-BANDED IN YUGOSLAV



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FIG 16. FREQUENCY OF

DOTTED BANDS IN YUGOSLAVI



C. nemoralis at the Southern limit of its range is that its structure differs considerably from that of those central populations so far studied in France and in Britain.

DISCUSSION AND CONCLUSIONS

Neither of the peripheral populations of Cepaea nemoralis studied showed any signs of unique races such as those found in Cleithromys, and in this respect they do not differ from central populations. In spite of this negative result, the study of populations of C. nemoralis at the limits of their distribution has been more than justified by the indirect evidence resulting on the causes of area effects.

Considered simply as area-effects, neither the Montrose nor the Yugoslav Cepaea populations support the theory that area-effects are determined by local climatic selection, as in neither case do the distributions of gene-frequency show any apparent relationship to local topographical factors might cause, for example, accumulation of cold air. This is particularly noticeable in the transects, both of which traverse remarkably uniform regions (sand-dune and polje respectively), and both of which nevertheless show considerable variations in gene-frequency.

The Northern populations studied show ~~an almost~~ complete absence of the Brown morph. Cain & Currey's claim that Browns are most common in the Northern part of C. nemoralis' range is therefore not borne out by this work. This finding casts considerable doubt on their explanation of the cause of

the Brown area effects on the Marlborough Downs.

The mere existence of colour and banding area effects at the Northern limit of C. nemoralis' distribution is in itself significant, as it suggests that ^{if} area effects are maintained in the face of intense selection by cold (which is presumably acting to prevent the species from extending its range), then environmental selective forces which are so small as to be virtually undetectable in most cases are unlikely to be the sole agents maintaining area-effects elsewhere in C. nemoralis' range.

The situation in the South is particularly interesting. Climatic selection seems to be causing great alterations in the frequencies of the colour genes, but to have relatively little effect on the relative frequencies of the genes for shell banding. This suggests strongly that these banding genes are in some way more deeply integrated into the gene complex than are those for shell colour. The colour genes are thus susceptible to intense environmental selection by high temperatures, while the frequency of the banding genes in any particular area is primarily a function of the genetic environment rather than the ambient temperature (or whatever else is limiting C. nemoralis' range).

It is probably significant in this connection that the Yellow morph has been shown to be more resistant to extreme conditions of various kinds than are the other colours.

Both the coadaptive and the selective theories of area effects may therefore be possessed of an element of truth, and Clarke's compromise between them may provide a satisfactory unitary hypothesis.

It appears that the genetic basis of Cepaea area-effects may be a complex phenomenon, with different genes showing different degrees of integration with the gene-complex. The degree of coadaptation may itself be a fairly labile attribute of a population - King (), for example, has shown that ~~six~~ stocks of Drosophila subjected to intense selection by DDT developed differently-integrated gene-complexes within twelve generations of selection, so that crosses between F_{12} lines showed significantly lower DDT resistance than did either parental line. Lewontin's experiments on Drosophila populations held in constant environments showed even more rapid evolution of different coadapted gene-complexes favourable to high or to low frequencies of a particular gene. Coadaptation may therefore develop rapidly and, as we have suggested in Cepaea, different genes may show different amounts of interaction with a coadapted complex of genes. In Cepaea, this may be based on an inversion system, whereby the abiding genes are held on an inversion bearing other genes which interact strongly with the animal's genetic environment, whereas the colour genes are not so strongly associated with such powerful elements of the gene-complex.

Area effects in other species are also likely to be based on a balance between genetic and environmental selection. Cavalli-Sforza's (8) finding that small isolated human populations show an increased variance in blood-group frequencies, and that classification of the human races according to such frequencies agrees well with classifications based on other characters is best interpreted as a response of blood-group frequencies to different genetic backgrounds in small isolated populations while, on a larger scale, related races have generally similar genetic backgrounds, and therefore have similar

gross proportions of the various blood groups (10). Allison's (1) work on "area-effects" in various haemoglobin variants in man, however, is equally likely to be a response of a particular gene (or group of genes) to environmental selection, in this case by disease.

In any event, area effects in any species deserve further study, not only because of the light which they may throw on human population genetics, but also because of their intrinsic evolutionary interest.

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