STUDIES ON THE ECOLOGICAL GENETICS OF *CEPAEA*.

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"I have, all my life long, been lying till noon; yet I tell all young men, and tell them with great sincerity, that nobody who does not rise early will ever do any good."

Saml. Johnson, 1773.

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I hereby declare that this thesis has been composed by myself and embodies the results of my own original research.

J. S. Jones.

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GENERAL INTRODUCTION

This thesis is concerned with the factors controlling the distribution of genes in natural populations of polymorphic landsnails of the genus Cepaea Held. Cepaea has an extensive polymorphism for shell colour and banding, and a great deal of information is available on the genetics of this polymorphism and on the distribution of morph frequencies in natural populations.

Perhaps the most remarkable recent discovery of population genetics is that there is a far greater degree of genetic variation at the biochemical level in natural populations of many organisms than had previously been supposed. Early workers assumed that only a small proportion of the loci in any population were polymorphic, and many of the mathematical models of theoretical population genetics were based on this postulate. Application of electrophoretic techniques to proteins has shown that the average level of heterozygosity in natural populations may be much higher than this; recent estimates have a mean value of about 40% (Mukai 1969). Lewontin & Hubby (1966) have suggested that essentially every locus in some Drosophila pseudoobscura populations may be polymorphic. Some species show greater or lesser amounts of polymorphism (see Manwell & Baker 1970 for review), and some classes of protein may be less polymorphic than others (Kojima et al. 1970). There is, however, little doubt that natural populations of many organisms do possess a very large amount of genetic variability.

A number of hypotheses attempt to explain how this variability is maintained. Some authors have argued that many protein variants are selectively neutral and that their frequencies are determined by random processes. Others postulate that very high mutation rates balanced by weak selection are responsible for at least some protein polymorphism. Kojima and his associates suggest that the selective values of the various alleles

may depend on their relative frequencies; this provides a mechanism of maintaining polymorphism without an impossibly large genetic load due to the segregation of unfit homozygotes. Several authors have published models whereby large numbers of polymorphisms may be maintained by heterosis and gene interaction (See Mukai 1969 for review).

Although mathematical speculations are of course invaluable in suggesting the nature of the mechanisms which may be available for the maintenance of polymorphism, their value is limited without a knowledge of how genes are distributed in natural populations and of the nature and magnitude of selective forces in the wild. The study of the distribution of allozymes in natural populations and of their associations (if any) with ecological factors is still at a very preliminary stage. Because of the practical difficulties of screening large numbers of individuals for protein variants, this is likely to be a laborious task. Complex systems of visible polymorphism based on a number of loci with known linkage relationships may provide a useful model against which the predictions of population genetics theory can be tested, particularly when a great deal is known about the ecology of the organism involved. Although it is possible that the factors responsible for the maintenance of protein polymorphism may be found to be quite different from those acting on most polymorphisms above the biochemical level, information derived from the study of the ecological genetics of visible polymorphisms is likely at least to be valuable in identifying the probable types of biological explanation which may be available for the maintenance of other types of variation in natural populations.

Most research on genes in populations has been carried out with Drosophila. The short life cycle of this animal and its giant salivary gland chromosomes make it ideal for laboratory experiments with artificial populations. As Drosophila is often rare, active and difficult to collect

very little is known about its ecology. It is therefore difficult to investigate the interactions of genetic polymorphism with environment in natural populations of this genus.

Land snails of the genus Cepaea have a number of advantages which make them almost uniquely suitable for some aspects of research in ecological genetics, although they do have corresponding disadvantages, such as a prolonged life cycle. They are frequently very common in a wide variety of habitats and are easy to collect. Their immobility means that populations sharing a common gene pool are relatively small and can be studied in detail. There is an easily scored polymorphism for shell colour and banding, and dead shells leave a record of which genes the animal possessed when alive. Shells can easily be marked for capture-recapture experiments, and the appearance of the dead shell may give an indication of the cause of death (Morris 1954).

C. nemoralis (L.) is the commonest British member of the genus. Its shell may be yellow, pink or brown, and may bear up to five dark bands. There are a number of variations in the expression of the bands, which may be fused together in various ways, may have reduced or unusually large amounts of pigment, or may have no pigment at all. The lip of the shell is usually black, but may be white. Body colour varies from black to reddish-brown to almost white.

The shell colour genes are allelic. The gene for brown shell is dominant to that for pink which is dominant to that for yellow. The locus controlling presence of absence of bands is linked to the colour locus, absence of bands being dominant to their presence. There is evidence of some inter-population variation in the recombination distance between these loci. Genes which reduce the band pigment to a series of dark flecks (punctate bands) modify its colour (orange bands), or

completely remove the lip pigment or lip plus band pigment (albolabiate and hyalozonate) are linked to the colour and banding loci. Loci not linked to each other or to the above group include a locus which reduces the normal five-banded pattern (scored as "12345", counting from top to bottom) (See Cain & Sheppard 1950) to one central band (pattern 00300) and another which suppresses the top two bands (pattern 00345). Many other variants have been described (Taylor 1914) and the mode of inheritance of some of these is known. The genetics of C. nemoralis has been investigated by Cain et al (1960), Cain et al (1968), Cain & Sheppard (1957), Cook (1967), Fisher & Diver (1934), Lamotte (1954), Murray (1963), and Wolda (1969c).

The closely related species C. hortensis (Müll) possesses most of the variants described above, although populations of this species are usually less polymorphic than are those of C. nemoralis. The genetics of the two species appears to be almost homologous (Murray 1962). C. vindobonensis Pfeiffer and C. sylvatica Drap. are Continental species which are described in more detail in chapter 3.

Polymorphism in C. nemoralis is very extensive (I have records of only 24 colonies which are monomorphic for both colour and banding out of a total of more than 2000 British samples containing at least twenty shells, and most of these show variation in, for example, band fusions), and has an ancient origin, as subfossil samples from the Neolithic show banding polymorphism (Diver 1929). Several early authors stated that variation in Cepaea is random and that natural selection is not important in controlling the distribution of varieties in this genus (Diver 1940; See Cain & Sheppard 1950). On the basis of an extensive survey of populations in France, Lamotte (1951, 1952) concluded that genetic drift is the most important factor affecting gene frequencies, as he could find no association between morph frequencies and environment and as mathematical treatment

of some of his data suggests that they accord with Wright's (1931, 1932, 1935, 1940) predictions for populations whose structure is determined primarily by random processes. In more recent publications, Lamotte (1959, 1966, 1968) has suggested that climatic selection may play some part in affecting the frequencies of the different morphs, although drift is also important in determining population structure.

Several other authors consider that environmental selection is the most important factor controlling the genetic structure of C. nemoralis populations. Populations of this species in the Oxford region tend to match the background upon which they live, beechwoods having a high frequency of pink and brown shells with the top two bands missing, while populations from grasslands are made up mainly of yellow shells with five bands (Cain & Sheppard 1950, 1954). This pattern of distribution seems to be due primarily to differential selection by thrushes acting against the less cryptic morphs (Sheppard 1951). Similar patterns of morph variation with background have now been found in other parts of the South of England (Currey et al 1964, Arnold 1966, Carter 1968b) and in France (Arnold 1970). Although the selective forces acting against conspicuous shells are large (Arnold 1966, Carter 1968a) and certainly too powerful to allow genetic drift to have much effect in the large populations found in these regions, the populations do not become monomorphic for the most cryptic morphs. There must therefore be some form of active maintenance of the polymorphism, which probably involves heterozygote advantage (Cain & Sheppard 1950, Cain & Currey 1963a). Other mechanisms such as frequency dependent selection by predators may have some local importance (Clarke 1962).

Not all populations of C. nemoralis have this pattern of morph distribution. Over large parts of the South of England and elsewhere, morph frequencies bear no apparent relation to the background upon which

the snails are living, although there may be intense predation. This type of population structure was first described by Cain & Currey (1963a,b) in C. nemoralis on theMarlborough Downs. Large ecologically diverse areas (which are enormous compared to the panmictic unit of Cepaea) are characterised by a limited range of colour and banding morph frequencies, while in adjacent and apparently similar regions the frequencies of these morphs are quite different. The populations do not in general match their backgrounds for shell colour and banding, in spite of thrush predation. Morph ratio clines between the different regions are often extraordinarily steep; in one locality on the Marlborough Downs, for example, there is a change in the frequency of yellow shells of 70% over a distance of only 130 metres, without any apparent environmental discontinuity. The clines may be stable over a number of years (Wolda 1969b) and may be maintained even when there is considerable gene flow (Day & Dowdeswell 1968). Cain & Currey have called such patterns of constancy of morph frequency over large areas without regard to background "area effects". The limits of the area effects for colour and banding do not necessarily coincide. Many of the steepest clines for banding morph frequency are in regions of relatively constant colour frequency, and vice versa.

Area effects have now been found in many parts of C. nemoralis' range, and are present in populations of C. hortensis (Cain & Currey 1963a, c, Cain et al 1969, Cameron 1969) and C. vindobonensis (see chapters 3 and 4). Rather similar geographical variations in gene frequency are also widespread in populations of other molluscs (Komai & Emura 1955, Mayr & Rosen 1956, Barker 1968, Clarke 1968). It is the primary purpose of this thesis to attempt to elucidate the causes of such patterns of gene distribution in Cepaea, and many of the area effects known to exist in this genus will be discussed in later chapters.

Phenomena similar to area effects in Cepaea also exist in natural populations of other organisms. The distribution of blue-flowered plants in some Linanthus parryae populations is rather similar to the distribution of shell colour and banding patterns in C. nemoralis on the Marlborough Downs, as this morph occurs only in "variable areas", which are ecologically very similar to the regions where only white flowers are found (Epling & Dobzhansky 1942). Some populations of D. willistoni and D. pseudoobscura show a local constancy of karyotype frequency in ecologically diverse areas which contrasts with surrounding populations, where the frequency of different inversions varies with the region's ecology (Dobzhansky 1962). The distribution of human blood groups may also be considered as analagous to Cepaea area effects, as there are great geographical variations in morph frequency which are usually independent of detectable environmental factors (Mourant 1954, Nijenhuis 1965).

It is clear that area effects in Cepaea may prove to be of much more than specialist interest. The mechanisms underlying this pattern of morph distribution are a matter of some controversy. Random genetic drift acting at the present time cannot be an explanation of area effects on the Marlborough Downs as the populations involved are far too large. There is also no evidence of a "genetic bottleneck" in historical times, and subfossil samples show that the location of the area effects has been remarkably stable (Cain & Currey 1963a). Cain & Currey suggest that climatic selection is responsible for at least some of these patterns of gene distribution. Their argument is as follows.

C. hortensis is a more Northerly species than is C. nemoralis and is therefore presumably more resistant to cold than is C. nemoralis. and In Britain the Northern limit of nemoralis parallels the summer isotherms, suggesting that summer temperature is the factor limiting this species'

distribution. On the Marlborough Downs, hortensis predominates in the valleys and nemoralis on the uplands. This is due to the valleys acting as frost hollows, so that because of the accumulation of cold air the temperature on clear summer nights drops to a level which can be tolerated by hortensis but not by nemoralis.

Dark brown shells are, these authors claim, commoner in the more Northern part of nemoralis' range than elsewhere. On the Marlborough Downs snails with dark brown shells are found mainly at the lower levels of nemoralis' distribution and also in the zones where this species overlaps with hortensis. These regions, according to Cain & Currey, are colder at night. Area effects for dark brown shell colour are therefore due to this morph's greater resistance to cold givingi it a selective advantage over the other shell colour morphs in frost hollows. The pink and yellow area effects are due to similar, but as yet undetermined, climatic selection. It is impossible to identify the selective forces causing area effects for shell banding in the Marlborough Down populations, although calculation shows that changes in the selective value of one homozygote of only a few percent could cause area effects as marked as those found on Downs. On the basis of further collections, Cain (1968) suggests that midbandeds are commoner in the warmer parts of the Downs, and that the frequencies of other banding morphs may also be affected by climatic selection.

Area effects have now been studied in many other regions. In general it has proved to be rather difficult to correlate morph frequencies with environmental selective forces. This is particularly true in places with a relatively uniform topography, such as Salisbury Plain (Cain & Currey 1963c), the banks of a river in Cambridgeshire (Goodhart 1962), and many sand dunes (Cain 1968, Clarke & Murray 1962, Clarke et al 1968, Jones 1966). Some apparent associations of morph frequency with topography or microclimate

have, however, been described. Cain (1968) found a strong association between the occurrence of dark brown shells and complex topography (which will allow accumulation of cold air) in British sand dune populations, and also some association (in one region at least) between the frequency of banding morphs and the aspect of the dunes. Populations at the heads of some Pyrenean valleys have a much higher frequency of unbanded shells than do those lower down (Arnold 1968). This is interpreted by Arnold as being due to unbanded shells' greater resistance to the accumulated cold air flowing into the valleys from the surrounding mountainsides on clear summer nights. A tendency for unbanded shells to be commoner on hillsides in the lower parts of these valleys is interpreted by him as being a result of this morph's greater resistance to hot and dry conditions (Arnold 1969). These apparent associations of morph frequency with microclimate, together with several similar examples, will be discussed at more length in the General Discussion of this thesis.

Because it is often very difficult to find an association between the distribution of morphs in area effects and ecological variables, other mechanisms of the origin and maintenance of area effects have been proposed. Goodhart (1963) argues that the differences between area effects are due to the action of the "founder principle" (Mayr 1963). Chance differences in the genetic constitution of the small scattered snail populations which first colonised the Downs have persisted because of the evolution of coadapted gene complexes. When these founder colonies expanded and met, hybrids between them were relatively unfit, so that a system of area effects separated by steep clines developed. Wright (1965) has analysed the probable evolution of Cepaea populations mathematically and reaches a rather similar conclusion. Goodhart's theory of the origin of area effects has been criticised by Cain & Currey (1963d) on the grounds that differently

coadapted gene complexes would probably not be equally successful in all environments, and that one would replace the others unless environmental selection is also acting. The geography of the clines also does not agree with what would be expected if they are hybrid zones.

A model of the evolution of clines has been developed by Clarke (1966). He proposes a situation where a large region is inhabited by a series of polymorphic populations, and where slight environmental differences from place to place locally favour one allele at the expense of another. Clines maintained by selective gradients will then be set up. In a region where one allele is common, selection will favour the genes which are compatible with it. Calculation shows that the spread of such modifying genes, if they satisfy certain conditions of interaction with the genotype involved, will cause steepening and in some cases even stepping of the cline. A step in the cline will take place preferentially at an environmental discontinuity, although such discontinuities are not essential for step formation. This process may lead to the formation of area effects separated by steep clines.

On the basis of their studies on the pattern of speciation in the snail Partula in the Society Islands, Clarke & Murray (1969) suggest that the evolution of area effects might continue until adjacent populations develop incompatible gene complexes, and that selection for reproductive isolation might then lead to semisympatric (or "parapatric") speciation. If this type of speciation does occur, it adds a new dimension of interest to the study of area effects in Cepaea.

There is clearly considerable controversy about the causes of area effects. Some workers emphasise selection by the ecological environment as the primary force determining the distribution of genes, while others consider that differences in coadaptation between area effects (originating either by random processes or as a result of selection) are the most

important factor in their maintenance.

There is, of course, a considerable body of evidence showing that geographically separated populations of many species do show differences in their genetic background leading to reduced fitness in the F_2 and subsequent generations of interpopulation crosses, or to similar reductions in fitness when a foreign chromosome is crossed into a population (see, for example, Vetukhiv 1953, 1954, 1956, 1957, Wallace 1955). Prakash & Lewontin (1967) have recently presented a more direct proof of coadaptation in Drosophila populations. There is as yet no direct evidence for coadaptive divergence between area effects. In populations of Partula taeniata there are area effects (which do not appear to be related to any detectable environmental variable) for high and low frequencies of purple shells. Where the cline of frequency of the gene for purple shell colour is steepest, there is a great increase in the frequency of banded shells, (which are rare elsewhere) together with some disturbances in the expression of shell banding. There are also correlated changes between the frequency of purple, mean shell length and the breeding condition of the snails. Clarke (1968) interprets this pattern as demonstrating that the cline is a region of hybridisation between differently coadapted genecomplexes. Two different Dutch C. nemoralis populations have been found to show great differences in behaviour and physiology (Wolda 1967); this may also indicate that geographically separated snail populations differ in a complex of genes, rather than merely in the frequency of their shell colour and banding alleles.

It is the purpose of this thesis to attempt to investigate the relative importance of environmental selection in determining the distribution of genes in natural populations of Cepaea. Populations of C. nemoralis have been studied at the southern limit of their range where

climatic conditions may be expected to be extreme (chapter 1), and this survey has been extended by a consideration of the association of morph frequencies with climate throughout the species' distribution (chapter 2). Morph frequencies have also been examined in Balkan C. vindobonensis populations living in a region with very marked local contrasts in topography and microclimate (chapter 3) and in another area with more uniform topography (chapter 4). An attempt to detect colour heterozygotes in C. nemoralis which if successful would have been relevant to the investigation of the ecological genetics of this species did not succeed, although it gave rise to some information on the biochemistry of the shell pigment and on probable differences in the absorption of solar radiation by shells of different colours (chapter 5). A subsidiary investigation on the distribution of Cepaea in Scotland is described in appendix 1. I have attempted to draw some general conclusions on the causes of area effects in a General Discussion at the end of the thesis.

CHAPTER 1

THE STRUCTURE OF A PERIPHERAL POPULATION OF *CEPAEA NEMORALIS*

INTRODUCTION

Peripheral populations are of considerable interest to evolutionary theory as they often exist in the face of environmental stress which prevents a species from extending its range. They may therefore demonstrate the effects of intense selective forces in a more convincing manner than do laboratory experiments, which usually depend on arbitrarily defined conditions of extreme selection. The reduction of gene flow into geographically marginal populations due to only one frontier being in contact with a source of new genetic variation, and the tendency of such populations to become completely isolated by colonisation of a new area means that peripheral populations may form particularly favourable material for the evolution of new species. Because of these factors, such populations have been widely studied.

Distinct forms and populations with an unusual genetic structure are present at the edges of the range of many species (Cook 1961). These may be relicts of formerly widespread types or may be specialised and genetically fragile populations which are likely to die out or to be overwhelmed by expansion of the main body of the species. Occasionally, however, small isolated peripheral populations will succeed in passing the "genetic bottleneck" of homozygosity due to genetic drift and will expand and attain a degree of heterozygosity which allows them to respond rapidly to selection, so that a new race, or even a new species, may evolve. Mayr (1963) has described many instances where this process has probably occurred.

As well as their importance in speciation, peripheral populations may play a part in maintaining the genetic flexibility of the parent species. Some *Drosophila* populations at the geographical limits of their range show

far less inversion polymorphism than do those at the centre (Carson 1955, Carson & Heed 1964) and therefore have a much higher incidence of crossing over than do central populations. The system of chromosomal polymorphism found in central populations, although it may allow the exploitation of specialised ecological niches, has the disadvantage of greatly restricting the release of latent genetic variability by recombination. Such populations are therefore specialised and inflexible. Peripheral populations cannot afford this loss of unfit segregating homozygotes and adapt to environmental change in an "opportunistic" fashion involving free recombination. They can therefore respond to selection much more rapidly than can central populations; this has been demonstrated experimentally by Carson (1958b). The marginal populations may act as an "escape mechanism" from possible overspecialisation by the main body of the population, as their system of selection allows rapid response to environmental changes, giving rise to new gene complexes which diffuse inwards to the centre of the species' range.

There has been little systematic study of geographically peripheral populations of Cepaea, although many workers have investigated the genetic structure of central populations of this genus. A large white-lipped race of C. nemoralis is found in the Dartry Mountains of Ireland and in the Pyrenees. Taylor (1914) considered these "peripheral" populations to be relicts of a once widespread race which is now found in fossil form in Germany. Cook and Peake (1960), and Arnold (1968), however, have found that there is considerable variation in the frequency of white lip and other characters in these populations. This could be due either to differing amounts of introgressive hybridisation between relict and new populations causing exchange of characters, or to the supposedly relict characters being in fact responses to local selection.

Irish populations are at the margin of the species' range only because of the intrusion of the Atlantic Ocean, and are not "peripheral" in the biological sense. Investigation of genuinely peripheral populations of C. nemoralis would be rewarding, as the factors limiting the geographical distribution of this species are quoted as evidence for Cain and Currey's theory of the causes of area effects.

I have found that the structure of Northern peripheral populations of C. nemoralis on the East Coast of Scotland is in general similar to that of the populations on the Marlborough Downs and in many others parts of Britain, as they show marked area effects for both colour and banding (Jones 1966). If Cain and Currey's theory of the causes of area effects is correct, as stated, we might expect Northern peripheral populations of C. nemoralis to contain a high percentage of snails with brown shells, which, these authors claim, are more resistant to cold than are the other shell colour morphs. The brown phenotype is, however, absent from the populations studied by Jones (1966) and further surveys have shown that it is at a low frequency throughout Scotland (Jones, unpublished; see chapter 2).

C. nemoralis reaches the Northern limit of its range in Scotland only 550 km. North of the Marlborough Downs. It may therefore be difficult to detect any effects of geographical differences in climate on gene frequency between these populations and those studied by Cain and Currey. This chapter describes the structure of some Southern peripheral populations of C. nemoralis in a region which is more than 1500 km. from the Marlborough Downs and which shows very marked differences in climate. These might be expected to have a detectable effect on the frequency of any genes which are liable to climatic selection in this species.

The Area Studied.

C. nemoralis reaches the Southern limit of its range in Spain, the South of France, North Italy, and the South of Croatia (Yugoslavia). The last area was chosen for this study of Southern peripheral populations, as it is furthest from the British Isles. The survey was concentrated on the Velebit region near the Adriatic coast of Croatia (fig. 1), as it seemed likely that Cepaea would be common in these limestone mountains.

Preliminary sampling showed that C. nemoralis was not present South of Gračac (fig. 1), and that the Southern limit was therefore North of this. The snails do not reach the limit of their range in this area simply because of the presence of an obvious geographical barrier, as habitats apparently suitable for C. nemoralis, in which C. vindobonensis was common, were found South of Gračac. These nemoralis populations are therefore presumably living in conditions which are marginal in the ecological as well as the geographical sense. Samples of C. nemoralis were collected in an area of approximately 5000 square kilometres, from Brod Moravice in the North to Gračac in the South, and as far East as Bihać. This species was most common in the Gacka area (around the towns of Otočac and Brinje), and the most detailed survey was carried out in this region.

The whole area is part of a limestone massif and has a typically karstic topography and vegetation. Large basins (the "polja"), which form the only level regions are surrounded by steep mountains up to 1500 metres high. The alluvial soils of the basins are often intensively cultivated, while the mountains are covered with short turf, open scrub-land, or, above 700 metres, dense beech and conifer forests. The area is described in more detail in chapter 3. A few samples were collected to the North and East of the area described in chapter 3. The geology and vegetation of these regions is in general similar to that of the main

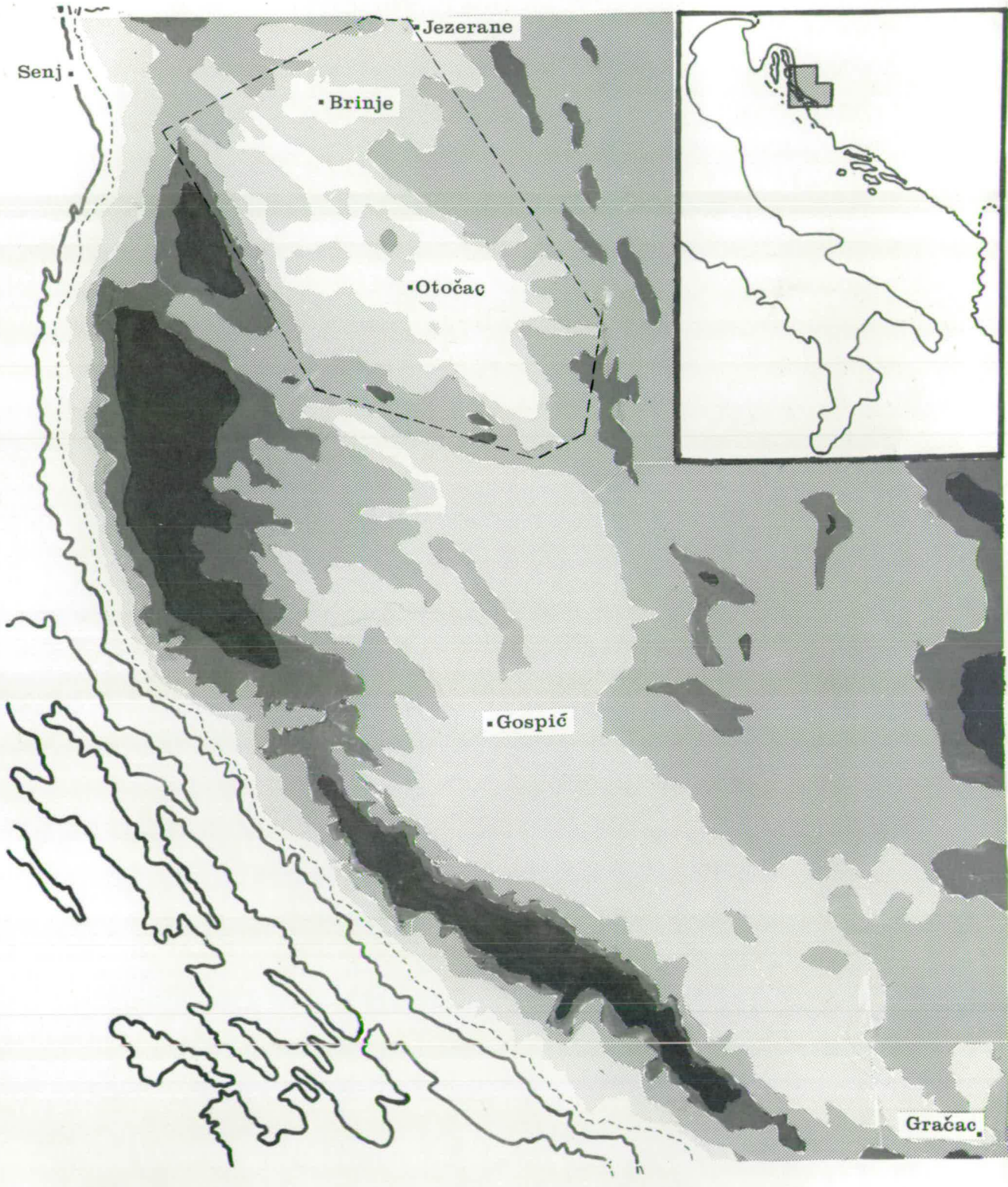
Figure 1.

Fig. 1. The Velebit Mountains.

Contours at 250 metre intervals.

Scale approximately 1:500,000.

Dotted line encloses main Gacka survey area (see fig. 17 and morph frequency maps).


Jezerane
Senj
Brinje
Otočac
Gospić
Gračac

survey area, although the country North of Jezerane (fig. 1) is more mountainous, with fewer basins, and is traversed by narrow river valleys. Extensive pine forests are found in the North-West of the survey area.

The Distribution of Snails.

The range of habitats in which C. nemoralis was found was in general similar to that of the closely related species C. vindobonensis, which was common throughout the area (See chapter 3). The two species were almost always found in association, although there was some tendency for C. vindobonensis to be commoner in the most arid and exposed places. Most of our nemoralis samples were collected from the hedgerows described in chapter 3. A few originate from other habitat classes such as "rough herbage", deciduous scrubland or beechwood. Habitats are described in more detail in chapter 3, and the habitat classes for our collections are given in table 4.

Distribution of Morph Frequencies.

Collection techniques were in general similar to those described by Cain & Currey (1963a) and other authors. Each sampling area (which in no case exceeded 100 metres radius and was usually much smaller than this) was searched carefully and all snails seen were collected. There were no significant differences in morph frequency between adult and young snails, or between live snails and those found dead. Except for the cases of fusions and of lip colour (which cannot be scored accurately in young snails (Cain & Sheppard 1950)) all snails collected were used in the analysis of morph frequencies. Sample scores are given in table 1. Morph frequencies are mapped in figures 2-6. Samples can be located by referring to the grid references in the tables and the grid squares on

figure 19.

i) Shell Colour.

Yellow shell colour is at an extremely high frequency throughout the main survey region (overall frequency = 94.5%). (Fig.2). This is not due merely to a local area effect for high frequency of yellow in the Gacka area similar to those found in parts of Britain, as yellow shells are at an equally high frequency throughout the 5000 sq. kms. from which samples were taken. Fig. 3, in which colour morph frequencies are mapped on the basis of ten-kilometre squares of the Yugoslav National Grid shows this clearly. There is therefore a real tendency towards monomorphy for shell colour in these southern peripheral populations of C. nemoralis.

No brown shells were collected. Pink shells tend to be grouped into a separate area effect in the central part of the Gacka region (mainly Srpsko Polje, Kompolje, Orovac, Rapajici and Brlog Stacija samples) although in no sample does the frequency of this morph exceed 54% (sample Brlog 2). Pink shells are almost absent from the southern part of the main survey area, the overall frequency of yellow being over 99%.

A disproportionately large number of samples was collected from the Central Gacka area effect for the presence of pink. If this small region is omitted from the calculation, the frequency of yellow over the whole survey area rises to 96.8%. This figure is likely to be a better estimate of the real average frequency of yellow shells in these southern peripheral populations than is the percentage of yellow shells considered over all samples.

ii) Shell Banding.

The pattern of distribution of the genes controlling shell banding differs somewhat from that of those controlling the colour of the shell.

The overall frequency of unbanded shells in Yugoslavia is 4.4%,

Figure 2.

Fig. 2. Frequency of Yellow Shells in the Gacka Area.

Scale approximately 1:150,000.

500 metre contour also shown.

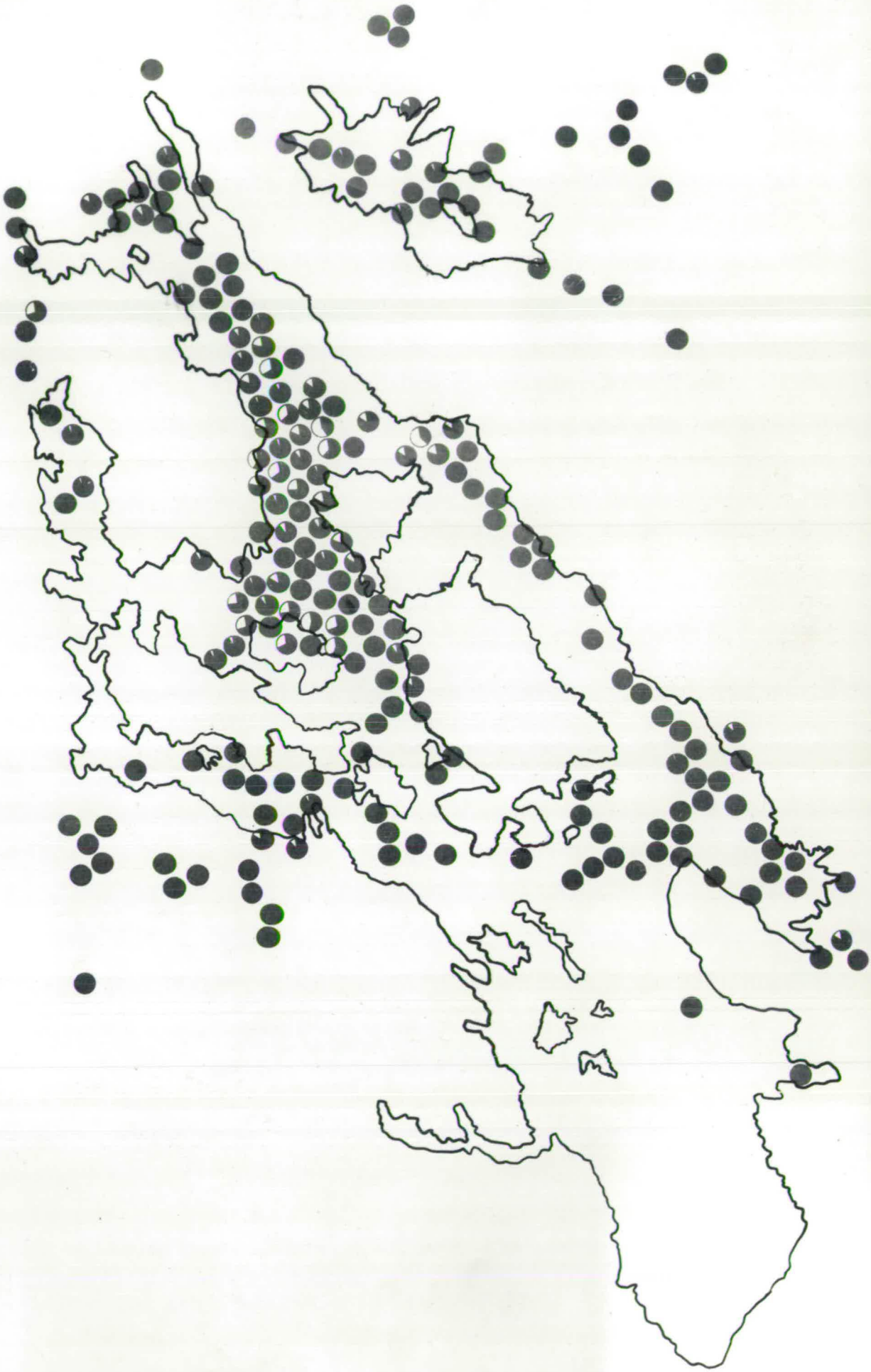
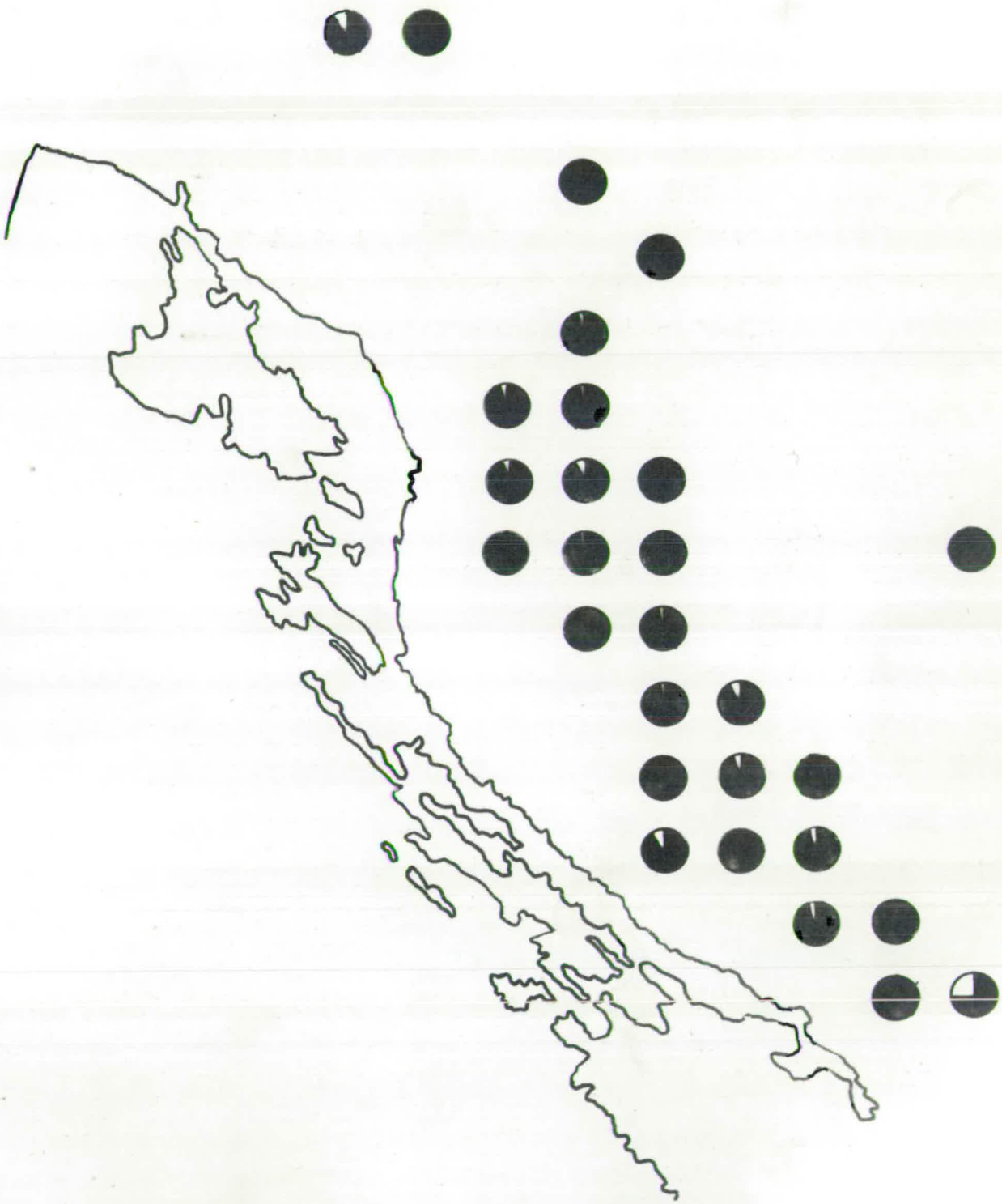


Figure 3.

Fig. 3. Frequency of Yellow Shells in C. nemoralis in the Velebit Mountains, arranged on the basis of the 10-kilometre squares of the Yugoslav National Grid.



compared to 22.4% in Britain. That of mid-banded is 21.2% of all banded shells, compared to 32.5% in Britain. It is difficult to compute the frequency of trifasciate shells (those with the top two bands missing) in which this condition is due to the presence of the T^{345} allele described by Cain et al. (1960), as there are many shells in which the absence of the upper bands is apparently due to a reduction in expressivity of punctate bands. The frequency of trifasciate among shells with at least three non-punctate bands is 2.4% in Yugoslavia, compared to approximately 3.5% in Britain.

Hyalozonate bands and orange bands occur sporadically at a low frequency. This situation is similar to that found in British C. nemoralis populations. With the exception of 4 white-lipped unbandeds in a sample (Perkovici 3) which also contained snails with hyalozonate bands, the white-lip phenotype was absent. The frequency of band fusions is rather low (2.7% of adult shells capable of showing fusions).

The overall frequencies of the major banding classes in Yugoslavia populations of C. nemoralis are not very different from those found in British populations. The frequency of unbanded snails is rather lower than in Britain as a whole, but this morph is at an almost equally low frequency over large parts of the British Isles such as the East of England from Hull southwards (overall frequency of unbanded = 10.8%). The frequencies of 00300, 00345, hyalozonate and orange banded are similar to those found in Britain. None of the major loci controlling shell banding show a tendency to monomorphy as marked as that found at the colour locus, and none of the differences in banding morph frequency between Yugoslav and British populations form part of a general trend throughout the range of the species, as is the case for the frequencies of the colour morphs (see chapter 2).

Punctate bands, in which the band pigment is reduced to a series of

Figure 4.

Fig. 4. Frequency of Unbanded Shells in the Gacka Area.

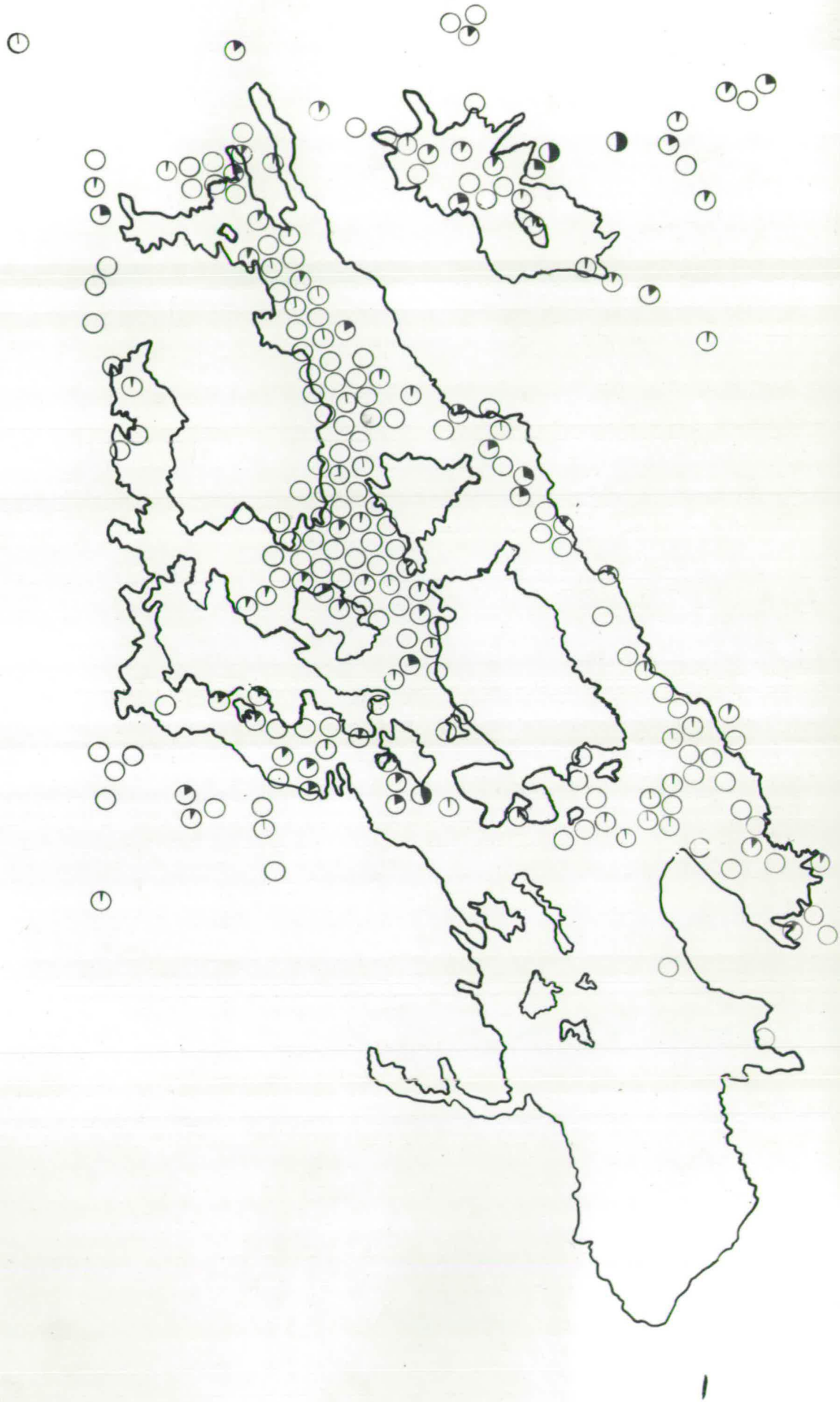


Figure 5.

Fig. 5. Frequency of Mid-banded Shells in the Gacka Area.

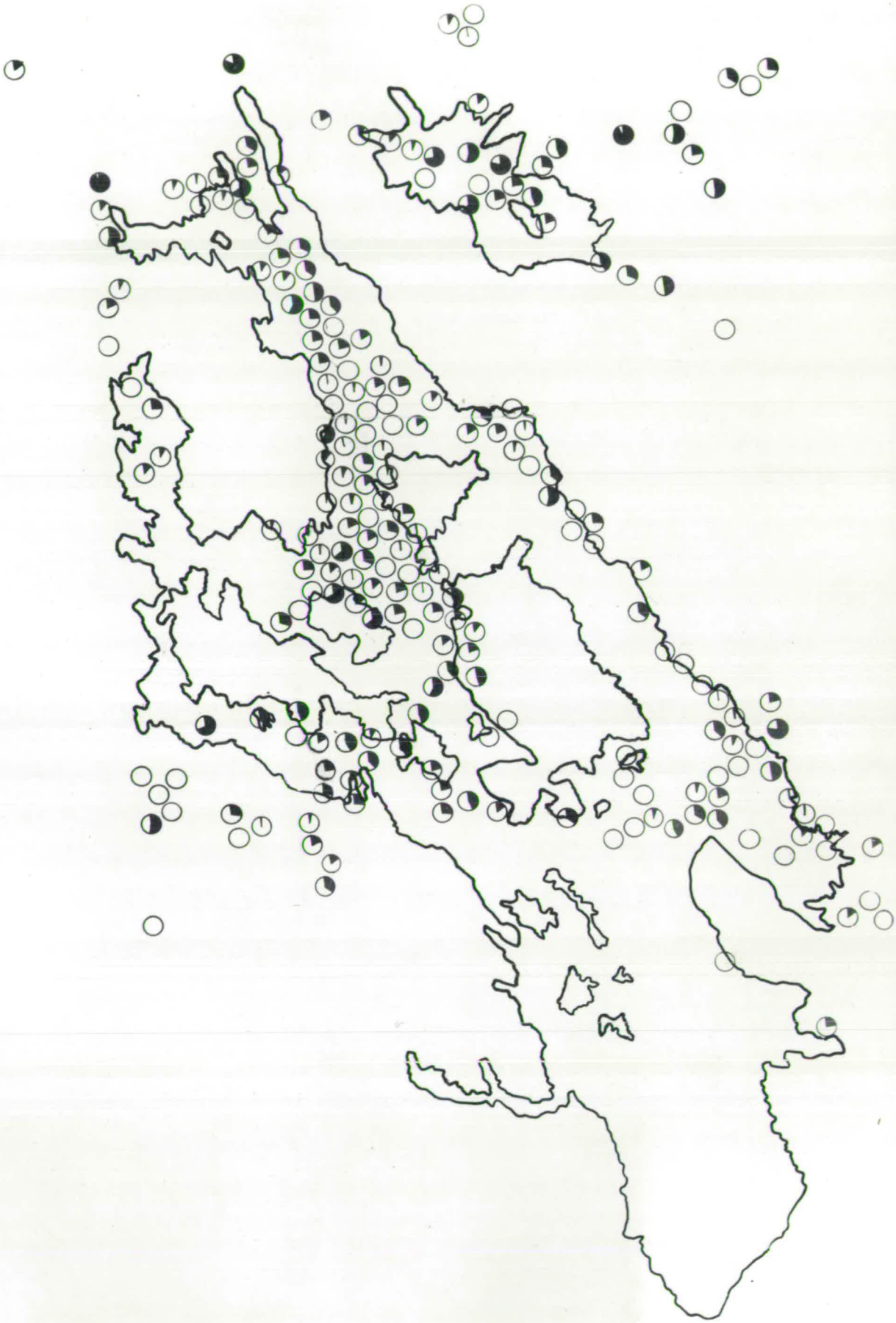
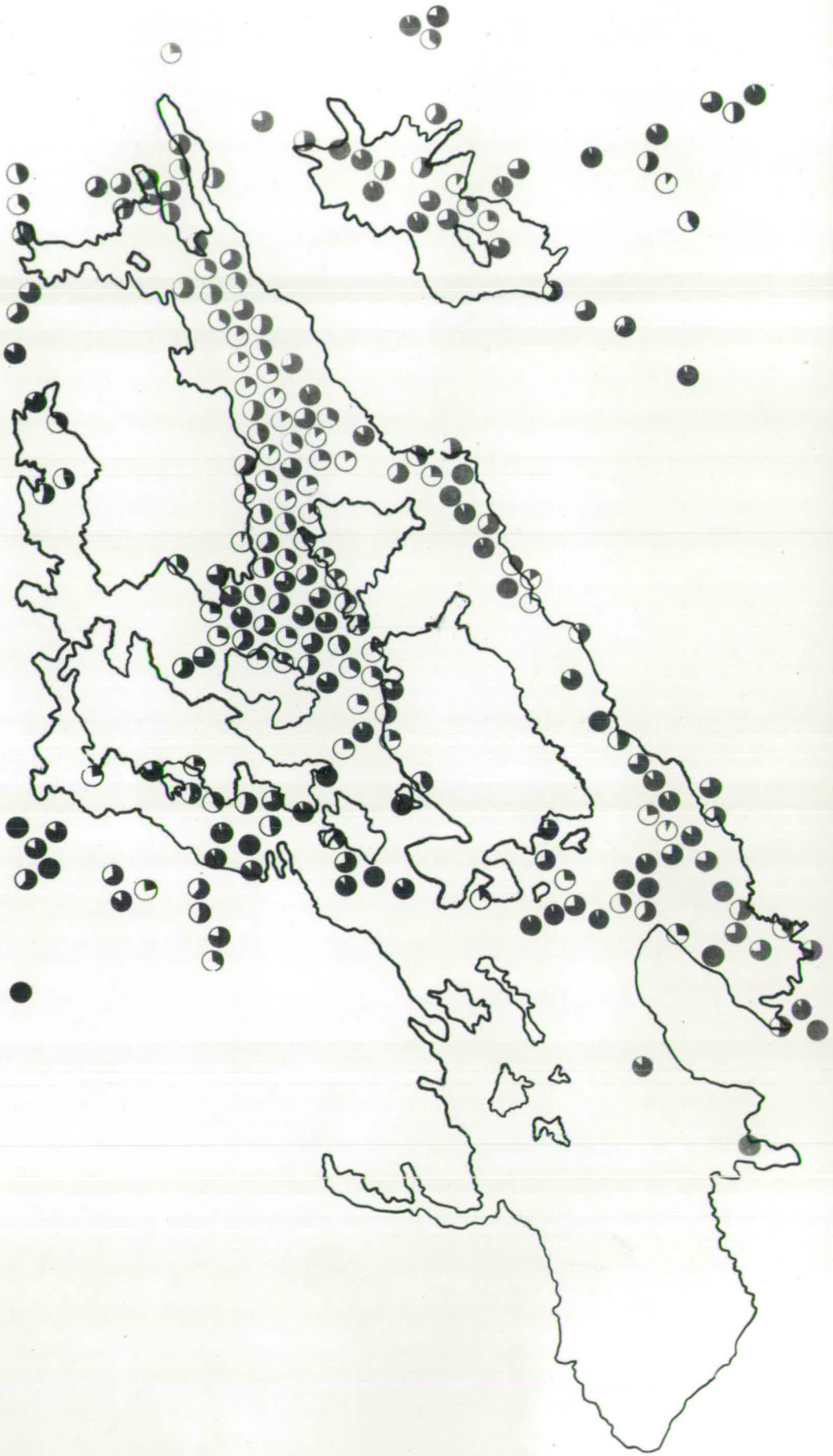


Figure 6.

Fig. 6. Frequency of Punctate Shells in the Gacka Area.



dark spots, are present at a relatively high frequency (51.8% of all bandeds). This frequency is considerably higher than that found in most British populations, although this is rather difficult to estimate accurately as some British authors do not give scores for this phenotype. In many punctate shells the pigment content of one or more of the bands is so diminished that the band is reduced to a faint punctate trace near the lip. Very frequently, punctate shells have one or more bands missing (patterns such as 02045 and 00045 being most common). This is probably due to a reduction in expressivity of the bands in individuals which also possess the allele for punctate banding, as non-punctate shells have a far lower frequency of this type of banding pattern (χ^2 = 12.417 $p < 0.001$). This phenomenon is similar to that described by Cain et al (1968) on the basis of breeding experiments. There are no obvious regularities in the geographical distribution of these reductions in expressivity, computed as the frequency of punctate shells (except midbandeds) with suppression of one or more bands, among all punctate shells.

Breeding experiments on French and British snails have demonstrated close linkage between the colour locus and that for punctate bands (Cook 1967, Cain et al 1968). There is often considerable within-colony linkage disequilibrium between such closely linked loci in C. nemoralis. There is no evidence of strong linkage disequilibrium between the colour locus and that giving rise to punctate bands in these Yugoslav samples, as 52% of the banded pinks are punctate, compared to 51% of the banded yellows. Only one sample (Srpsko Polje 16) contains a "significant" excess of punctate bands in one of the colour classes, but this is no more than what one expects to find, purely by chance, if the 88 samples containing punctate shells of both classes are considered separately. This lack of disequilibrium may suggest that the locus for punctate banding in these

Yugoslav populations is less closely linked to the colour locus than in the snails investigated by Cain et al (1968). The Yugoslav punctates also differ in appearance from those previously described, as the dark flecks on the punctate band are separated by uninterrupted shell ground colour, instead of by a noticeable pale band. This character may therefore be controlled by a different locus from that investigated by these authors.

Yellow shells show a much greater tendency towards reduction of band pigmentation in punctates than do pinks, so that there is a higher frequency of missing bands in yellow punctates than in pinks (sign test; $p < 0.001$). This tendency for pinks to show greater expressivity of the bands than do yellows may be similar to the situation described by Wolda (1969c) for Dutch, by Goodhart (1962) for English, and by Clarke et al (1968) for Irish C. nemoralis, where certain band fusions are much commoner in pink than in yellow shells. It may also be analagous to the tendency of brown C. hortensis to have more band fusions than do yellows (Cain et al 1969) and to that of C. vindobonensis with fully pigmented bands to show a greater degree of fusion of the bands than do shells with reduced band pigmentation (see chapter 3). Wolda interprets his findings as being due either to strong selection against fusions in yellow, or to linkage between the fusion loci and the colour locus. An alternative explanation for this excess of more heavily banded shells in pinks, which is perhaps more satisfactory as it does not invoke strong selection or otherwise unproven linkage, is that the gene for pink shell colour in C. nemoralis has a pleiotropic effect on the expression of banding, so that the darker pink shells have a tendency to produce more dark band pigment. Similar interactions between the colour and banding loci are already known - for example, five-banded shells show reduction of the

intensity of the ground pigment between the bands (Taylor 1914, Cain & Sheppard 1950) and snails bearing the lurida and hyalozonate modifiers of band pigmentation sometimes show suppression of ground colour (Murray 1963, Cook 1967).

The geographical distribution as well as the overall morph ratios of banding morph frequencies in the Velebit Mountains is rather different from that of the colour morphs (figs. 4, 5 and 6). There is little tendency for adjacent samples to have similar frequencies of most of the banding morphs, in contrast to the situation at the colour locus, where samples containing pink shells show a tendency to be grouped together. This is most marked for the mid-banded and punctate phenotypes; for example, there is a change in the frequency of midbanded from 2% to 69% to 3% over 500 metres between samples Srpsko Polje 16, 15 and 13, while the frequency of yellow alters only from 75% to 86% to 97%. There is no clear tendency for any region to have an average frequency of midbanded which differs markedly from that of any other region, although there are many very localised variations in morph frequency throughout the study area.

Similar extremely steep clines occur for the frequency of punctate bands; between samples Podbrdje 2 & 3 there is a change in the frequency of this morph from 32% to 92% within 400 metres. Many similar examples could be quoted from throughout the survey area. As in the case of midbanded there is no apparent tendency for any regional group of samples to have a higher frequency of punctate than any other, although there is everywhere very marked within-group variation in morph frequency.

The frequency of trifasciate shells (computed among non-punctates only) is rather low. There is no clear tendency for snails of this phenotype to occur more commonly in one region than in another.

The pattern of distribution of unbanded shells is generally parallel to that of the other banding morphs, as it occurs sporadically throughout the survey area. A number of steep clines in the frequency of unbanded were found - for example, between samples Price 2 and Zakulje 1 there is a change in morph frequency of 0% to 32% within 300 metres. There is some tendency for slightly larger regions to have elevated frequencies of this morph; thus, unbandeds were present in all four samples at Poljice, reaching a frequency of 44% in Poljice 2. Similarly, areas around Krizpolje have a relatively high frequency of unbanded shells. However, the general pattern of variation at this locus remains one of local fluctuations in gene frequency, with no very clear indication of large areas of high or low frequency comparable to those found in British C. nemoralis populations.

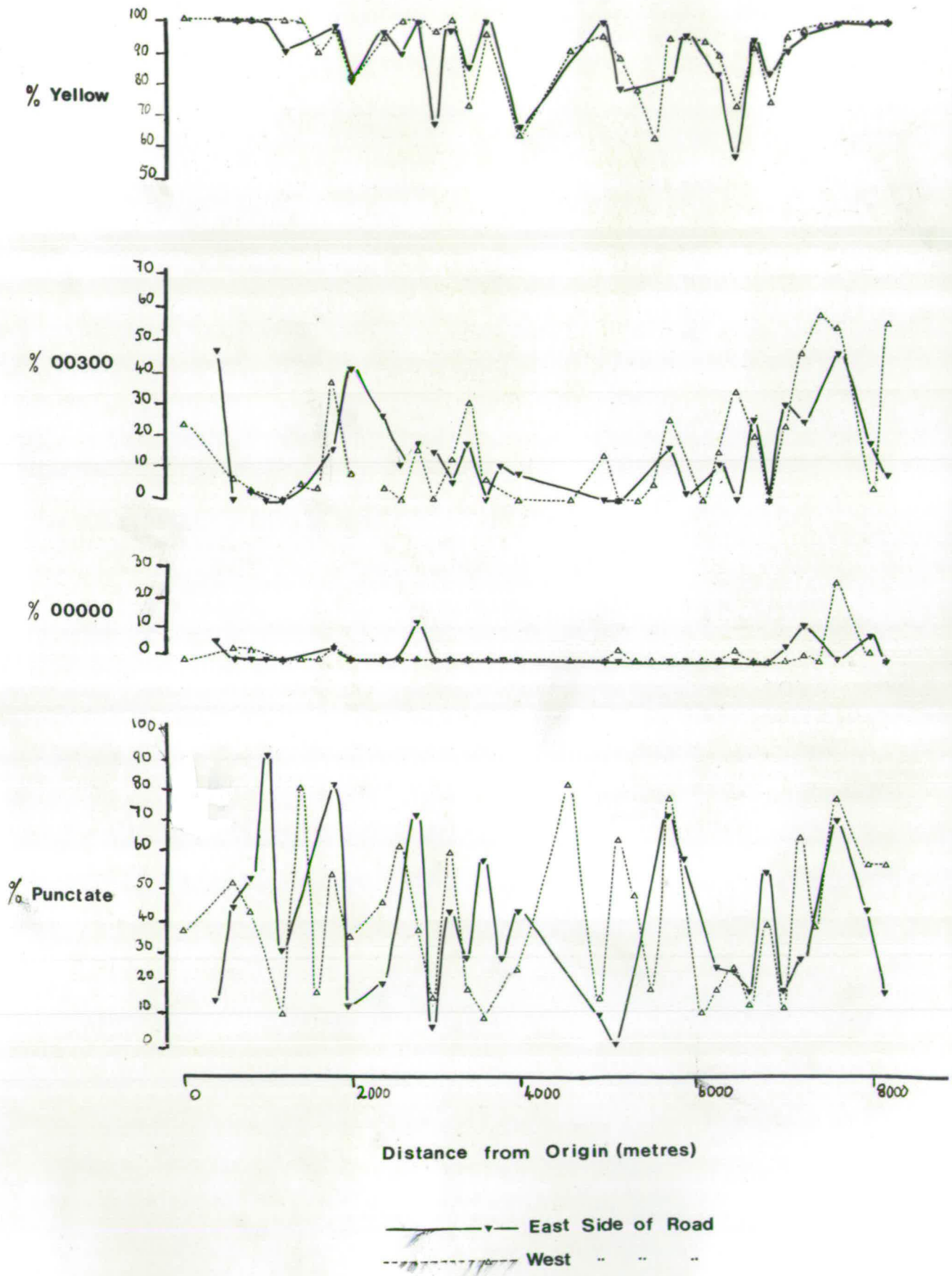
The pattern of distribution of the colour and the banding morphs was compared by means of a transect across the main area effect for presence of pink. (Rapajin Do., Rapajici, Brlog Stacija and Kompolje samples). 46 localities at 200 metre intervals along the main Otocac - Zuta Lokva road were examined. The road, which is approximately 15 metres wide, is bordered along most of its length by rather uniform hedgerows of blackthorn (Prunus spinosa) and hawthorn (Crataegus) fronted by a ditch containing long grass and broad-leaved vegetation and overhung by occasional plum trees (Prunus domestica). Snails were found only on the hedgerow, and not in the ditch or on the trees. Wherever possible, pairs of samples were collected on opposite sides of the road, although at many localities a suitable hedgerow was present on one side only.

Figure 7 shows the morph frequencies along the transect. There are marked differences in the patterns of distribution of the various morphs. Yellow shells are at a frequency of 100% at the North and South ends of the transect, and this morph is also at fixation for at least 5 km. in

Figure 7.

Fig. 7. Morph Frequencies along the Transect.

Origin is at South end of transect.


% Yellow
100
90
80
70
60
50
% 00300
70
60
50
40
30
20
10
0
% 00000
30
20
10
0
% Punctate
100
90
80
70
60
50
40
30
20
10
0
0
2000
4000
6000
8000
Distance from Origin (metres)
East Side of Road
West

each direction North and South of this series of samples. Pink shells make their appearance approximately 1400 metres from the South end of the transect and become more common until a frequency of 45% pink is reached (8800 metres). The frequency of this morph then drops gradually until the gene for yellow shell colour again reaches fixation at 10,000 metres from the South end of the transect. Unbanded shells are at a very low frequency in this region, so that it is rather difficult to ascertain any regularities in their distribution within the transect. There is a tendency for this morph to be relatively commoner at the North and South ends of the transect.

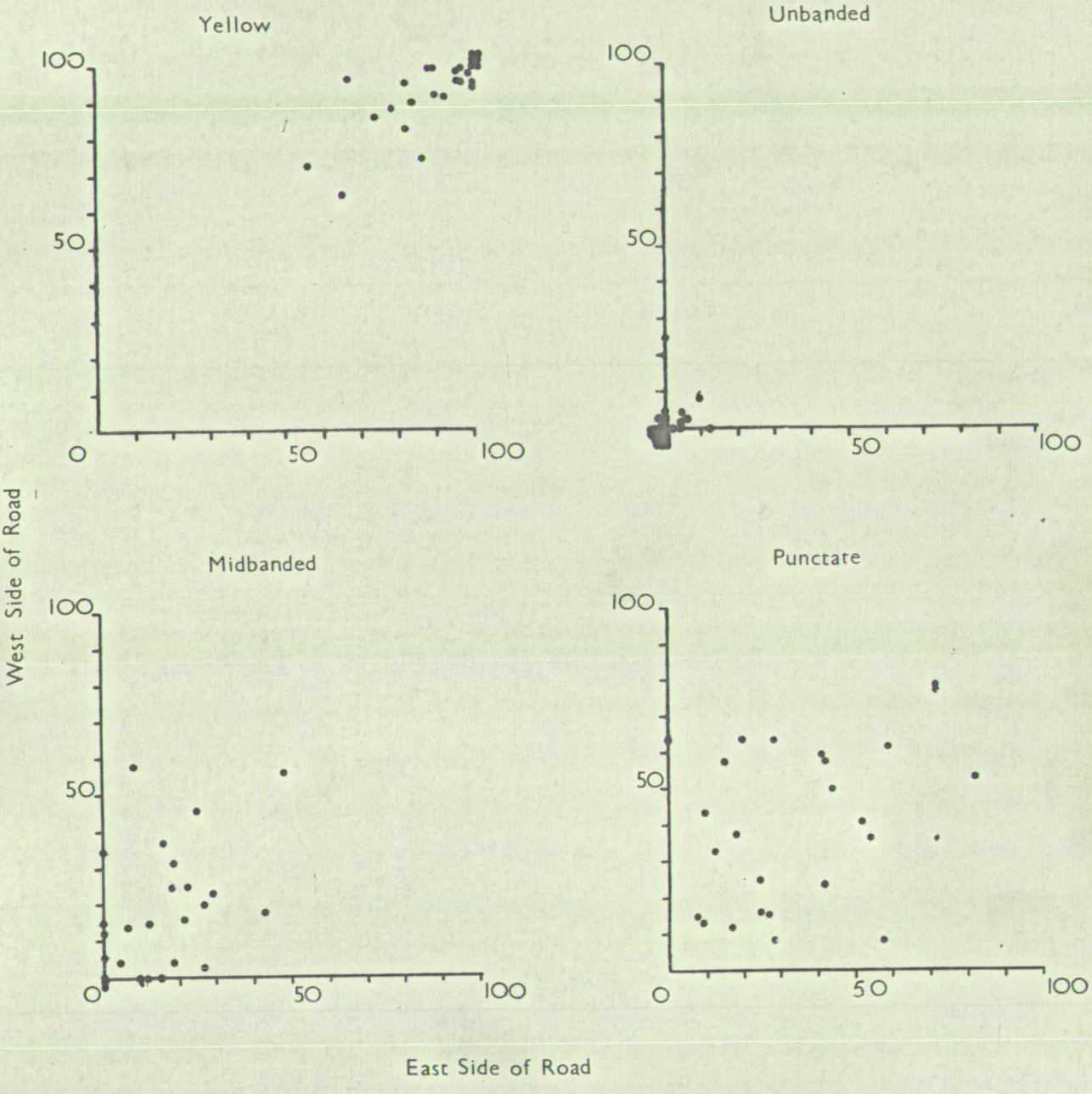
There are violent fluctuations in the frequency of midbanded and punctate shells along the transect. This is particularly marked in the case of punctate bands, which varies in frequency by 60% within 200 metres in several places. No consistent trends in the frequency of these morphs are visible along this 9-kilometre length of hedgerow, and this reflects the situation found in the study area as a whole.

Comparison of gross morph frequencies over all samples on opposite sides of the road gives no evidence of any tendency for one side of the road to differ from the other in the overall frequency of any morph. The microgeographical distribution of morphs was investigated by comparing morph frequencies in the 26 pairs of samples collected on sides of the road (fig. 8). There is a very significant positive correlation between the frequency of pink shells on opposite sides of the road (Spearman rank correlation coefficient $r_s = 0.69 : p < 0.001$). The correlation between the frequency of midbanded shells is barely significant ($r_s = 0.30 : p < 0.05$). There is formally no correlation between the frequency of unbanded shells on opposite sides of the road ($r_s = 0.22$: N.S.) but as the overall frequency of this phenotype is so low, not much can be deduced from this.

There is therefore very intense geographical differentiation of the frequencies of the genes controlling the midbanded and punctate band

Figure 8.

Fig. 8. Comparison of Morph Frequencies in Pairs of *C. nemoralis* samples.


Yellow
Unbanded
Midbanded
Punctate
100
50
0
50
100
West Side of Road
East Side of Road

phenotypes over a distance of only 15 metres across a road.

DISCUSSION.

Two aspects of the structure of these populations will be discussed; these involve comparison of their overall morph frequencies with those of populations elsewhere in the species' range, and consideration of the geographical distribution of morphs within the area studied.

1) Comparison with other populations.

The distribution of the frequencies of the major morphs throughout the range of C. nemoralis is considered in more detail in chapter 2 of this thesis. Factors affecting the average frequencies of these morphs in Yugoslavia compared to Britain will not therefore be discussed at length here.

The frequency of yellow shells is much higher in these Southern peripheral populations than in Britain. Comparison of the climates of the Velebit and the South of England shows that the Yugoslav populations are living in much warmer conditions than are the British. The mean Summer temperature (May - September) of the Gacka region is approximately 18.0°C, while that of the Marlborough Downs is approximately 15.5°C (Hidromet. Zav, N. R. Hrvatske 1958, Booth 1966). Similarly, the mean temperature in the warmest month is 20.5°C in the Gacka compared to 16.0°C on the Downs.

Although the Yugoslav study area is much warmer than the Marlborough Downs, there is little difference in the rainfall of the two regions. The average precipitation during the Summer half year (April - September) is approximately 450 mm. in the Gacka area, compared to approximately 380 mm. on the Downs (Ministry of Housing, N.D.). This difference is a relatively minor one in pluviometric terms; thus, even within the South of England the summer rainfall varies from 500 mm. in Cornwall to 220 mm.

in London, while the mean summer temperature varies only from 15.5°C. to 17.0°C. The average relative humidity in the Summer months is also rather similar in the Velebit and the South of England (Thran & Broekhuizen 1965). The total amount of summer rainfall does not appear to be of primary importance in determining the differences in morph frequency between peripheral and central populations.

It therefore seems that the warm conditions at the Southern limit of the species' range favour the yellow phenotype over the pink and brown, although they have less effect on the frequencies of the major banding morphs when compared with those in British populations. This conclusion is in agreement with the results of a comparison of morph frequencies with climate throughout the range of C. nemoralis (chapter2). Shell colour thus appears to be more responsive to the effects of climate than is shell banding. There is a considerable body of evidence (which will be discussed in the following chapters) from other investigations on Cepaea suggesting that the genes controlling shell colour are more susceptible to identifiable environmental selection than are the banding genes. This may be relevant to our understanding of the causes of area effects in this genus (see General Discussion).

ii) Distribution of Morph Frequencies within the Velebit Populations.

The distribution of morph frequencies within these populations shows several interesting features which may be valuable to an investigation of the factors causing area effects in Cepaea.

a. Associations with Background.

Most of our samples were collected from a restricted range of background vegetation. It is therefore rather difficult to establish any correlation which may exist between morph frequency and background from these collections. There is little evidence that visual selection is

having an effect on colour morph frequencies. Only one out of six samples from dense beech woodland contains pink shells; this proportion is not significantly different from that found in non-woodland samples. There is also no evidence that banding morph frequencies are affected by selective predation. Predated shells make up less than 1% of the total collected, and at least on the basis of this evidence it seems unlikely that predation involving shell breakage is an important selective factor in these populations.

b. Associations with Topography.

The survey area shows very striking variations in topography, which are discussed at length in chapter 3 of this thesis. Large basins surrounded by mountains are the main relief feature. These basins are known to be very active frost hollows when cold air flows into them from the mountain-sides on clear nights (see chapter 3 for references). C. nemoralis was found both in the basins and on the hillsides, and has a range of height from 420-670 metres above sea level. I have attempted to investigate any associations which may exist between morph frequency and a sample's location in a basin or on a hillside, and between morph frequency and height.

The great local variation in intensity of sampling (with a large excess of samples being collected in one low-lying basin) and the highly skewed distribution of most phenotype frequencies makes statistical analysis of this data very difficult. Simple tests of the association between morph frequency and height above sea level, and morph frequency and a measure of the sample's association with a basin (the inter-contour distance - see chapter 3) using the methods of rank correlation (Kendall 1948) give several highly significant association between the frequency of all morphs and height above sea level, and a highly significant association between the frequency of pink shells and inter-contour distance.

These apparent associations are, however, clearly greatly affected by the disproportionately large number of samples collected in the transect across Srpsko Polje basin at 420m. above sea level. Omission of this small region (less than 2% of the whole survey area)from the analysis causes radical changes in the sign and magnitude of the correlation coefficients. I have attempted to separate the effects of topography on morph frequency from geographical effects due to uneven intensity of sampling by comparing morph frequencies in sample pairs.

Starting at the South-West corner of the survey area, samples were paired with the nearest sample at a different height. A radius equivalent to the distance between the two samples was drawn round each member of the pair. The adjoining sample pair was taken as the nearest pair of samples which could be set up without their twin radii overlapping those of the first pair. A similar process was carried out for samples with different values of the inter-contour distance index. In this way the effect of disproportionately large numbers of samples in some regions is minimised - for example, the Srpsko Polje-Kompolje area provides only 4 sample height pairs, although over 60 samples containing ten or more snails were collected in this region.

Comparison of morph frequencies in the 27 such pairs of samples at different heights, and 12 pairs with different inter-contour distances shows no significant association of the frequency of any morph with either of these variables over the survey area as a whole. The main area effect for presence of pink shells is in a basin, and the boundaries of this area effect coincide fairly closely with the edges of the basin. However, some large basins do not contain any pink shells, and pink shells occur sporadically in samples from the hillsides.

It is possible that the existence of an area effect for the presence of pink, the darker shell colour, in the Srpsko Polje-Kompolje basin (which is known to be an active frost hollow - see Chapter 3) represents a selective response by these populations to microclimate similar to that found in *C. nemoralis* on the Marlborough Downs (where dark brown shells predominate in frost hollows) and in *C. vindobonensis* in the Velebit

mountains (see chapter 3). It is, however, difficult to draw final conclusions on any association of morph frequency with topography which may exist in the populations described in this chapter, as only one area effect for pink shell colour can be distinguished and as the frequency of the banding morphs shows great local fluctuation.

c. Microgeographical Distribution of Morphs.

The pattern of distribution of allele frequencies at the colour locus differs somewhat from that found at the loci controlling shell banding. One large region has an overall frequency of pink shells which is clearly different from that found elsewhere in the survey area, while none of the banding morphs show such clear large-scale differentiation of morph frequency. Differences in the microgeographical distribution of morphs will be discussed here with particular reference to the transect described earlier in this chapter.

This series of samples shows that populations separated by only fifteen metres across a road may have very different frequencies of the alleles controlling the midbanded and punctate shell banding patterns, but tend to have rather similar frequencies of the alleles at the colour locus. The pattern of gene frequency distribution along the road is much the same as that found on comparing pairs of samples. Although the 200 metre interval between samples is too great to permit detailed analysis of the fluctuations in frequency of midbanded and punctate along the road, there appear to be many very steep clines in the frequency of these morphs, with no clear trends in their frequency in the area as a whole. The samples in the central part of the transect have a frequency of pink shells which clearly differentiates them from the samples at the North and South ends. The structure of these populations is rather similar to that of the populations in longitudinal habitats described by Goodhart (1962) on an artificial

river embankment and by Wolda (1969a) along roadsides in Holland. The degree of local differentiation at the banding loci in Yugoslavia is even greater than that found in these English and Dutch populations.

The region of moderately elevated frequencies of pink shells which is traversed by the transect is clearly different from the rest of the survey area in its frequency of the shell colour alleles, and seems to be similar to the area effects described by Cain & Currey as there is a relative constancy of morph frequency over an area vastly larger than C. nemoralis' panmictic unit. The uniformity of habitat in the transect region makes it difficult to establish that lack of correlation with background which is, strictly speaking, part of the definition of an area effect. The very small regions of high or low frequency of the alleles for midbanded and punctate shells may or may not represent a phenomenon closely analagous to the area effects on the Marlborough Downs and elsewhere; this problem is discussed by Wolda (1969a). In any event investigation of such localized patterns of gene distribution in Cepaea is likely to provide valuable information on factors which may control gene distribution on a larger scale in this genus.

Unfortunately there is at present no information on gene flow in these populations. Borg (quoted by Wolda 1969a), who worked on Dutch population in which morph frequencies varied in the same way along opposite sides of a road found that 2-3% of the adult population crossed the road during one active season. Simple measurement of the movement of individuals is likely to give an overestimate of the amount of gene flow as the reproductive success of emigrants is often considerably less than that of animals in their home population (Labine 1966, Ehrlich & Raven 1969). Lomnicki (1964) has shown that Helix pomatia introduced into a natural population are likely to survive less well than are the native snails.

This species also shows strong homing behaviour (Edelstam & Palmer 1950), as may C. nemoralis (Cain & Currey 1968). This will also tend to lead to overestimation of the probable amount of gene flow from simple measurement of the short-term movement of individual snails.

Movement of Cepaea along linear habitats which are not interrupted by a barrier is more extensive than the movements described by Borg (Goodhart 1962, Day & Dowdeswell 1968). We rarely saw live snails in the herbage below the hedgerow along which the transect was taken, and never on the road itself, although they were continuously distributed along much of the hedgerow.

It therefore seems likely that gene flow in our study area will be much less restricted along the hedgerows than across the road. The net amount of gene flow is probably less than in the populations studied by Borg, Goodhart and Wolda; Cepaea's movement is very dependent on the amount of moisture available as the snails aestivate under dry conditions (Cameron 1970). Although total rainfall in the Velebit mountains is similar to that on the Marlborough Downs, rain falls as torrential storms separated by long dry periods (Hidromet. Zav. 1958), so that the snails are inactive for long periods of time. The road is therefore likely to be a fairly effective barrier to snails.

The road is approximately fifteen metres wide. It is rather difficult to envisage the nature of a microclimatic selective agent which could show consistent differences in its mode of action over distances as short as this, particularly in the topographically uniform region of the transect. The The divergence in banding morph frequency on opposite sides of the road may therefore be due to factors other than environmental selection. As discussed above, gene flow across the road is probably somewhat restricted. It therefore appears that genetically rather isolated

populations living close together show consistent differences in the frequencies of midbanded and punctate shells, but tend to have similar frequencies of pink shells. This suggests that environmental factors are less important in controlling banding morph frequency in these populations than are factors associated with gene flow, while the similar climatic environments found in pairs of samples separated by fifteen metres give rise to rather similar frequencies of the alleles at the colour locus.

The pattern of gene distribution in the transect appears to represent a situation where banding morph frequencies vary in a way which is rather independent of the environment, while the frequencies of the colour morphs appear to be more responsive to the effects of environmental selection. Several apparently similar instances of this phenomenon will be discussed later in this thesis. These populations provide an unusual opportunity to investigate the effects of gene flow on population structure. It will clearly be necessary to estimate the amount of gene flow across the roads and along the hedgerows and to examine the structure of populations separated by similar distances along the hedgerow as across the road before finally accepting or rejecting the argument discussed here on the effects of genetic isolation on C. nemoralis populations living in very similar environments. I hope to be able to carry out this research in the future.

Both the investigation of microgeographic distribution of gene frequencies in this southern peripheral population and comparison of its overall morph frequencies with those elsewhere in C. nemoralis' range have provided valuable information on factors which may affect the genetic structure of Cepaea populations. The following chapter extends the investigation of large-scale variation in gene frequency in C. nemoralis to include populations throughout the species' range.

CHAPTER 2

THE DISTRIBUTION OF MORPH FREQUENCIES THROUGHOUT THE RANGE OF *CEPAEA NEMORALIS*.

Most previous research on *Cepaea* has been concerned with the detailed investigation of populations living in a restricted area. Several authors claim to have detected local variations in the frequency of some morphs in *C. nemoralis* which appear to be correlated with microclimate, although the general importance of local climatic factors in controlling area effects in *Cepaea* remains a matter of some controversy. Any genes which do show a selective response to microclimate might be expected to show changes in frequency throughout the range of *C. nemoralis* which can be correlated with large scale climatic trends. Such a situation is known to occur in *Drosophila*. In *D. robusta*, for example, the frequency of some inversions changes by up to 60% over 12 kilometres with a height range of 1000 metres in the Smoky Mountains, and by a similar amount in 1000 kilometres from the North to the South of the species' distribution in the U.S.A. (Carson 1958a). This chapter reports the results of an investigation of geographical variations in morph frequency throughout the range of *C. nemoralis*.

There have been some previous attempts to detect climatic trends in *Cepaea* populations, although as they have been based on limited data they have in general not been very successful. Cain and Currey (1963b) quote what little information is available on the geographical distribution of dark brown shells in *C. nemoralis* as evidence for their climatic theory of the causes of area effects. Lamotte (1966) considers that in French populations of this species there is a positive relationship between the frequency of unbanded shells and mean July temperature, and a negative one between the frequency of yellow and mean January temperature. These

results are based only on a consideration of four climatic zones in France. Central European populations have been investigated by Schilder & Schilder (1957), who were unable to find any associations between morph frequency and climate.

I have attempted to bring together all available data on C. nemoralis populations, and to investigate any association of morph frequency with a number of climatic variables.

Information about morph frequencies has been obtained from several sources.

i. Great Britain.

Data on British C. nemoralis populations from the following papers are incorporated in this survey: Cain 1968; Cain & Currey 1963b; Cain & Currey 1963c; Cain & Sheppard 1950; Cain & Sheppard 1952; Cain & Sheppard 1954; Cameron 1969; Carter 1968; Clarke 1962; Clarke & Murray 1962; Currey, Arnold & Carter 1964; Currey & Cain 1968; Day & Dowdeswell 1968; Goodhart 1956; Goodhart 1958; Goodhart 1962; Murray 1966; and Sheppard 1952.

The following unpublished data were also utilised: Arnold 1966; manuscripts of Captain C. Diver held in the British Museum (Natural History); Jones 1966; personal communications from Mr. D.A. Briscoe, Professor A.J. Cain, Professor B.C. Clarke, Mrs A.W. Ford, Dr. J.J.D. Greenwood, Mr. P. Harvey, Mr D. Heath, Mrs. N.F. Macmillan, Mr. C.R.D. Reynolds, and Mr T. Warwick. I am grateful to all these individuals for allowing me to make use of their unpublished samples. My own unpublished collections in Scotland are also included in the survey.

Morph frequencies in British C. nemoralis populations arranged on the basis of the ten kilometre squares of the National Grid are given in table 2. Figure 9 shows the distribution of these C. nemoralis samples in Britain.

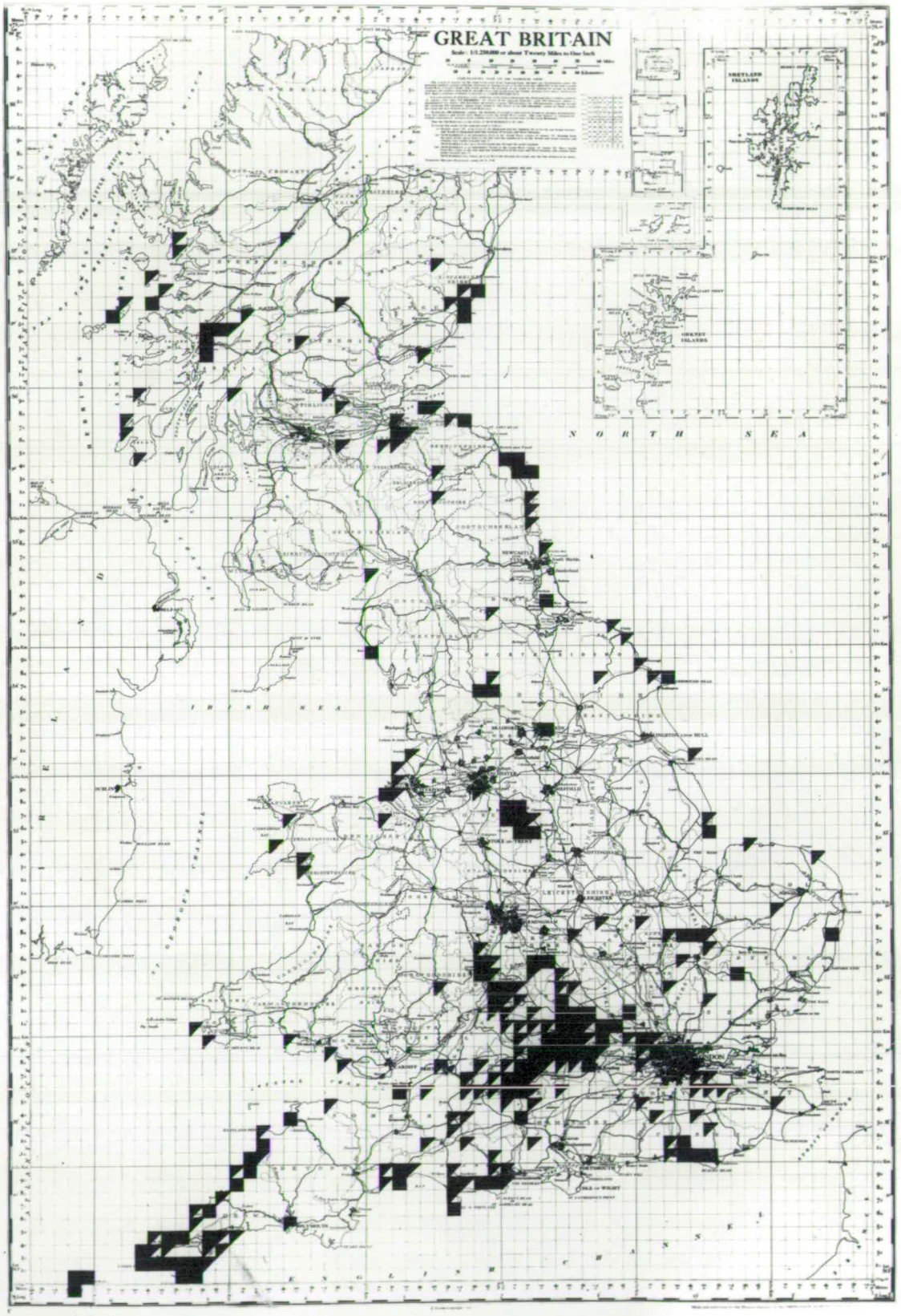
British samples were lumped together for the purposes of this survey

Figure 9.

Fig. 9. Distribution of Cepaea nemoralis Samples in Britain.

■ 10-kilometre squares containing at least 100 snails in 5 or more separate samples.

◤ 10-kilometre squares containing less than 100 snails, or more than 100 snails in less than 5 separate samples.


GREAT BRITAIN
Scale : 1/1,250,000 or about Twenty Miles to One Inch
SHETLAND ISLANDS
ORKNEY ISLANDS
NORTH SEA
IRISH SEA
ENGLISH CHANNEL

on the basis of the 100-kilometre squares of the National Grid. As there is often very great local variation in morph frequency, only squares containing at least 500 snails from five or more separate ten-kilometre grid squares were used in the analysis. Most squares contain far more snails than this - for example, square SU (South Central England) contains 34,872 C. nemoralis from 32 10-kilometre squares. The Scottish 100-kilometre squares in general contain fewer snails than do the English.

Only samples containing at least twenty shells were used when plotting morph frequency histograms for English populations. Samples containing at least ten shells were utilised for the Scottish histograms. Banding morph frequencies are computed among non-brown shells only, as dark brown snails show disturbances in the expression of shell banding. The frequency of midbanded snails is expressed as a percentage of banded shells, as the gene for absence of bands is epistatic to that giving rise to the midbanded phenotype. For the same reason, the frequency of 00345 shells is computed among shells with three or more bands. In the morph frequency histograms for banding, only samples containing at least twenty (or in Scotland at least ten) non-brown shells are used. The frequency of midbanded and trifasciate shells is computed only in samples containing at least ten shells capable of expressing these characters.

ii. Ireland.

Irish sample scores are taken from the papers of Cain 1968; Cameron 1969b; Clarke, Diver & Murray 1968; Cook & Peake 1960; and Cook & Peake 1962. Some Irish samples were taken from the manuscripts of Captain C. Diver held in the British Museum (Natural History). I am grateful to Dr. J.J.D. Greenwood for making a number of his unpublished Irish samples available to me. Mrs. N.F. McMillan of the Liverpool City Museum kindly allowed me to score and utilise her own samples, and made available a large number of

unscored random samples collected by Mr A.W. Stelfox and Mr R. Welch in the early part of this century. I am indebted to Mr Stelfox for information about his samples and for permission to score them and to use them in this research.

Irish samples were lumped together on the basis of the 100-kilometre squares of the Irish National Grid. As in the case of Great Britain, only squares containing at least 500 snails from five or more 10-kilometre grid squares were used in the analysis of the association of morph frequencies with climate. Morph frequencies for use in morph frequency histograms were calculated using the same criteria as those applied to Scottish samples.

iii. France and Spain.

The most important source of data on these regions is the work of Lamotte (1951, 1959, 1966). Lamotte, without giving details of individual samples, groups his results on the basis of arbitrarily defined sub-divisions of France (for example, "Paris region", "Massif Central"), and I have retained this arrangement. Most ofhis regions contain a very large number of snails, although one ("Mediterranean Region") has only 674 shells. The data of Guerrucci-Henrion (1966) (Brittany) and Arnold (1968) (Pyrenees) has also been utilised, together with the results of my own unpublished collections in the Eastern Spanish Pyrenees.

The frequencies of midbanded and trifasciate shells in French and Spanish samples have been corrected as far as possible for the effects of epistasis as described above. It has not been possible to correct banding morph frequencies for the effect of the gene for dark brown shell colour, as Lamotte does not state the frequency of dark brown shells in his samples. It seems likely, however, that this morph is relatively rare in France (Arnold 1970, Lamotte 1951, Cain & Currey 1963a). Morph frequency histograms have been extracted directly from the publications of Lamotte. To these I have added morph frequencies from the sources

described above, computed according to the criteria used for English samples.

iv. Central and Eastern Europe.

A large amount of information on C. nemoralis from these regions has been published by Schilder & Schilder (1957). I have analysed only their German data, as their samples from other regions are often very small (for example, there are less than 100 snails from the whole of Italy) and as many of their non-German samples are taken from the literature or from museum collections, which often do not represent a random sample of the snail population living in the collection area. Most of the German samples were collected at random by the authors themselves, and are therefore suitable for inclusion in this survey. Schilder & Schilder's samples are grouped together in their paper on the basis of German "Lander", and this arrangement has been retained. Morph frequencies in their distribution maps are given only to the nearest 10% (or in some cases to the nearest 20%). I have taken morph frequency as the average of the frequencies given in their maps, so that a frequency of 15%, for example, is assigned to one of "10-20%". I have also made corrections for epistasis as far as possible.

Unfortunately Schilder & Schilder's data are presented in such a way as to make it impossible to extract sample scores from their tables. I have therefore not been able to prepare histograms of morph frequency for German C. nemoralis populations.

Samples from Southern peripheral populations in Yugoslavia (chapter 1) have also been included in the survey. Almost all these samples originate from one 100-kilometre square of the Yugoslav National Grid.

The whole analysis is based on approximately 505,000 C. nemoralis (see table 3).

Climatic Data.

Information on climate was gathered from several sources. British (together with some Irish) climatic data are tabulated in the publications of the Meteorological Office (Booth 1963, 1966, Ministry of Housing, N.D.). Most of the information on European climate was extracted from the work of Thran & Broekhuizen (1965), who give a large number of readings from some five hundred meteorological stations throughout Europe. Supplementary works were consulted for sunshine data (Arlery 1961, Atlas de France, N.D., Meteorological Office, 1956), and for information on the climate of the Pyrenees and of Yugoslavia (Hidromet Zavod NR Hrvatske 1958; Nuevo Atlas de España, 1961.)

In places where there is much climatic variation within the region where the snails were collected, I have attempted to give an "average climate" for the whole area. In mountainous regions I have taken the average near the midpoint of C. nemoralis' range of height. This reduces distortions due to climatic readings from high mountain peaks.

The Distribution of Morph Frequencies.

Figs. 10-13 show the distributions of colour and banding morph frequencies throughout Britain and Europe. There is a large amount of variation in the frequency of all the morphs. The average frequency of yellow varies from 16% (North-East Scotland) to 97% (Eastern Spanish Pyrenees), of unbanded from 1% (North Wales) to 63% (Spanish Pyrenees), of midbanded from approximately 0% (North Germany) to 79% (Derbyshire) and of trifasciate from 0% (Scotland) to approximately 70% (Central Germany). This species therefore shows almost as much variation in morph frequency on a large scale as on a microgeographic one.

There is an obvious general tendency for the frequency of yellow to be higher in the Southern part of C. nemoralis' distribution. None of the

Figure 10.

Fig. 10. Frequency of Yellow Shells in British and European Populations of C. nemoralis.

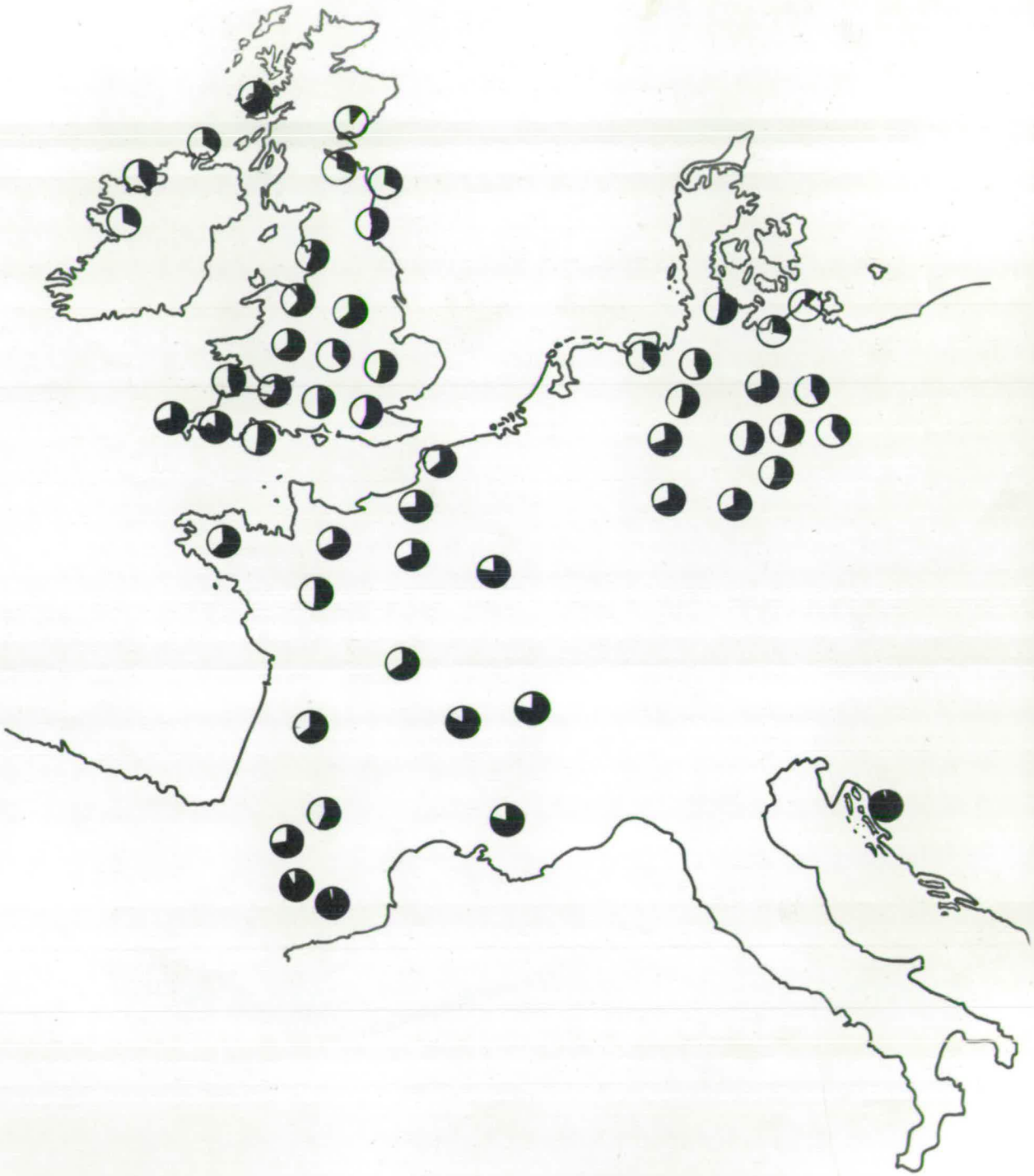


Figure 11.

Fig. 11. Frequency of Unbanded Shells in British and European Populations of C. nemoralis.

Figure 12.

Fig. 12. Frequency of Midbanded Shells in British and European Populations of C. nemoralis.

Figure 13.

Fig. 13. Frequency of 00345 shells in British and European Populations of C. nemoralis.

banding morphs show such a tendency, and regional variation in banding morph frequency do not show any detectable relationship to the region's distance from the Northern or Southern limits of the species' range. This is clearly demonstrated in the morph frequency histograms shown in fig. 14. These histograms also show that the higher frequency of yellow in the Southern part of the range is not due merely to the presence of a number of large samples with a disproportionately high frequency of this morph distorting the real frequency of yellow shells in these areas, but represents a genuine North/South cline. The median frequency of yellow rises from 39% to 49%, to 58%, to 65%, to 95%, to 100% with distance from C. nemoralis' Northern limit. None of the banding morphs show such regular clines. There is a tendency for the median frequency of unbanded to be higher in some Southern populations (particularly in the Pyrenees), but this tendency is reversed in the Yugoslav Southern peripheral populations, which have an extremely low frequency of unbanded shells. There are no detectable regularities in the frequencies of midbanded or 00345 shells.

Associations of Morph Frequency with Climate.

A multiple regression analysis was carried out of the association of the frequencies of yellow, unbanded, midbanded and trifasciate shells with summer (May - September) mean temperature, January mean temperature, July mean temperature, mean maximum temperature in the hottest month, hours of bright sunshine in summer, and precipitation in the summer half - year (April - September). There is a significant positive association of the frequency of yellow shells with climate, the best relationship being with summer mean temperature ($Y = -84.6 + 9.1X$: $p<0.001$) (fig. 15). The frequencies of unbanded and midbanded are not significantly associated with any of the climatic variables tested. There is a negative regression of the frequency of trifasciate on January mean temperature ($Y = 25.1 - 4.8X$: $p<0.001$). It is difficult to decide whether this is due to a

Figure 14.

Fig. 14. Morph Frequency Histograms for British and European Populations of C. nemoralis.

The continuous lines connect median frequencies in each area.

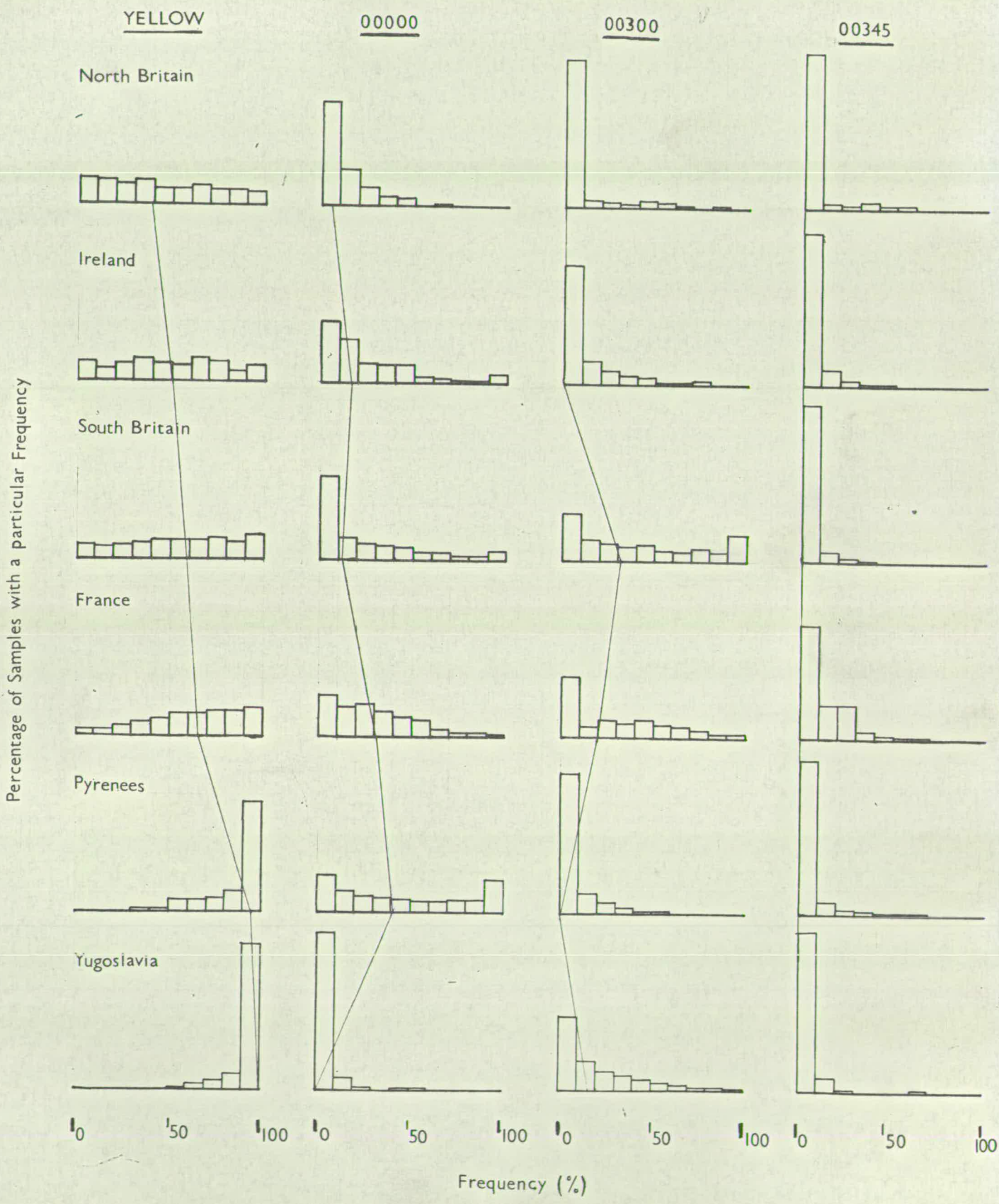
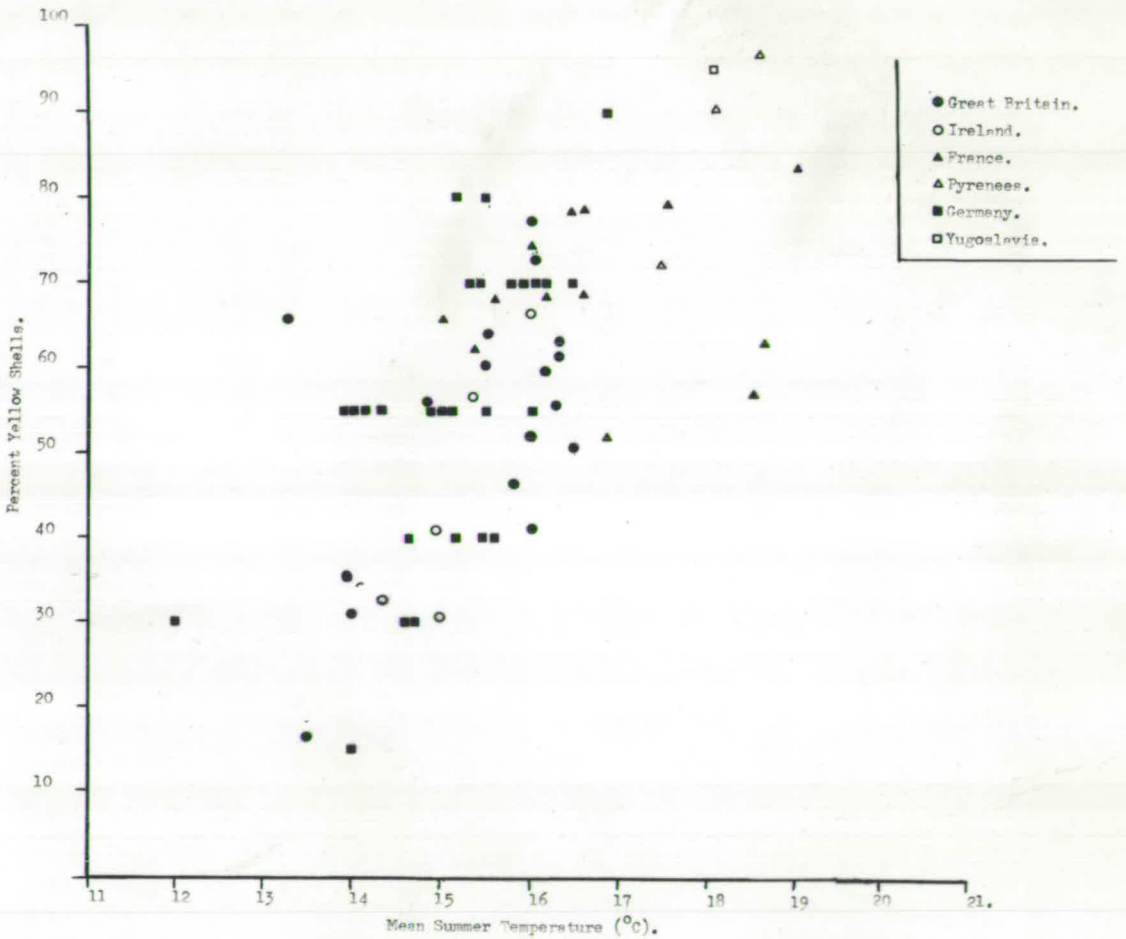

YELLOW
00000
00300
00345
North Britain
Ireland
South Britain
France
Pyrenees
Yugoslavia
Percentage of Samples with a particular Frequency
0
50
100
Frequency (%)

Figure 15.

Fig. 15. Association of the Frequency of Yellow Shells with Mean Summer Temperature in British and European Populations of *C. nemoralis*.


100
90
80
70
60
50
40
30
20
10
Percent Yellow Shells.
11
12
13
14
15
16
17
18
19
20
21.
Mean Summer Temperature (°C).
Great Britain.
Ireland.
France.
Pyrenees.
Germany.
Yugoslavia.

genuine climatic effect, however, as a large part of this association is clearly due to the presence of several samples in one part of Germany (which has a very low January mean temperature) with a frequency of trifasciate shells far higher than that found elsewhere. It is therefore difficult to separate simple geographical effects in the distribution of this phenotype from those due to climate. This is unlike the situation found at the colour locus, as the association of the frequency of yellow shells with climate holds true throughout the range of C. nemoralis and is not unduly affected by one climatically extreme region with a high frequency of yellow. The gene for punctate banding is also at a high frequency in this area of Germany (Schilder & Schilder 1957); this may modify the expression of shell bands to give a trifasciate phenotype even when the major gene described by Cain et al (1968) is not present. In Yugoslavia, for example, the frequency of trifasciate rises from 2.4% among non-punctate shells to 14 % when punctate shells are included in the calculation. Wolda (1969) has shown that the 00345 phenotype may also be produced by multifactorial modification of the expression of other genes. The geographical distribution of this phenotype does not, therefore, reflect the distribution of any single gene at all accurately.

Discussion.

There is a very clear cline in the frequency of the gene for yellow shell colour throughout the range of C. nemoralis. None of the genes controlling the number of bands on the shell show such regularities in their distribution. The cline in colour morph frequency is not due simply to selective predation and to differences in the background upon which the snails live between Northern and Southern populations. Many of the most Northerly Scottish samples come from open habitats similar to those described by Cain & Sheppard (1954), while the majority of samples known

to originate from woodland are from the South of England and Northern France, in the central part of C. nemoralis' distribution. In any event, differences in habitat have a relatively small effect on overall phenotype frequencies throughout a region even when selective predation is known to be acting in one part of it. Omission of all woodland samples in the National Grid 100-km. square which includes the Oxford region changes the overall frequency of yellow only from 50.2% to 53.2% and that of unbanded from 20.2% to 18.1%. These habitat differences are much less marked than the geographical variation described in this chapter. At least some of this geographic variation shows a clear association with temperature.

Many ectothermic animals are known to possess dark-coloured forms in the colder parts of their distribution. Arctic insects frequently show black pigmentation which completely obscures wing-patterns found elsewhere in the range (Downes, 1962, 1964). Less extreme instances of melanism in cold climates are found in butterflies (Hovanitz 1942), moths (Kettlewell 1961), lady-beetles (Dobzhansky 1933), Collembola (Rapoport 1969), and in the snail Helicella itala (Cain et al 1969). This analysis of morph frequencies throughout the range of C. nemoralis has shown that the frequencies of at least the shell colour phenotypes in this species show a very similar association with climate, light-coloured yellow shells being at a high frequency in warmer regions, while the dark-coloured pink and brown phenotypes predominate in the cooler parts of the species' distribution. Any overall association of banding morph frequency with climate is weaker than that found at the colour locus.

Some of the minor genetic variants (but not the major banding genes) in C. nemoralis may also show this pattern of distribution. Shells with fused bands are at a much lower frequency in Yugoslavia (2.7% of shells capable of showing fusions) and the Ter valley (4.7%) than in Scotland,

which is the only part of Britain for which reasonably complete data are available (overall frequency of fusions = approximately 31%). This trend may be consistent over the whole of C. nemoralis' range (Schilder & Schilder 1957; see map 73). All the live snails collected in Yugoslavia and the Ter valley had light-coloured bodies; this contrasts with the situation found in Britain, where the body wall is often saturated with black pigment (Cain & Sheppard 1952; Jones, unpublished data). As punctate bands are common in North Germany (Schilder & Schilder 1957) the high frequencies of this phenotype found in the Pyrenees and in Yugoslavia are not part of a regular cline throughout C. nemoralis' range.

Some experiments on the temperature tolerance of different morphs in C. nemoralis accord with the observation that yellow shells are at an advantage in hot places, although with the exception of the work of Wolda (1963, 1965, 1967) our knowledge of the physiology of Cepaea is very limited. The response of C. nemoralis to environmental changes in experimental colonies may depend upon the region from which the snails originate rather than upon their shell phenotype (Wolda 1963); this finding casts considerable doubt on the value of physiological experiments in which the snails used do not all come from exactly the same locality.

Wolda (1963) investigated the survival of the different morphs in an artificial colony. Comparison of oviposition frequency in two summers showed that "red" (pink plus brown) snails tended not to oviposit much more frequently than did yellows in the warm and dry summer, but that there was no difference between colour morphs in the cool wet summer. There was no significant difference between summers in the oviposition frequencies of the various banding morphs. Different coloured shells also showed considerable differences in the variance of clutch size between the two years, but this was not apparent between the different shell banding morphs. Bandeds showed greater overall survival than unbandeds within the red shell

colour class, but survival differences between banding morphs were much less marked than were the fertility and survival differences between shell colour morphs. Results from this artificial colony are therefore generally in agreement with the patterns of association of morph frequency with temperature described here. Wolda's (1965a) finding that drought does not affect overall fertility of the different morphs differently also accords with my observation that morph frequency throughout the range of C. nemoralis is not correlated with rainfall. Laboratory experiments have not fully elucidated the nature of the selective action of temperature in the colony (Wolda 1967). The effects of high temperature were rather complex and depended on an interaction between colour and banding. The variance of clutch size in the laboratory was far greater than in the field experiments; these laboratory experiments probably do not represent the selective responses of different morphs in natural populations very accurately.

Sedlmair (1956) has also investigated survival in field experiments. She found that yellow C. hortensis survived better than pinks in a hot summer; in C. nemoralis, however, pinks survived better (although yellows were more active). Experiments on the survival of different C. nemoralis morphs are described by Lamotte (1959). Analysis of his data on the survival of 211 snails exposed to the heat of a strong bulb at 35°C for 40 hours shows that yellows survive better than pinks and unbandeds better than five-bandeds. Both these results are significant at the 5% level. Lamotte does not give the data for his other experiments, but examination of the percentage survival quoted after 40 hours at 35°C in a dry atmosphere shows that the differential survival of yellows over pinks is much greater than that of unbandeds over five-bandeds, and that to obtain a significant difference in survival of the banding morphs from these percentages it would be necessary to examine several thousand snails.

His percentage survival of snails kept at - 8°C for 3 hours shows a higher survival of yellows than pinks (a result opposite to that expected from the evidence described in this chapter and in the General Discussion) and of unbandeds than bandeds. To obtain significance for either of these results it would be necessary to use several times the number of snails used in the experiment for which Lamotte does provide full data. It seems unlikely that this number of snails was in fact examined; Lamotte's results are therefore of limited value in the investigation of any differences in temperature tolerance between morphs in Cepaea.

Much of the evidence available on differences in temperature tolerance between morphs accords with the observations described in this chapter that yellow C. nemoralis are more resistant to high temperatures than are pinks. There is some indication from laboratory experiments that the banding morphs may show differences in temperature tolerance; the evidence for this is in general less satisfactory than is that demonstrating differences between different coloured shells. The results of survival experiments are rather confused. Apparently contradictory results may often be due to using snails from different populations which show interpopulation differences in survival obscuring any differences in the resistance of the shell colour or banding morphs.

The probable mode of action of the selective agent responsible for these associations with climate, and the response of the various phenotypes to environmental selection will be considered at length in the General Discussion of this thesis. It is sufficient to mention here that there is a considerable amount of evidence showing that the colour of the body surface in many organisms has a marked effect on heat input in sunshine, and that this often has a profound influence on the animal's physiology and its ability to tolerate extreme temperatures. The association between the frequency of the shell colour morphs in C. nemoralis and environmental

temperature described in this chapter is likely to be due primarily to such differences in the efficiency of absorption of solar radiation by shells of different colours. The apparent lack of an overall association between banding morph frequencies and climate may reflect a general tendency for the frequencies of the genes controlling the number of bands on the shell to be less responsive to the effects of environmental selection than are the frequencies of the shell colour genes. Such differential responses to climatic selection may be relevant to our understanding of the forces controlling gene distribution in Cepaea on the microgeographical as well as on the large scale. This hypothesis is discussed at more length in the General Discussion of this thesis.

CHAPTER 3

AREA EFFECTS IN CEPAEA VINDOBONENSIS.

Introduction.

This chapter describes the pattern of variation in Yugoslav populations of the snail Cepaea vindobonensis Pfeiffer. C. vindobonensis has a much simpler system of shell polymorphism than does the more widely-studied C. nemoralis. Taylor (1914), for example, describes one hundred and sixty colour and banding variants in C. nemoralis, and it is easy to compute that even when the calculation is restricted to characters whose mode of inheritance is known there are over 20,000 possible combinations of the various alternatives for shell, lip and body colour, and number and pigmentation of the bands.

There are several instances where the study of a polymorphism in one species has given valuable information on an apparently homologous polymorphism in a closely related species. This is that case, for example, in the mimetic butterflies Papilio polytes, P. memnon and P. dardanus (Sheppard 1967). In the genus Cepaea, Clarke (1960) has shown that in some areas C. hortensis responds to differential predation by thrushes in a manner analagous to C. nemoralis, although it utilises different genes to achieve a similar effect. Any direct attempt to determine the relative importance of environmental selection and coadaptation in controlling gene frequencies in one species from investigation of a related species is, however, not necessarily valid. The sibling species D. pseudoobscura and D. subobscura, for example, have quite different genetic systems, D. pseudoobscura showing very marked coadaptive divergence between geographically separated populations (Vetukhiv 1953, 1954, 1956, 1957), while crosses between D. subobscura populations from as far apart

as Scotland and Israel show no sign of the F_1 heterosis and F_2 breakdown in fitness characteristic of coadaptation. (McFarquhar & Robertson 1963).

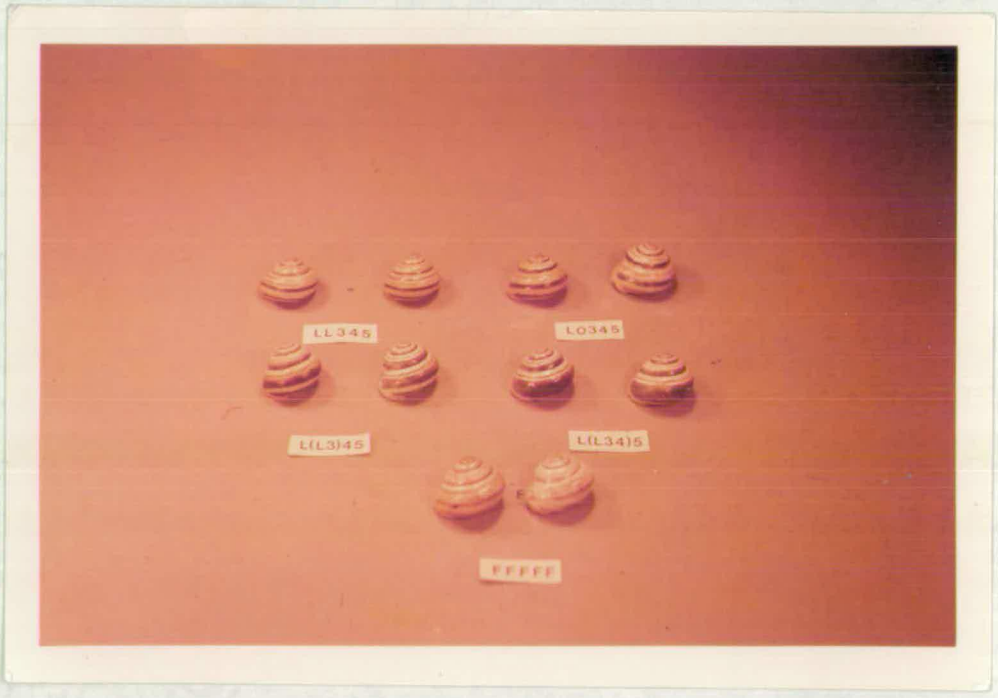
Four species of Cepaea - nemoralis, hortensis, sylvatica and vindobonensis - have been described (Perrot & Perrot 1938). C. nemoralis and C. hortensis populations have been investigated in detail in several places. C. sylvatica, which lives in the Alps, shows less variation than either of these species, and its population genetics has not been studied.

C. vindobonensis is the most Eastern species in the genus Cepaea, as it is distributed from Austria to the Caspian and from North Greece to Poland. It can be distinguished from other Cepaea spp. by the fine striations on its shell. There is no obvious polymorphism for shell ground colour, nearly all specimens being a uniform drab grey. Young shells sometimes appear to be slightly yellow, but this is due merely to the colour of the periostracum (which is bleached in older specimens), as can be shown by scraping off the periostracal layer.

C. vindobonensis has some banding polymorphism (fig 16), although it is not nearly as variable in this respect as is C. nemoralis. Most shells in my samples have five bands, although the second band is sometimes missing (band formula "10345"). A few other variants, such as 12045, occur at a very low frequency. Band fusions are often found, the most common types having the second and third ("1(23)45") or second, third and fourth ("1(234)5") bands fused together, although other fusions, such as 1(23)(45), also occur at a low frequency. Unlike band fusions in C. nemoralis and C. hortensis, in which the point on the shell where the bands fuse together is so variable that fusions can safely be scored only in adult shells, fused bands in C. vindobonensis always coalesce at a very early stage in shell growth. They can therefore be scored accurately even in young shells.

Figure 16.

Fig. 16. C. vindobonensis - Major Morphs.


LL345
LO345
L(L3)45
L(L34)5
FFFFF

C. vindobonensis also shows variation in the intensity of pigmentation of the bands. Bands 3, 4 and 5 are usually dark and heavily pigmented, but bands 1 and 2 are almost invariably narrow with reduced pigmentation, and are light brown in colour. I have called such bands "light" bands (designated by "L" in the band formula), giving morphs such as LL345, L(L3)45, etc. In some specimens, all the bands show reduction of pigmentation, so that the shell has five straw-coloured bands. The degree of pigment reduction may be so great that the shell appears on cursory examination to be unbanded, a condition that seems to be equivalent to Férussac's var. pallescens (see Schilder & Schilder 1957). No genuinely unbanded shells (var. balcanica) were found. I have called the banding pattern resulting from this type of reduction of pigment "faint" banding, and have designated such bands as "F" in the band formula. Faint banding is probably not homologous with morphs such as "orange banded" in C. nemoralis (Cain et al 1960) as the vindobonensis faint bands are lighter in colour than are orange bands and the lip colour of both faint and normal vindobonensis is brown. This is unlike the situation in nemoralis, where shells having the gene for orange bands also show alterations in the colour of the lip.

There is evidence of an interaction between fusions of the second and third bands and faint banding, as there is a very significant deficiency of F(FF)FF snails in samples containing LL345, L(L3)45 and FFFFF shells (sign test; $p < 0.001$). Because of this, the proportion of fusions of the second and third bands has been calculated among non-faint-banded snails only.

There is at present no direct evidence that the shell banding morphs in C. vindobonensis have a genetic basis (although a breeding programme has been started). As the very similar banding polymorphisms in C. nemoralis and C. hortensis are known to be genetically determined, it

seems likely that the polymorphism in C. vindobonensis will also be found to be under genetic control. The constancy and discrete nature of the banding variants may be considered as circumstantial evidence for the genetic basis of the variation. Faint banding is unlikely to be the result of a direct effect of the environment decolorising the bands, as faint-banded shells have a fully pigmented lip although the pigmentation of the bands may be greatly reduced.

The parallel between the genetic systems of C. nemoralis and C. hortensis is so close as to amount almost to complete homology, suggesting that the polymorphism may have developed before speciation took place (Cook & Murray 1966). C. vindobonensis and C. sylvatica differ from C. nemoralis and C. hortensis in a number of anatomical characters, and the two groups have different chromosome numbers (25 for vindobonensis and sylvatica; 22 for nemoralis and hortensis) (Perrot & Perrot 1938). The mechanism of inheritance of the shell banding morphs in C. vindobonensis may therefore be found not to be closely homologous with that in C. nemoralis and C. hortensis. In particular it seems possible that the mode of inheritance of band fusions may differ in C. vindobonensis. This character is much more clear-cut than in other species, and shows none of the continuous variation in the degree and time of onset of band fusion found in C. nemoralis which, together with the results of breeding experiments (Cain et al 1960, Wolda 1969c), suggests multifactorial inheritance of fusions in this species.

THE AREA STUDIED

The main area in which C. vindobonensis populations were investigated was in the Velebit Mountains of North Yugoslavia (fig 1).

The Velebit region was chosen in the first instance because C. nemoralis was known to reach the Southern limit of its range in the

area, and populations of this species were investigated in conjunction with those of C. vindobonensis (See Chapter 1). It also has the advantage of possessing a great deal of topographical variation, with abrupt changes from one type of topography to another, which might be expected to demonstrate very clearly any effects of topography and thus of microclimate on gene frequency distribution.

Most of the samples were collected within a region of approximately 100 kilometres by 30 kilometres, stretching from Jezerane in the North to Gracac in the South (fig. 1). The most detailed survey was carried out in the area drained by the River Gacka (fig. 17). The survey to the South of this (in the Lika drainage area) was considerably less intensive. (fig. 18)

The whole region forms part of a very extensive limestone massif. Most of the limestones are Cretaceous, but Jurassic limestones also occur. All the rocks have been extensively fractured and folded, and the topography is in general typically karstic. Because of solution of the limestone by rainwater, most of the water circulation is underground, and much of the surface becomes pitted by enclosed hollows of some hundreds of metres in diameter ("dolina"). As the limestone is very pure, solution of the rocks leaves little residue for the formation of soils, so that large areas have a very thin soil cover. The seaward slopes of the Velebit mountains (which are up to 1700 metres high in this region) have developed into a stony desert, although the Eastern slopes of the range show local exposures of shales and sandstones which have allowed the development of slightly more fertile soils (Anon. 1944).

Large basin - the "polja" - form a major relief feature in the area. They are usually formed by block faulting (Cvijic 1918), and are often very extensive - the main Lika basin, for example, has an area of some 200 square kilometres. The rivers which cross the basins have in the

Figure 17.

Fig. 17. The Gacka Survey Area.

Scale approximately 1:150,000.

Contours at 500, 600, 700 and 800 metres.

See also figure 1.

▲ Position of recording thermometers.

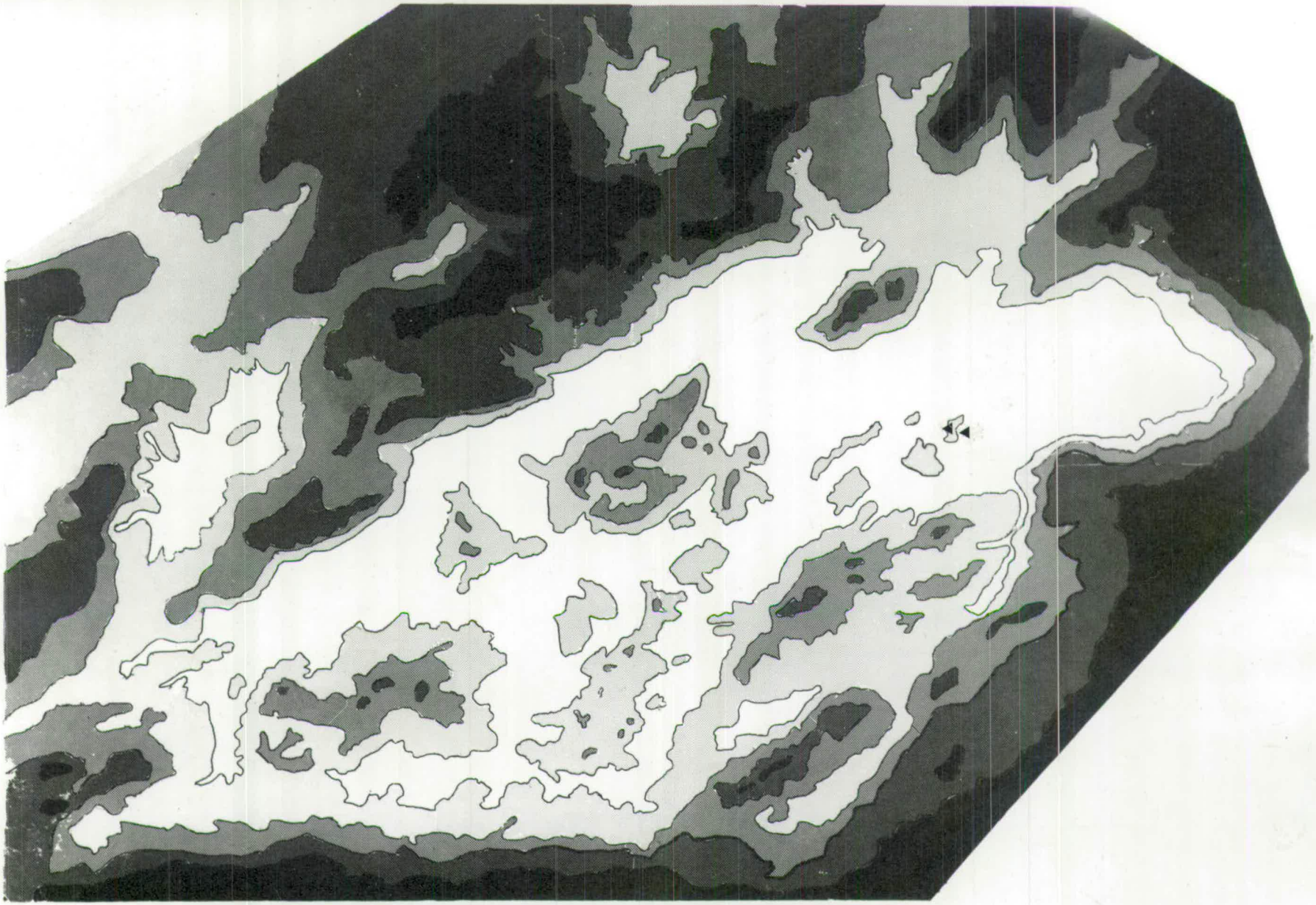


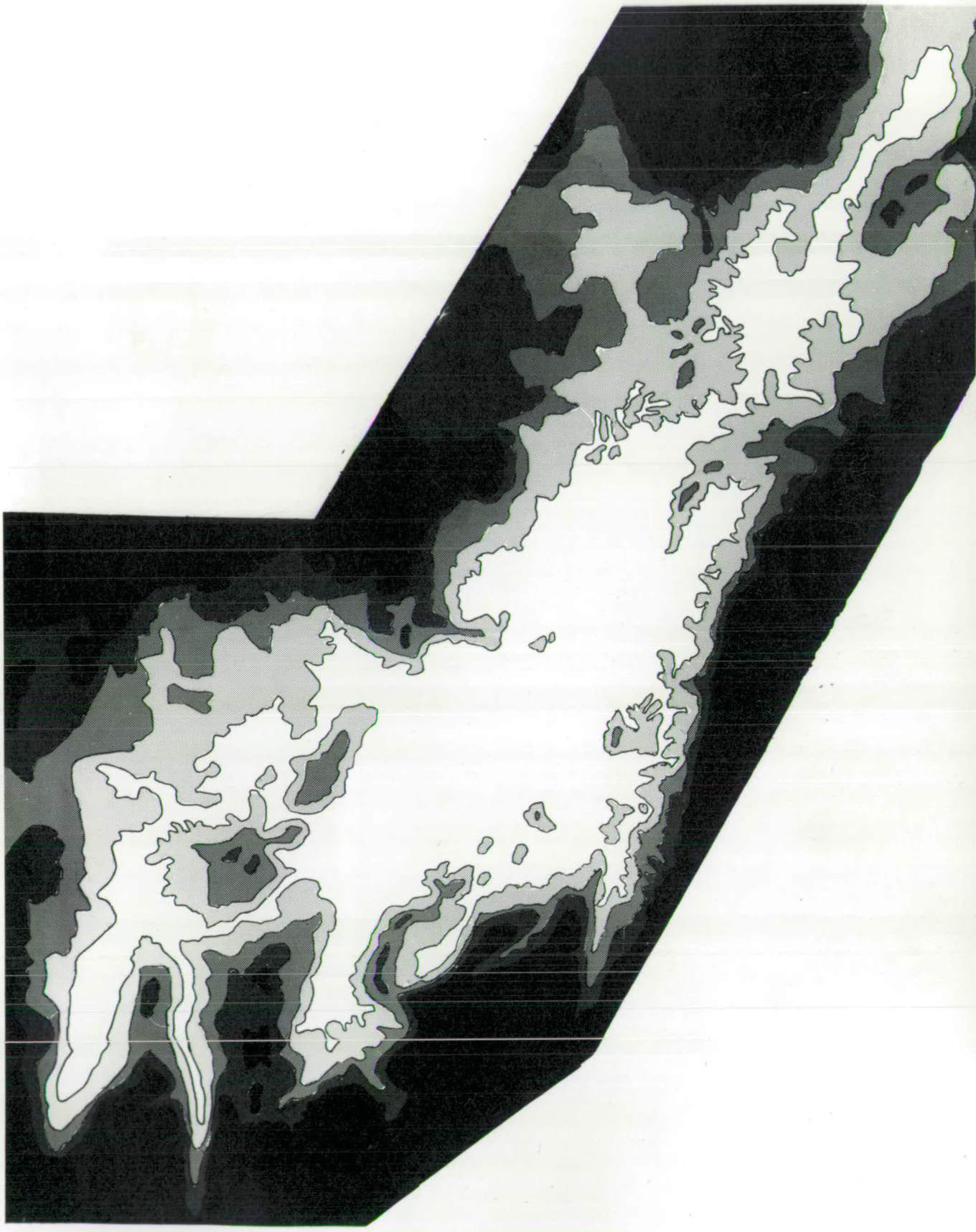
Figure 18.

Fig. 18. The Lika Survey Area.

Scale approximately 1:300,000.

Contours at 600, 700, 800 and 900 metres.

See also figure 1.



past deposited layers of silt, so that the basins are remarkably level.

There are thirteen separate basins of different sizes in the region studied. Although the height of their floors above sea level varies considerably (Srpsko Polje near Otocac being at 420 m., Brinje Polje at 460 m., and Letinac Polje near Brinje at 620m., for example), all the basins show the characteristic level floor. In one of the basins in the Lika group it is possible to travel in a straight line for over 20 km. with a height range of less than twenty metres, although most of the basins are much smaller than this. All the basins are surrounded by steep mountains which are over 1000 m. high.

Vegetation.

The vegetation of the area shows much local variation which is correlated with the karstic topography. It is described in detail by Turrill (1929). The seaward slopes of the Velebit have a Mediterranean ecology, with a coastal belt of evergreen shrubs or "pseudo-macchie" and pines (mainly Pinus halipensis) which gives way first to forests of laurels (Laurus nobilis) and other low trees interspersed with expanses of bare limestone and, towards the summit of the Velebit, to conifer forest and sparse grassland.

The Eastern side of the Velebit has a Central European ecology with few Mediterranean influences. The alluvial soils of the basins are often intensively cultivated, with many hedgerows made up primarily of hawthorn (Crataegus spp.) and blackthorn (Prunus spinosa) sometimes associated with ivy (Hedera helix) brambles (Rubus spp.) and broad-leaved vegetation, and overhung by plum trees (Prunus domestica). Outside the basins, open karst woodland or scrub made up of clumps of ash (Fraxinus ornus), beech (Fagus sylvatica), sessile oaks (Quercus spp.) and hazel (Corylus avellana) may develop, in conjunction with hedgerows

of blackthorn and hawthorn. There is often much bare rock. Above about 700 m. beech is dominant, and frequently forms dense forests with little undergrowth. Conifers (mainly spruce Picea abies and Pinus spp.) are found above about 1400 m., and usually merge into the beech community, although there are a few pure conifer forests.

Distribution of Snails.

Cepaea is absent from the seaward slopes of the Velebit and from dense beechwoods on the landward side. Both C. vindobonensis and C. nemoralis are found in the basins and on the lower slopes (up to 670 m.) of the surrounding mountains. Most samples contain both species of Cepaea, and there is no obvious tendency for the two species to differ in their range of height. There is a higher frequency of unmixed colonies of C. nemoralis or C. vindobonensis in the Lika area than in the other regions, but there is no apparent tendency for unmixed colonies to be more common at greater heights or outside the polja.

Most of the polje samples were collected from the hedgerows described above, but some (for example Bjeljevine 2) are from thickets of bramble and broad-leaved vegetation corresponding approximately to Cain & Sheppard's (1950) "rough herbage" class. A few are from other types of habitat, such as the edges of beechwoods (e.g. Poljice 4), or sparse herbage growing on stone walls or fences (e.g. Brlog Stacija 5). Many of the non-basin samples were collected from hedgerows, but a number of these samples originate from scattered clumps of beech and hazel or from "rough herbage". The habitat classes for these collections are given in table 4. Collection localities and habitat classes for the main survey area are mapped in fig. 19.

Distribution of Morphs.

Collection techniques were similar to those described for C. nemoralis (chapter 1). As there were no significant differences in morph frequency

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Figure 19.

Fig. 19. Collection Localities and Habitat Classes for the Gacka Survey Area.

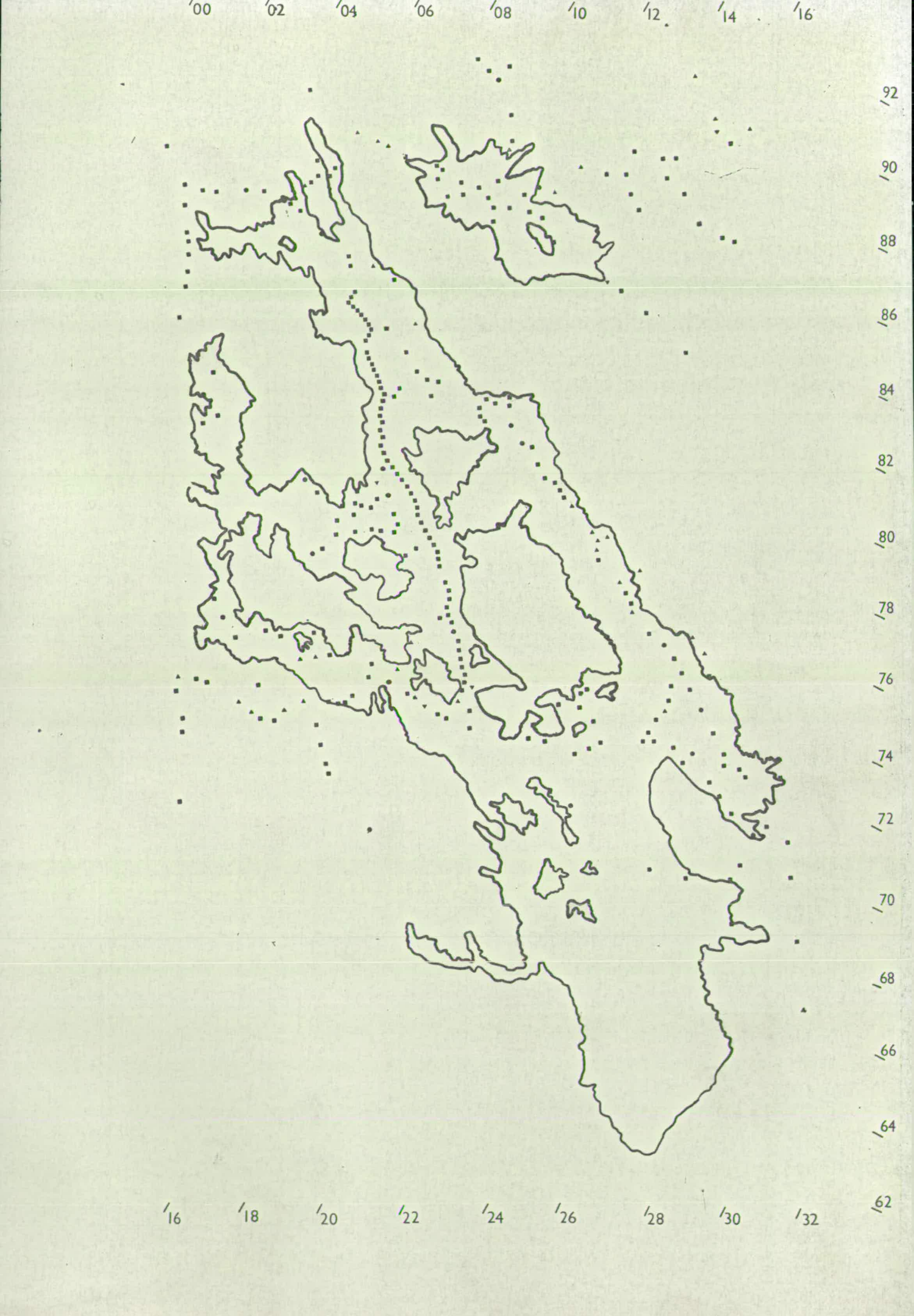
■ Hedgerow.

● Rough Herbage.

▲ Scrub.

▼ Deciduous Woodland.

Grid squares of the Yugoslav national grid also shown.


'00
'02
'04
'06
'08
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'12
'14
'16
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76
74
72
70
68
66
64
62
'16
'18
'20
'22
'24
'26
'28
'30
'32

between adult and young snails, or between live individuals and those found dead, all snails collected were used in the analysis of morph frequencies. Sample scores are given in table 4. Morph frequencies are mapped in figs. 20-23.

i) The Gacka Area.

There are marked variations in morph frequency throughout this region

a) Band Fusions. (fig. 20)

L(L3)45 shells are at a relatively high frequency in the central part of the Gacka survey area (Srpsko Polje - Kompolje - Brlog Stacija samples). This morph is much rarer elsewhere in the Gacka region, and its frequency does not usually rise much above 5%. This is the case, for example, around Koljevici and Krizpolje, where no L(L3)45 shells were collected. The transition between places with a high and those with a low frequency of this morph is often quite abrupt - at Orovac, there is a decrease from 63% to 14% L(L3)45 shells along 400 metres of apparently uniform hedgerow. This difference in morph frequency is maintained, with few exceptions, for more than five kilometres in either direction. L(L34)5 shells were found only in a restricted region in the central part of the Gacka.

b) Missing Bands.

Snails with the second band missing occur sporadically throughout the region with little tendency for concentration within a particular district, although some places - e.g. Podum - have a slightly higher frequency than others.

c) Faint Bands. (fig. 21)

There is very marked regional localisation of faint-banded snails, which are absent from the samples in the central part of the Gacka survey, although they reach a high frequency in other parts of this region (for example around Zuta Lokva and Jelvica). There are

Figure 20.

Fig. 20. Frequency of L(L3)45 and L(L34)5 in C. vindobonensis in the Gacka area.

L(L3)45 - black.

L(L34)5 - stippled.

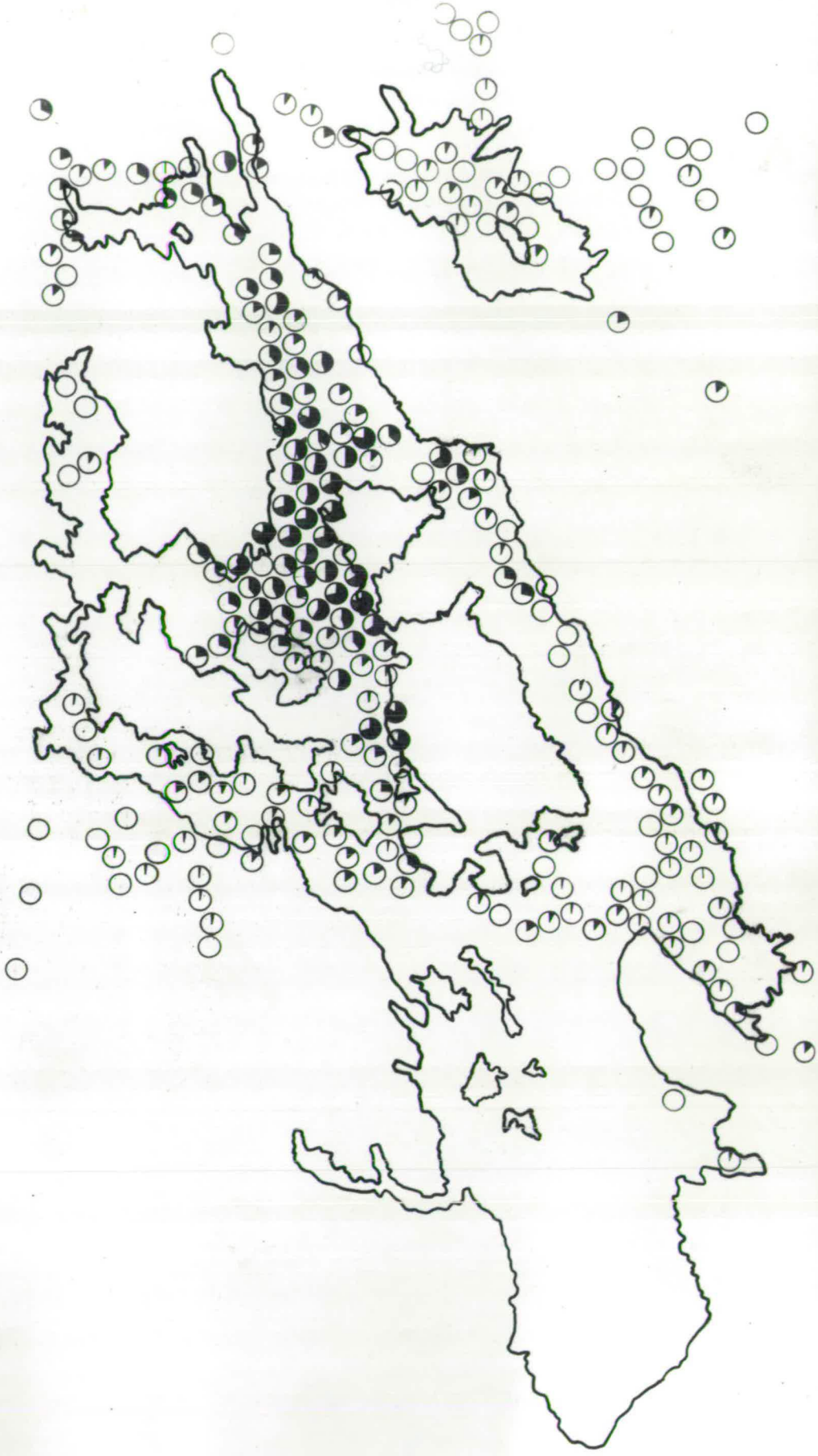
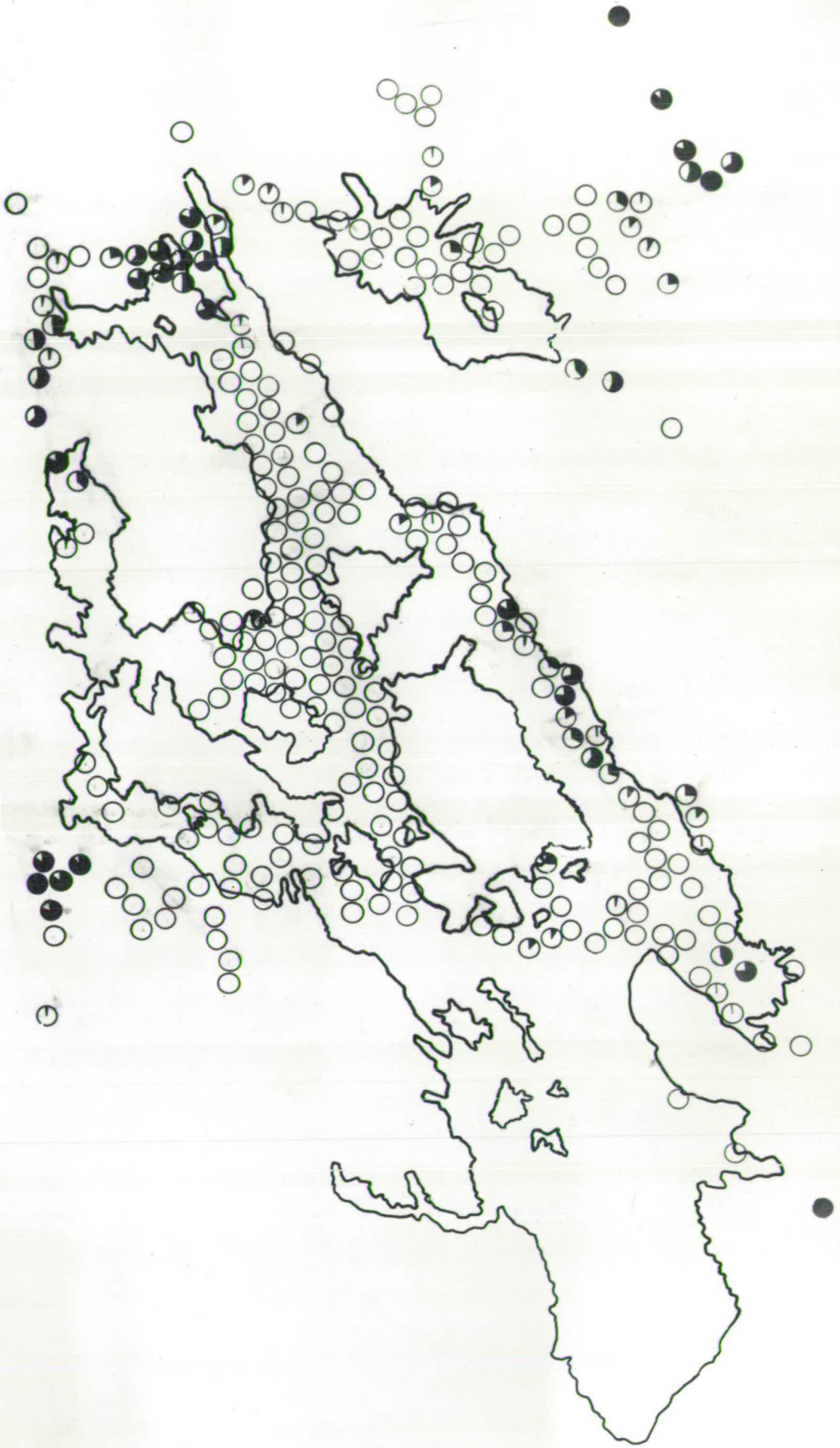


Figure 21.

Fig. 21. Frequency of Faint Bands in C. vindobonensis in the Gacka Area.



several steep clines in morph frequency - at Poljane, for example, there is a change from 0% to 83% faint-banded snails within 150 metres.

ii) The Lika Area.

Although this region was sampled less intensively, local variations in the frequencies of all morphs can be distinguished.

a) Band Fusions. (fig.22)

L(L3)45 shells are more common in the North than in the South of the Lika. The overall frequency of this phenotype is considerably lower than in the Gacka, and there is no indication that any region has a frequency of L(L3)45 as high as that found in the central part of the Gacka. No L(L34)5 shells were collected in the Lika survey area.

b) Missing Bands.

In the Lika region, snails with the second band missing are considerably more common than in the Gacka, and this phenotype reaches a frequency of over 50% in several samples. Samples with a high frequency of missing bands show a marked tendency to be grouped together. This is particularly noticeable in the South of the Lika.

c) Faint Bands. (fig.23)

The distribution of faint bands is similar to that found in the Gacka survey, as this phenotype is absent from some areas but reaches a higher frequency in others. The overall frequency of faint bands is higher than in the Gacka.

The general pattern of morph distribution in these populations of C. vindobonensis is rather similar to that described by Cain and Currey for the distribution of shell colour and banding phenotypes in C. nemoralis populations on the Marlborough Downs.

Association of Morph Frequency with Environment.

i) Background Vegetation.

There is no significant association between the frequency of any

Figure 22.

Fig.22. Frequency of L(L3)45 in C. vindobonensis in the Lika Area.

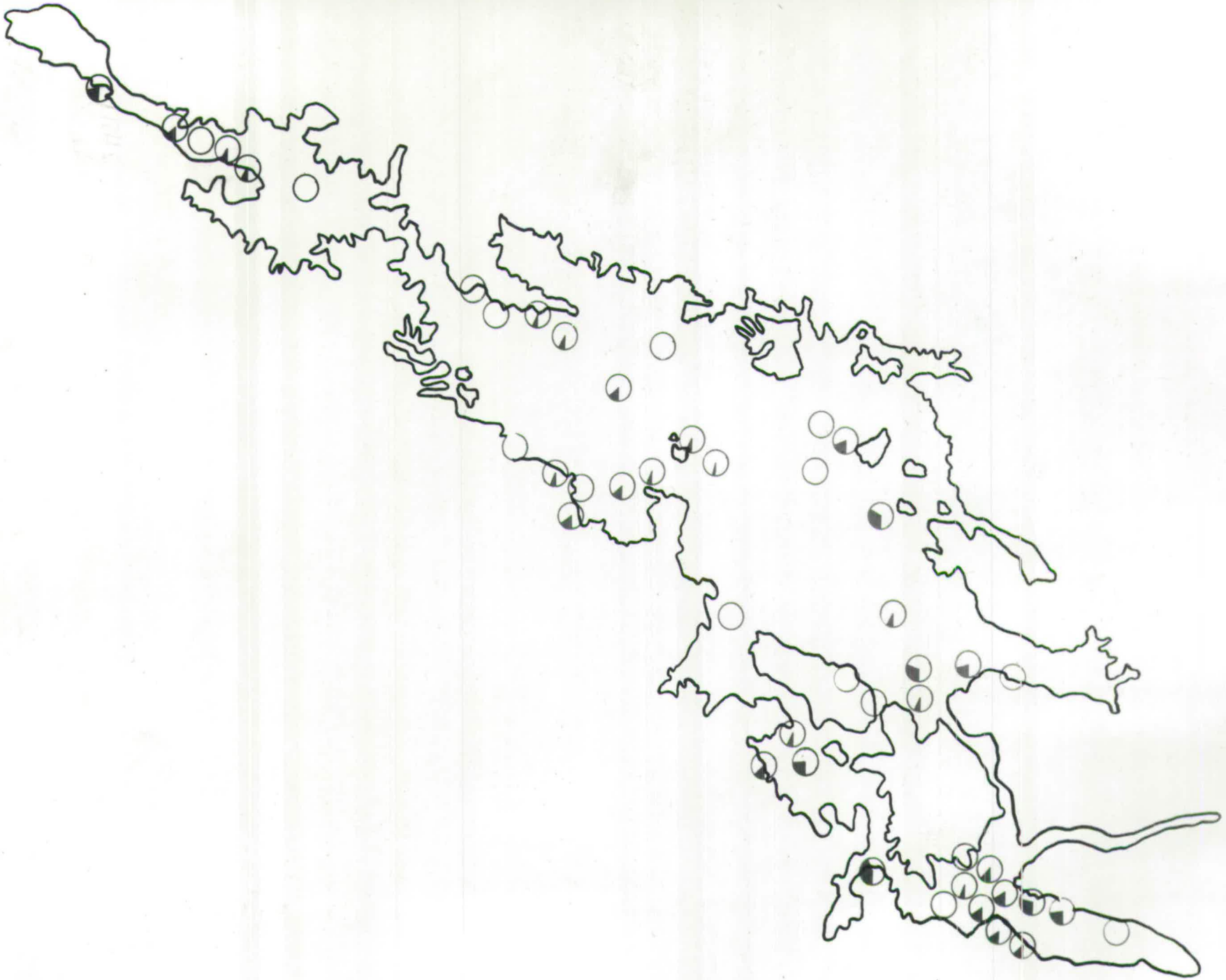
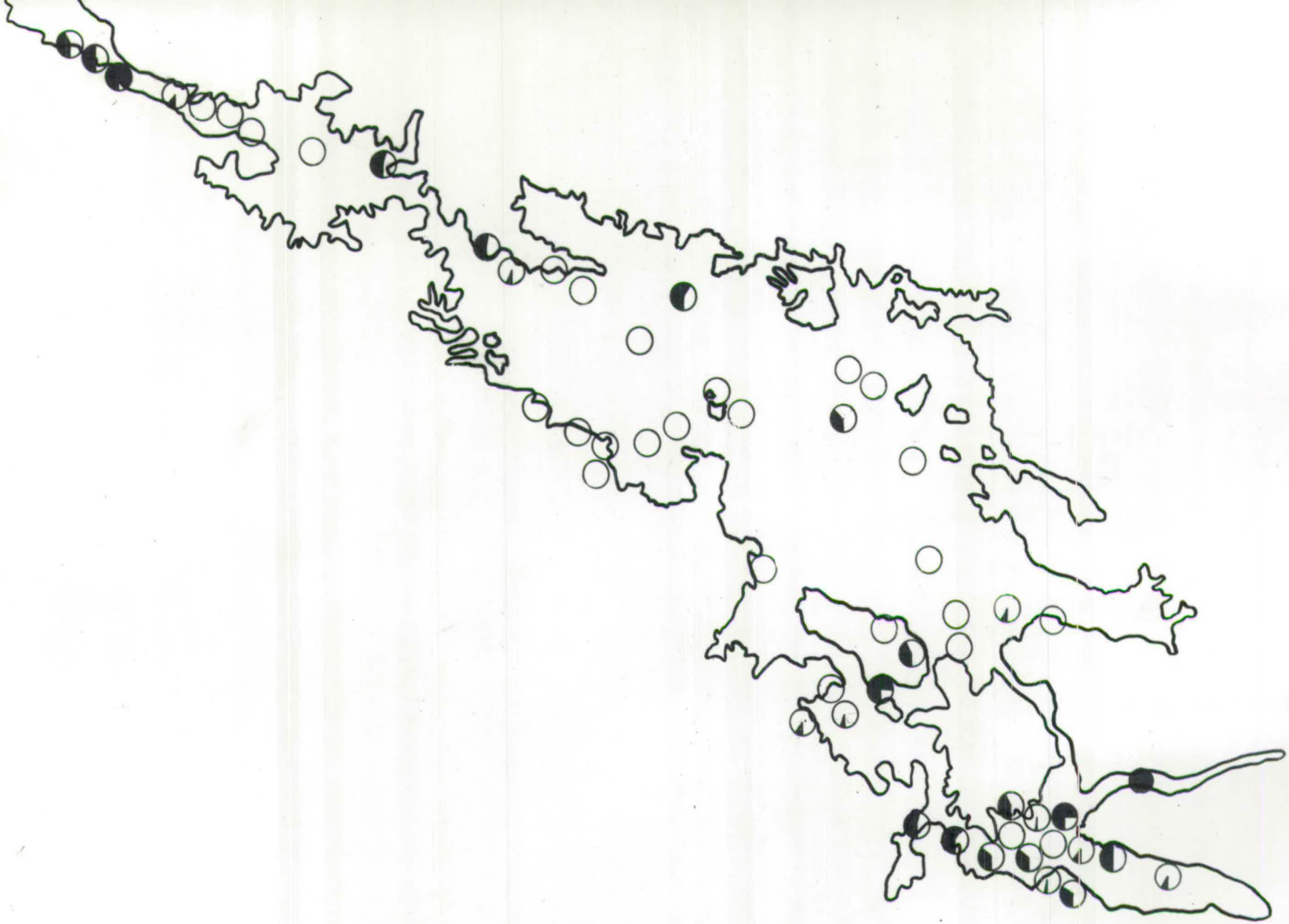


Figure 23.

Fig. 23. Frequency of Faint Bands in C. vindobonensis in the Lika Area.



morph and background vegetation (classified as Hedgerow, Rough Herbage and Beech). The range of types of vegetation in which snails were found is considerably more restricted than in Cain and Sheppard's Oxford collections. It is therefore rather difficult to establish any correlation of morph frequency with background which may exist in C. vindobonensis from our collections.

As the constancy of morph frequencies over large regions described above bears no evident relation to background vegetation, these patterns of variation in C. vindobonensis can be classified as "area effects" as defined by Cain and Currey (1963a).

No interspecific association has been found for the frequencies of different morphs in mixed colonies of C. nemoralis and C. vindobonensis comparable to that found by Clarke (1962) to exist between C. nemoralis and C. hortensis, despite the fact that the two species were nearly always found in coexistence. Clarke suggests that the interspecific association found by him is due to the behaviour of predators, which apply the same "searching image" to both species. Predation involving shell breakage does not seem to be an important cause of mortality in C. vindobonensis in this region, as only 9 of the 15,000 shells collected were predated, all of these having the gnawed appearance characteristic of rodent-predated shells (Cain 1953). The C. nemoralis populations living in the area may be more liable to predation, as 95 of the 11,000 nemoralis collected were predated. This may be a function of the thicker shell of C. vindobonensis and of its more inconspicuous appearance.

ii) Topography.

The geology of the Velebit Mountains has given rise to very marked local variations in topography, the most striking of which are the large basins surrounded by mountains. I have attempted to quantify the levelness of each sampling site. The distance on the map from the

sampling point to the nearest 20m. contour was measured. This line was then extended back through the sampling point until it reached a contour in the opposite direction and this distance was also measured. The two distances from sample to contour were added to give a "polje index". Height above sea level is the other main topographical variable, and this was taken from the 1:50,000 map (Geografskog Instituta J.N.A., 1956).

a) Faint Bands.

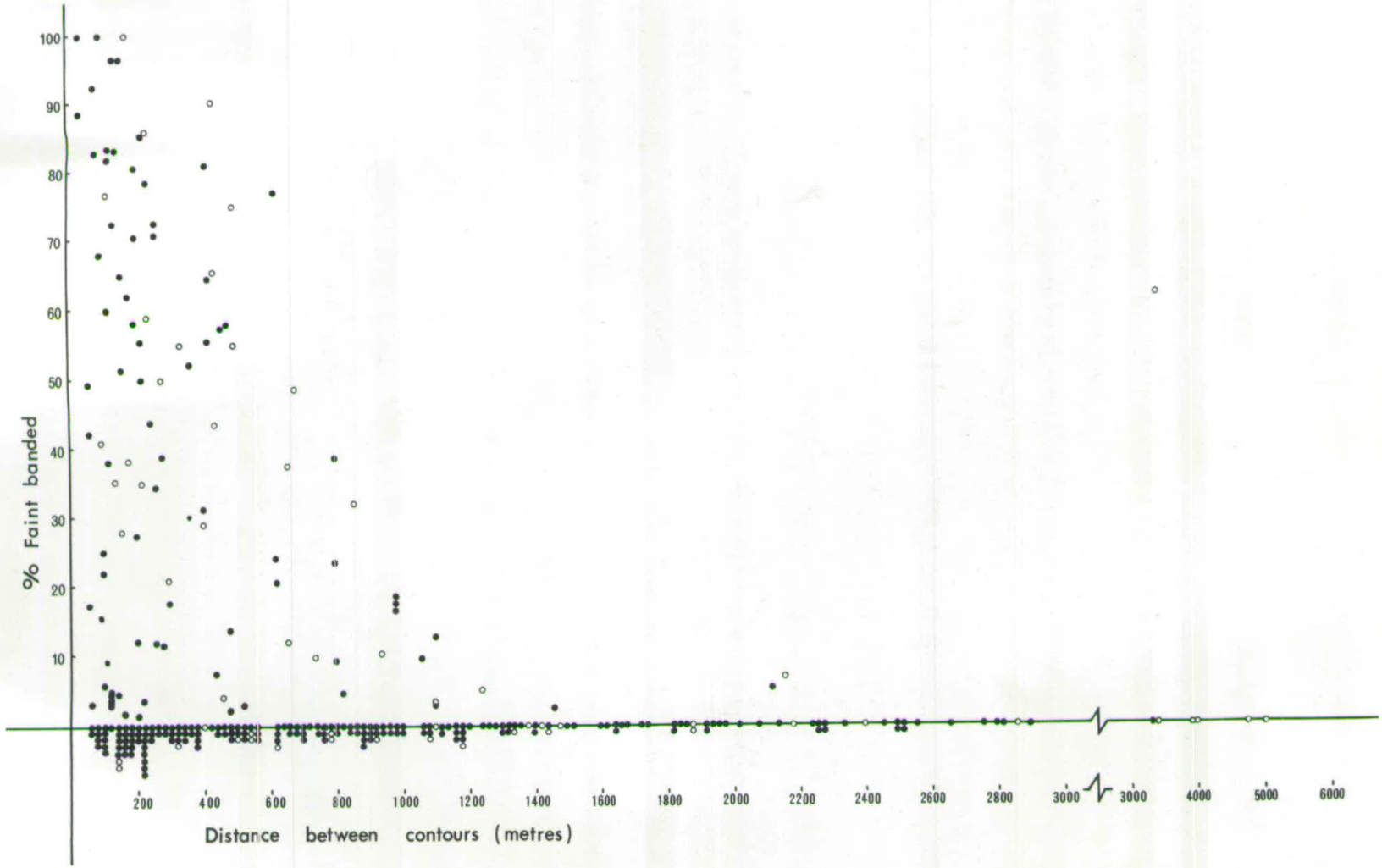
The maps of the frequency of this morph (figs.21+23) show that in general faint-banded snails occur only in non-polje areas, although not all non-polje samples contain faint-banded snails. Figure 24 shows the association between the percentage of this morph and the distance between contours. This demonstrates clearly that faint-banded snails are found only in samples with a low polje index - i.e. in those collected away from the basins - and that the frequency of the morph where it does occur is negatively related to the polje index, samples having the highest percentage of faint-banded snails being found only on the steepest hillsides. Only one sample (Pavlice 2, in the Lika survey area) out of a total of 331 samples containing more than ten snails does not agree with this pattern of morph distribution, as although it is in an extensive basin (distance between contours = 3400 metres), 61% of the 44 snails collected were faint-banded. The collection was made from a thicket of hawthorn. The nearest sample containing more than ten snails is 5 kilometres away (at Ribnik), and this contains no faint-banded individuals. Although the area surrounding the aberrant sample was searched carefully, only 9 C. vindobonensis (noneof which were faint-banded) could be found. It seems possible that this dense isolated colony of C. vindobonensis living in a restricted area may be a recent introduction from outside the basin, or alternatively (although this is perhaps less likely) that genetic drift has given rise to a high

Figure 24.

Fig. 24. Association of the Frequency of Faint Bands in *C. vindobonensis* with Distance between Contours.

● Gacka samples.

○ Lika samples.


% Faint banded
100
90
80
70
60
50
40
30
20
10
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
2600
2800
3000
3000
4000
5000
6000
Distance between contours (metres)

frequency of faint bands.

The very significant negative relationship between the frequency of faint bands and the flatness of the sampling site is not due merely to geography (with all the samples containing this morph being concentrated in one region which is not a basin), as 11 separate area effects for faint bands can be distinguished, none of which (with the exception of Pavlice 2) is in a basin. Similarly, again with the exception of the single colony at Pavlice 2, none of the 13 basins studied contain high frequencies of faint banding.

b) Other morphs.

L(L3)45 shells reach a high frequency in the samples in the central part of the Gacka survey area, and are rather rare elsewhere in the Gacka and throughout the Lika region. L(L34)5 shells are even more restricted in their distribution, as they are found only in Srpsko Polje in the central Gacka. This pattern of distribution makes it difficult to separate any associations of morph frequency with topography from simple geographical effects due to the concentration of these samples in one small region. This situation is quite different from that found when considering the distribution of faint banded shells, as the apparent association of this morph with topography is consistent over a number of geographically separate populations. The central Gacka area effect for high frequencies of L(L3)45 is not associated with the levelness of the sampling site, as its boundaries overlap both a basin and a region of steep hillsides. L(L34)5 shells are found only in one basin, but their distribution is so restricted that it is difficult to make any statistically valid statements about the significance of this.

The region where band fusions reach their highest frequencies is nearly all less than 460 metres above sea level. However, other low-lying parts of the survey area (e.g. Brinje Polje, at 460 m.) have a very low

frequency of shells with fused bands. Further sampling of new areas is necessary before we can establish any correlation which may exist between the frequency of band fusions and height above sea level or any other topographical variable.

Shells with the second band missing occur sporadically at a low frequency throughout the Gacka region. There seems to be no tendency for this morph to occur preferentially on hillsides or in basins, or for its frequency to be associated with the sample's height above sea level. Although the overall frequency of L0345 shells is considerably higher in the Lika than in the Gacka, no clear associations with topography are discernible in this area.

DISCUSSION.

Previous work on area effects in C. nemoralis has shown that it is often difficult to correlate morph frequencies with environmental selective forces. This chapter describes the structure of populations of a species with a considerably simpler system of polymorphism living in a region with striking local variation in topography. There appears to be an association between the frequency of at least one of the morphs in this species and topography. It may be possible to deduce the nature of the selective forces acting on morph frequency from a consideration of this association.

a) Faint Bands.

The polja, which are large basins surrounded by mountains, provide ideal conditions for the development of temperature inversions (during which cold air flows from the mountainsides into the basins, which therefore act as frost hollows) in calm clear weather. The development of such inversions in Yugoslav polja has been studied quite intensively because of the importance of this ponding of cold air to agriculture.

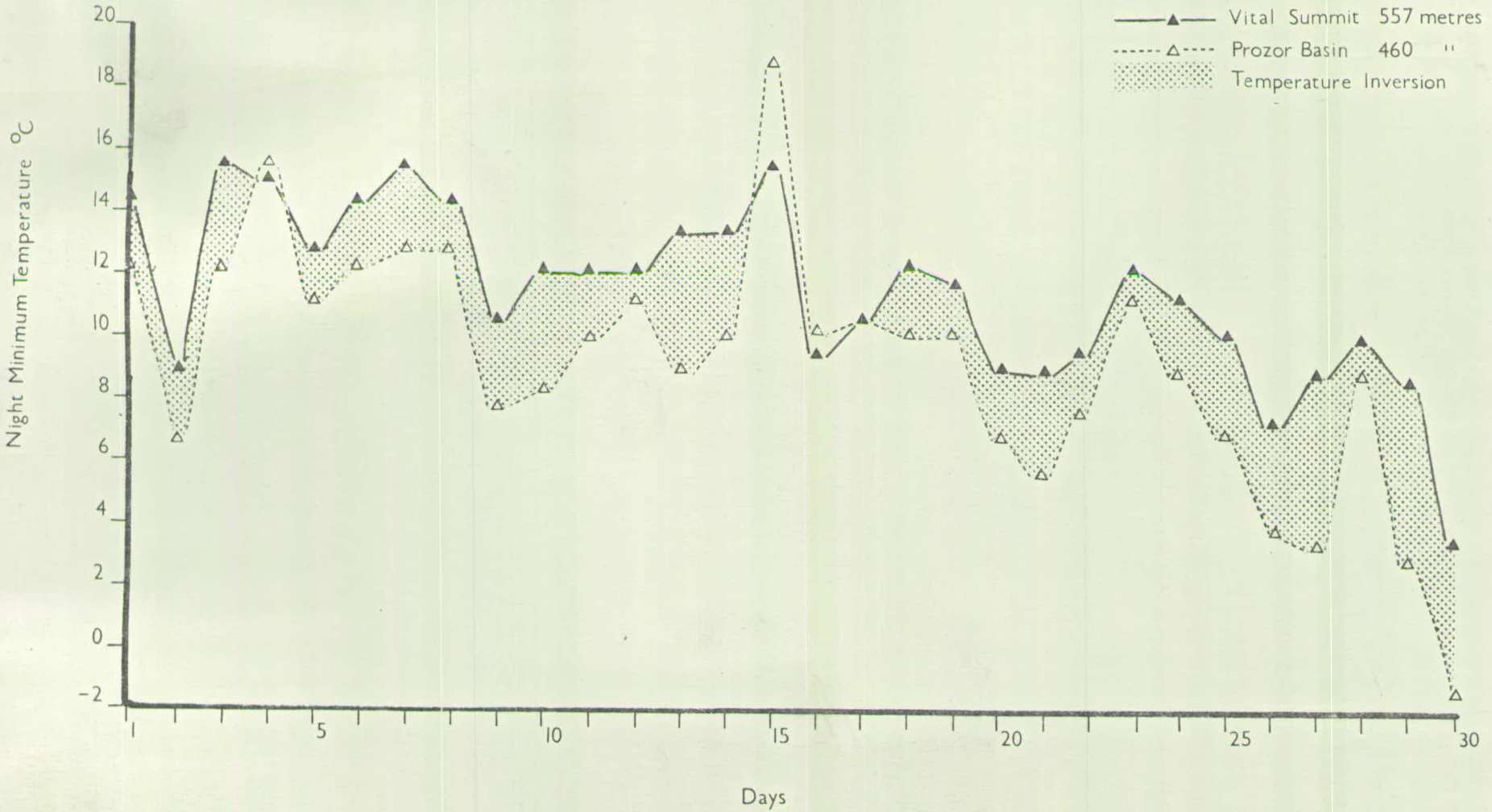
In Slovenia (North Yugoslavia), for example, the lowest recorded temperature is in Babnopolje (780 m.), where an extreme of - 32°C has

been recorded, whereas the temperature at the adjacent summit of Obir (1200 m.) does not fall below -27°C (Anon. 1944). Detailed measurements of the vertical air temperature gradient in the basin of Ljubljana (150 km. N.N.W. of the Gacka region) (Bernot 1957) show that temperature inversions develop frequently under anticyclonic nonditions. Inversions may persist for up to a week under suitable conditions, although summer inversions (during which the floor of the basin is an average of 3°C colder than the adjoining hillsides) are usually reversed during the day.

A small amount of information is available on the development of temperature inversions in the polja where C. vindobonensis was collected. Gospic, in Lika polje (564m.) commonly experiences temperatures 8°C below those at Ostarije (924 m.) in the surrounding mountains, the difference in temperature occasionally being as much as 17°C (Anon. 1944). The development of temperature inversions in the main survey area was investigated by measuring night minimum temperatures in free air 1 metre above ground level using recording thermometers. Unscreened thermometers were placed at the base of an isolated hill (Vital) in the main Gacka basin at 460 m., and also on its summit at 560 m. (see fig. 17). Minimum temperatures were measured at these stations on 30 consecutive nights in August and September 1971. Figure 24b shows that inversions of temperature developed on 26 of these nights, the lower station usually having a minimum temperature approximately 2°C below that of the upper, although the difference in temperature was sometimes as much as 5.6°C. The mean minimum temperature over this period at the summit of Vital was 11.4°C, and at its base 9.1°C. This difference in mean minimum temperature over a height range of 100 metres is comparable to that found at the same time of year over a distance of 900 kilometres between Western Scottish and Northern French climatic stations at sea level (Booth 1966). Unpublished data from the climatic stations at Licko Lesce (463 m.) and Stipanov Gric (1200 m.) kindly made available by the Croatian Hydrometeorological

Figure 24b.

Fig. 24b. Night Minimum Temperature at two Climatic Stations.


Vital Summit 557 metres
Prozor Basin 460 "
Temperature Inversion
Night Minimum Temperature °C
20
18
16
14
12
10
8
6
4
2
0
-2
1
5
10
15
20
25
30
Days

Institute shows that inversions developed in this basin even between points with a height difference of 750 m. on 39% of the nights in June, July and August 1967 and 1968. We often saw mists lying in other basins in the early morning while the surrounding mountains were clear, and as this pattern is typical of the development of temperature inversions, it seems likely that these were acting as frost hollows also.

Faint-banded snails are found almost exclusively away from the basins. If, as seems very likely, faint banding is not directly induced by the environment, this suggests that the selective force determining the distribution of this phenotype is in some way associated with the reduced ability of snails with faint bands to withstand or recover from the cold conditions caused by the accumulation of cold air at night. It is interesting to note that in the C. nemoralis populations studied by Cain & Currey (1963a) and Cain (1968), the darkest shell colour morph (dark brown) is found in frost hollows. Darker shells in both these species may therefore be more resistant to the climatic conditions found in frost hollows. This may be a function of the dark shells' ability to warm up more rapidly by solar heating in the early morning after an inversion of temperature. This hypothesis will be discussed in the General Discussion of this thesis.

The distance between contours was measured for Cain & Currey's samples on the Marlborough Downs, using a 1:25,000 Ordnance Survey map. There was no correlation between the frequency of any of the morphs and this index. As the topography of the Marlborough Downs is very different from that of the Velebit, the presumed frost hollows being dry valleys or sloping areas rather than extensive level basins surrounded by mountains, the distance between contours is not a very satisfactory measure of any tendency to accumulate cold air on the Downs. The absence of any correlation between this parameter and the frequency of brown shells in C. nemoralis does not therefore indicate that the regions in which

browns are found on the Downs are not frost hollows.

b) Other Morphs.

As there are no clear associations of the frequency of shells with fused or missing bands with topography, it is difficult to speculate on the nature of any microclimatic variable which may exert a selective effect on these morphs in the Velebit. The absence of any association between the frequency of L(L3)45 and LO345 and any tendency of the sampling site to accumulate cold air suggests that the ability of snails with these phenotypes to withstand extremes of low temperature is unlikely to be important in controlling their distribution. There is some indication that shells with band fusions are commoner in the lower parts of the survey area. These regions have a higher mean temperature (but not a higher mean minimum temperature) than that found elsewhere, and are also drier. Precipitation in the Velebit is, however, very dependent on aspect (Penzar 1959), and there is no evidence that the frequency of fusions is correlated with this variable.

Although it is possible that the frequency of phenotypes other than faint banding in C. vindobonensis may be affected by microclimate, the populations described in this chapter do not provide any convincing evidence for this.

This investigation of a species of Cepaea with a simple system of shell polymorphism living in a region of striking variations in topography has revealed one rather clear association of morph frequency with microclimate. The following chapter describes populations of C. vindobonensis living in a topographically rather uniform environment. The possible relevance of gene distribution in C. vindobonensis to our understanding of area effects in the more widely studied C. nemoralis will be considered in the General Discussion.

CHAPTER 4

AREA EFFECTS IN ROMANIAN POPULATIONS OF CEPAEA VINDOBONENSIS.

As there are marked associations between morph frequency and environment in Yugoslav populations of C. vindobonensis, another less extensive survey of this species was carried out in Romania, 1000 kilometres East of the Velebit study area. This allowed a comparison of morph frequencies in populations living in different climatic and topographical conditions which might help to identify the environmental factors affecting morph frequencies on a smaller scale.

The Area Studied.

All Romanian samples were collected in the Dobrogea, which lies between the Danube and the Black Sea (fig. 25). The Southern part of the region consists mainly of low relief, and although the North Dobrogea is hillier, the highest point in the survey area is only 250 metres above sea level. The topography of the Romanian study area is thus very different from that of the Yugoslav.

Most of the region is made up of Palaeozoic and Mesozoic rocks with a few outcrops of limestone near the coast. The majority of the soils are loessic and over much of the area have developed into fertile chernozems which, although usually calcareous, may be strongly leached.

Much of the Dobrogea has a steppe ecology which is dominated by typical "steppe meadows" of Poa bulbosa, Euphorbia stepposa, and other vegetation resistant to aridity. There are a few extensive forests in the Northern hills, and several parts of the steppe have become modified to "silvosteppe", which possesses many woods. In the South-West of the region these woods consist mainly of Quercus cerris and Q. frainetto, but elsewhere in the Dobrogea other oaks (Q. pubescens, Q. sessilis and Q. pedunculiflora) predominate. A few of the woods are made up almost exclusively of the false acacia Robinia pseudoacacia, and this species

occurs sporadically in most of the oakwoods. As the canopy of these woods is usually quite dense, there is little undergrowth and the ground is covered with leaf litter.

The silvosteppe includes regions of bushes and scrub (made up mainly of Syringa vulgaris, Fraxinus ornus and low-lying oaks) which often develop around the edges of the oakwoods but may also be found in isolation (Societatea Stiinte Naturale R.S.R. 1966).

Distribution of Snails.

C. vindobonensis is absent from the steppe meadows but is often very common at the edges of woods and in the scrub areas of the silvosteppe. Most samples were collected from leaf litter in oakwoods, or from open scrub. A few originate from other habitat classes; for example, Hagieni 2 was collected from a bramble thicket on a small limestone outcrop, and Babadag 10 from a region of heavily overgrazed oak scrub with a few stunted young oaks and much bare ground.

Unfortunately the survey was carried out during a cold dry period near the end of the snails' active season (late September 1968), and although C. vindobonensis was often very common, most of the samples collected consist only of dead shells. As these sometimes become bleached, and as there is occasionally some resemblance between a partially bleached shell with normal bands and a faint-banded shell, there is some danger in overestimating the frequency of faint bands. All shells which showed signs of this type of bleaching were discarded, and this source of error is unlikely to have led to considerable inaccuracy in estimates of morph frequency.

Distribution of Morphs.

There are marked differences in the frequencies of the various morphs between Romania and Yugoslavia, and there are area effects for the morphs found in the Dobrogea (figs. 25+26 ; table 5).

a) Faint Bands.

Shells with reduced band pigmentation are commoner in the Romanian samples than in the Yugoslav, with an overall frequency of 16% in the Dobrogea compared to 11% in the Velebit Mountains. There is an area with low frequencies of this morph in the South-East corner of the Dobrogea. (fig. 25).

b) Other Morphs.

L(L3)45 shells are at a far lower frequency in the Dobrogea than in Yugoslavia. Only 9 of the 1885 snails collected have this banding pattern, and in two of these the second and third bands are fused only after an obvious shell breakage and repair. This compares with an overall frequency of 17% L(L3)45 in the Velebit Mountains, No L(L34)5 shells were found.

There is a considerably higher frequency of shells with missing bands in Romania than in Yugoslavia (44% compared to 4%). There is an area of lower frequencies of shells with the second band missing in the central part of the Dobrogea (fig. 26).

Association of Morph Frequency with Environmental Factors.

i) Background Vegetation.

Habitats were classified into "wood" and "non-wood". There is no association between the frequency of any of the morphs and habitat class, and morph frequency is constant over large areas irrespective of background vegetation. This pattern of morph distribution is therefore analagous to the area effects found in C. nemoralis on the Marlborough Downs. There is little evidence of predation in C. vindobonensis in the Dobrogea, 100 out of 1885 / shells being predated.

ii) Topography.

The relief of the Romanian study area shows far less variation than does that of the Yugoslav, most of the region consisting of low rolling

Figure 25.

Fig 25. Frequency of Faint Bands in C. vindobonensis in the Dobrogea.

Scale approximately 1:800,000.

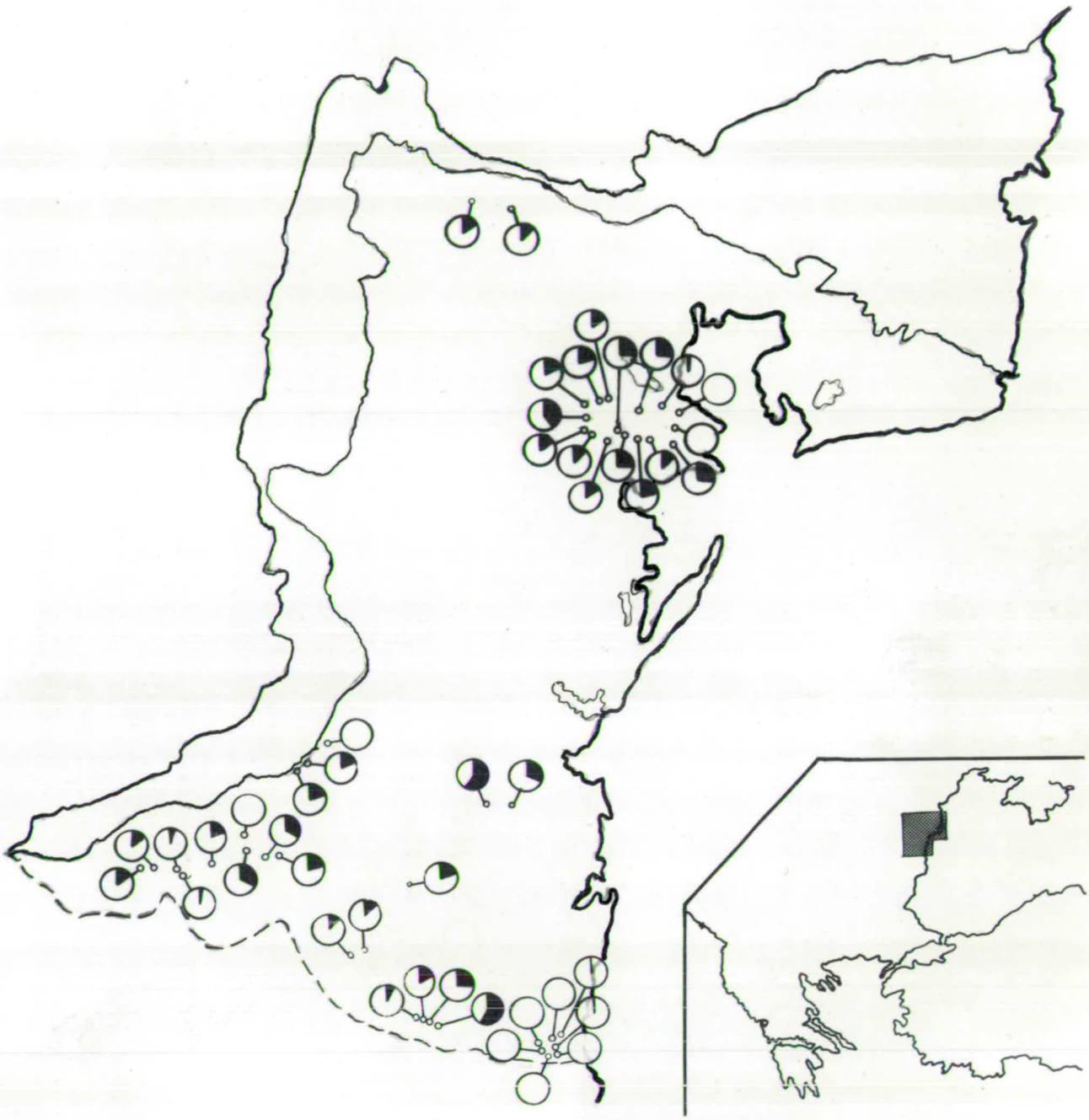
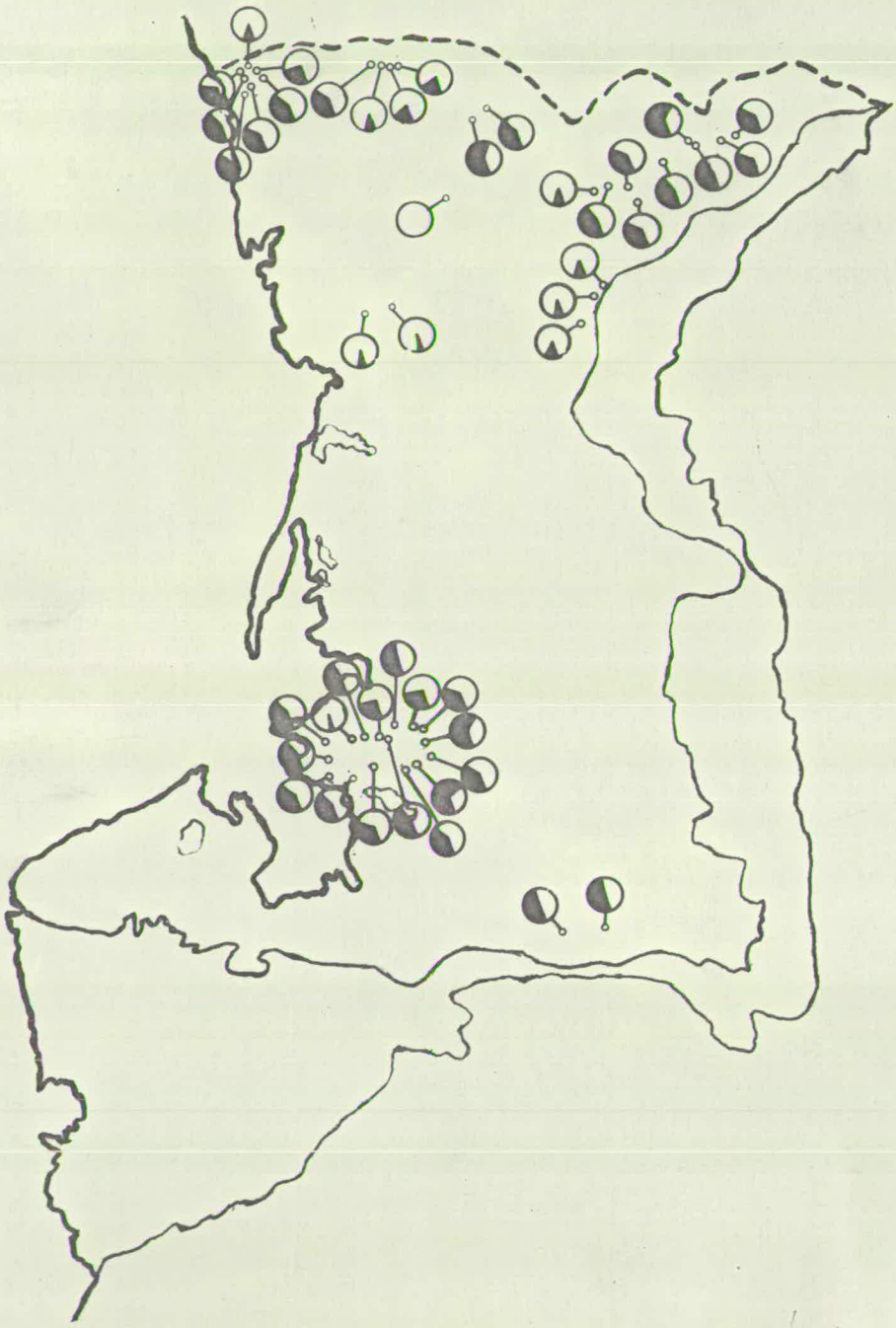


Figure 26.

Fig. 26. Frequency of L0345 in C. vindobonensis in the Dobrogea.



steppe. There is no association between the frequency of any of the morphs and height above sea level, nor (as far as could be deduced from the map) between morph frequency and any tendency to accumulate cold air.

In general, then, the pattern of morph distribution in C. vindobonensis in the Dobrogea is analagous to that found in the Velebit, although the overall frequencies of the morphs involved are very different, and there is no apparent relation between morph frequency and any environmental factor.

DISCUSSION.

The overall climate of the Dobrogea is much more continental than is that of the Velebit, the winters being colder and the summers much hotter and drier (Atlas Geografic RSR 1965). During the snails' active season, there are no nights as cold as those found in the Yugoslav polja. At Gospić, in the Velebit, for example, from 1946-1955 there were frosts every month of the year except July and August (Hidromet. Zavod N.R. Hrvatske), while in the Dobrogea as a whole there were no frosts between early April and the end of October (Atlas Geografic RSR 1965). This frost-free period covers almost the whole of the snails' active season in this region (Dr. D. Grossu; pers. comm.). In 1955, the last year for which figures are available for both areas, the frost-free period at Constanța (Dobrogea) was 12th April-21st November, (Anuarul Meteorologic, 1955) while at Gospić it was 1st June-17th September. The average absolute minimum and mean night temperatures are also considerably higher at Constanța than at Gospić.

Comparison of gene frequencies between only two geographically separated populations allows only the most preliminary speculations on the nature of climatic or other differences which may be responsible for differences in their genetic structure. Chapter 2 of this thesis shows that there are many marked large-scale geographical fluctuations in morph frequency in C. nemoralis which, when considered in the context

of gene frequency distribution throughout this species' range, can clearly be seen not to be due to easily identifiable climatic selection.

It is nevertheless interesting to note that faint-banded shells in C. vindobonensis, which appear to be commoner in the less cold parts of the Velebit Mountains, are also commoner in the Dobrogea, which is much warmer in summer than is the Velebit. Similar selective factors may therefore control both microgeographical and large-scale variations in the frequency of this phenotype. In the absence of any evidence apart from overall frequencies in the two populations described in this thesis as to the nature of any climatic variable which may affect other morphs in C. vindobonensis, it is impossible to decide whether the frequency of shells with the second band missing and shells with band fusions responds to climatic selection.

It appears from the limited data given by Schilder & Schilder (1957) that var. pallescens (faint banding) is commoner in the warmer South and South-East parts of C. vindobonensis' range, while there are no detectable regularities in the geographical distribution of the frequency of 00345 shells. This is the pattern which would be expected if the faint banded phenotype is indeed at an advantage in warm conditions, while the distribution of 00345 shells is independent of climate. The large-scale distribution of genes in C. nemoralis shows a rather similar tendency for the frequency of the major genes controlling the number of bands on the shell to be independent of climate, while the frequency of some other genes is closely correlated with temperature. This will be considered further in the General Discussion.

CHAPTER 5.

AN INVESTIGATION OF CEPAEA SHELL PIGMENTS.

This chapter describes the results of an investigation of the shell colour pigment of C. nemoralis. I have attempted to develop methods of measuring small differences in colour which might allow the detection of heterozygotes in this species, and have also examined the probable effects of shell pigmentation on heat input in sunshine.

i) Detection of Colour Heterozygotes.

Deviations from the Hardy-Weinberg equilibrium in a large genetically isolated random-mating population may indicate that selection is affecting its genetic composition. These deviations can be detected only if the three possible classes of genotype at a locus can be distinguished from each other. In many cases, dominance leads to heterozygotes being phenotypically indistinguishable from one of the homozygotes. In other instances, however, - such as in the wing patterns of the moth Panaxia dominula (Fisher & Ford 1947) - dominance can be seen to be incomplete. As dominance may often be a function of the expression of a gene (see Fisher 1958), detection of heterozygotes is more frequently possible as the level of investigation approaches that of the gene. This has been the case in investigation of X-linked muscular dystrophy, where heterozygotes (who show no gross phenotypic abnormalities) have an increased level of serum creatine kinase (Walton 1969). Perhaps the clearest example of heterozygote detection is given by the work of Nolte (1959 a, b), who found that heterozygotes for some alleles at the white eye locus in D. melanogaster can be distinguished from the dominant homozygote by spectrophotometric assay of the amount of eye pigment, although dominance appears to be complete on simple visual examination of the eyes.

In C. nemoralis nearly all the banding variants whose mode of

inheritance is understood show complete dominance. Cain et al (1960) found that shells heterozygous for the ground colour genes Dark Pink and Yellow usually show no visible difference in colour from homozygous Dark Pink shells. In the majority of individuals known from breeding experiments to be Pale Pink/Yellow heterozygotes, however, the shell has a yellow tip, and in some cases the yellow coloration extends for a considerable distance down the shell. Similar incompleteness of dominance may occur in Brown/Yellow and Brown/Pink heterozygotes. About ten percent of these heterozygotes show complete dominance, so that the presence of the recessive gene's pigment on the tip of the shell is not a character which can be used to detect deviations from the Hardy-Weinberg equilibrium with any degree of accuracy.

The existence of visible incompleteness of dominance in some colour heterozygotes suggests that application of techniques more sensitive than visual observation might allow detection of heterozygotes in colour classes other than Brown or Pale Pink, and might increase the accuracy of heterozygote detection in these classes. Development of an accurate method of heterozygote detection would render possible several new aspect of research with Cepaea.

d) Heterozygote Advantage and Maintenance of the Colour Polymorphism.

Many polymorphisms are believed to be maintained by heterozygote advantage, whereby the heterozygote is selectively superior to both homozygotes. The selective forces involved are sometimes surprisingly large, - for example, although humans homozygous for sickle-cell haemoglobin have at least a 90% reduction in fitness, the heterozygote's superior resistance to malaria maintains a frequency of up to 40% heterozygotes in some African populations (Allison 1956). Cain & Currey (1963a) have pointed out that although morph ratios in C. nemoralis populations may be altered by selective predation, the polymorphism must be maintained by an opposing selective force, which probably involves heterozygote advantage.

They calculate that the selective advantage of heterozygotes over homozygotes in non-area effect regions is likely to be of the order of 5%.

If heterozygotes could be distinguished, the accuracy of this estimate could be tested by comparing the proportion of heterozygotes in snails hatched in the laboratory with the proportion in adult snails in natural populations, or by breeding from parents whose genotypes have been scored and comparing the observed and expected frequencies of heterozygotes in the offspring. Prout(1965) has shown that net fitnesses cannot be estimated from information on genotype frequency in a population determined by counting genotypes at the same stage of development in two successive generations, unless the selective process has been completed at the time when the genotypes are observed. As we have little information on the stages in the lifecycle when natural selection might act in Cepaea, it will be necessary to examine genotype frequencies in at least three parent/offspring transitions in order to estimate fitness (Prout 1969). This might be an obstacle to any attempt to measure the action of heterozygote advantage.

Clarke (1962) suggests that another mechanism - "apostatic selection" - may help to maintain polymorphism in Cepaea. Predators tend to take a disproportionately high proportion of the common varieties of a polymorphic species and a correspondingly low proportion of the rarer morphs. This is due to the development of a "searching image" by the predator, whereby it becomes conditioned to associating one particular morph with food. Such behaviour may maintain a polymorphism in which the rarer morphs are always at a selective advantage.

As this mechanism of maintenance of polymorphism is a function of predator behaviour, there should be no consistent excess of heterozygotes in stable populations whose polymorphisms are maintained solely by apostatic selection. Development of a method of heterozygote detection

in Cepaea might render possible an estimate of the relative importance of heterozygote advantage and other types of selection by comparing the actual excess of heterozygotes with the excess calculated by Cain and Currey to be necessary to maintain the polymorphism. Because of its low mobility, Cepaea would also be ideal material for field experiments on the ecological manifestations of heterozygote advantage.

b) Heterozygote Detection and Area Effects.

Theories of area effects which emphasise direct response of gene frequency to selection by the environment (see General Introduction) predict that there will be no gross deficiency of heterozygotes in the clinal zone between two area effects, as this cline represents a region where there is a gradient in some selective factor, and not a zone of hybrid disadvantage between two balanced genecomplexes. Coadaptive theories, however, suggest that inter-area hybrids will be selectively inferior, as they belong to neither of the parents' "adaptive peaks". There should therefore be a deficiency of inter-area heterozygotes in a cline.

If application of a heterozygote-detection system revealed a gross deficiency of heterozygotes in a cline, we would be justified in claiming that the maintenance of each area effect involved some degree of co-adaptation. The absence of such a deficiency of heterozygotes, however, is not necessarily a proof that coadaptation is unimportant in the maintenance of area effects. Clarke's (1966) model of steepening clines predicts that the accumulation of modifiers results first in one homozygote becoming selectively disadvantageous when placed in the genecomplex of the area effect for the other homozygote, and then in the inter-area heterozygotes themselves becoming disadvantageous. The existence of coadaptation will therefore be revealed by a deficiency of heterozygotes within the cline only in the later stages of evolution on this model. The presence of heterozygote advantage can legitimately be deduced from

observed zygotic distributions only if the composition of the genepool is stable (Wallace 1958). Gene frequencies are in the course of alteration in a steepening cline, and the possibility of this source of error giving an apparent heterozygote advantage should be bornein mind when examining clines. In steep clines a situation may arise where F_1 hybrids between two coadapted genecomplexes show heterosis while the majority of the F_2 recombinants do not survive because of the breakdown of balanced gene-complexes. Immigration into the cline from each area effect may give rise to a situation where F_1 luxuriance maintains an excess of heterozygotes which masks any deficiency of inter-area heterozygotes due to the break-down of fitness in the F_2.

ii) Shell Pigmentation and Solar Heating.

It is possible to predict the thermal response of an object to radiation from a knowledge of the spectrum of the incident radiation and of the absorption of different wavelengths by the object itself. In chapter 2 of this thesis I have shown that there is an association between the frequency of the shell colour morphs throughout the range of C. nemoralis and environmental temperature. Analysis of the spectral characters of C. nemoralis' shell pigments may indicate whether differences in heat input in sunshine are likely to be important in controlling such associations of gene frequency with climate in this species.

The Shell and its Pigment.

The shell of Cepaea consists of crystals of calcium carbonate (in the form of aragonite) embedded in a proteinaceous matrix of conchiolin, and covered by a thin periostracum, which is a layer of quinone-tanned protein (Comfort 1951b).

Little is known about the biochemistry of the shell pigments of land pulmonates, although Comfort (1951a) has shown that the shells of many marine molluscs are coloured by acid-soluble pyrroles and porphyrins

(especially uroporphyrin). Comfort has also worked on the ground pigments of the helicids Polymita picta and C. nemoralis. In P. picta (but not C. nemoralis) the pigment could be peeled from the decalcified shell and was also slightly soluble in acidified 2-chloro-ethanol. Attempts to decolourise the shell by feeding both species with melanin inhibitors failed. Comfort suggests, nevertheless, that at least some of the ground pigments of land molluscs may be melanins.

Helmcke (1935) also found Cepaea shell pigments to be intractable, as they were not soluble in a wide variety of organic solvents. He named them as Xanthocochlin (yellow), Phaeocochlin (pink), and Melanocochlin (brown). Emberton (1964) chelated the shell with Ethylene-diamine-tetra-acetic acid (EDTA), but was unable to separate the pigment from the chelated mixture. A number of histochemical tests carried out on the pigment in situ failed to identify it with any accuracy.

Although Cepaea shell pigments have proved difficult to handle, their possible importance to our understanding of the ecological genetics of this genus makes further investigation very desirable.

Materials, Methods and Results.

Early experiments were carried out using C. nemoralis shells collected from various localities in the South of England. When it became necessary to analyse complete samples, collections from the Scilly Isles, from Mounts Bay in Cornwall, and from Montrose Dunes were utilised. Whenever possible, unbanded shells were used, but when banded shells had to be examined, the band pigment was found to be considerably more inert than the ground colour pigment; it had no apparent effect on the results of the ground pigment experiments. Most of the work was carried out on pink and yellow shells, as few brown shells were available.

i) Removal of the Periostracum.

Shells bearing a periostracum gave a yellowish solution (the colour of

which did not depend on the colour of the shell used) when refluxed with organic solvents. This was not obtained when shells without periostraca were used, and in subsequent experiments the periostracum was removed by boiling the shell for 10 minutes in saturated sodium hydroxide solution, which hydrolyses the periostracal proteins. The shells were then washed in running water overnight to remove residual NaOH.

Old shells often show periostracal darkening which obscures the ground pigment. After removal of the periostracum the various morphs can be clearly distinguished - this might prove to be useful in cases where it is impossible to distinguish between the colour morphs, as in the Clarke et al (1968) study of sand-dune populations, where it was difficult to separate pale brown shells from the other colour morphs.

ii) Removal of Pigment from the Shell.

a) EDTA.

Shells were immersed in Tetrasodium EDTA for one week at room temperature. This chelating agent causes shells to disintegrate leaving a pale yellow solution irrespective of the colour of the shells used. Adsorption of the EDTA - shell - pigment complex onto carboxymethyl and diethylaminoethyl celluloses disclosed the presence of a strongly negatively charge yellowish substance in the complex, which could not be disassociated from the cellulose when eluted with solvents of different polarity and different pH.

EDTA-pigment complexes were investigated no further, as the colour of the complex shows no relation to that of the shell used, as the strongly anionic element could not be removed from charged cellulose, and as Emberton's (1964) work on spectrophotometry, chromatography, and partition extraction of EDTA - shell - pigment complexes shows that the different colour morphs give apparently identical EDTA complexes, and that the pigment cannot easily be extracted from the complex.

b) Enzymatic Digests.

Comfort (1951b) states that "the pigments of almost all the higher molluscs appear to be chemically incorporated in the protein of the shell". Attempts were therefore made to remove the pigment from the shell with proteases.

1) Pancreatin.

This complex protease was used in preference to others as it hydrolyses bonds in a relatively undiscriminatory fashion. 5 gm of washed fragments of yellow, pink and brown shells were incubated with 2.5 mg of pancreatin (British Drug Houses) in 10 ml of phosphate buffer pH7 at 36°C for 12 hours. No colour was lost from the shells and none appeared in the solution.

2) Papain.

5 gm of washed fragments of yellow, pink and brown shells were incubated with 0.05 ml of papain (Sigma Chemical Corporation) activated by 0.05 gm L-Cysteine in 10 ml of pH 7 phosphate buffer at 37°C for 12 hours. No colour was lost from the shells and none appeared in the solution.

Under these conditions, proteases do not release pigment from the shell. This may mean either that the pigment is not attached to protein, or that the pigment with any associated protein is held in the interstices of the aragonite crystals of the shell where it is protected from the action of the protease.

c) Organic Solvents.

Yellow, pink and brown shells were refluxed for a minimum of eight hours in petroleum spirit, tetrachloromethane, methanol, ethanol, diethyl ether, formaldehyde (as formalin), acetone, ethyl acetate, benzene, and α-hydroxytoluene. None of these solvents gave any positive results.

Emberton (1964) states that shells immersed in 2-chloroethanol for

a week at 60°C show some reduction of the ground pigment, although Comfort (1951a) found that acidified 2-chloroethanol had little effect on the ground pigment of C. nemoralis. Fragmented shells were left standing for 20 weeks at 25°C and heated for 3 hours at 70°C with neutral and acidified 2-chloroethanol. Neither of these treatments had any apparent effect on the shell pigment - the difference between this result and that of Emberton may be due to the different reaction conditions used. None of the experiments with 2-chloroethanol suggest that the shell pigment is easily soluble in this substance, and this line of approach was therefore pursued no further.

Shells heated at 80°C for 3-4 hours in glacial acetic acid gave murky solutions whose colour approximated closely to that of the shell used. 95% acetic acid was a more effective solvent than was glacial, as it erodes the outer layer of the shell and appears to release pigment molecules. Addition of 10% solid phenol to this solution slightly increased the rate at which pigment was removed from the shell, but for reasons of convenience most of the experiments described below were carried out using only 95% acetic acid as solvent.

d) Acid Etching Experiments.

Emberton states that "acids, however dilute, destroy the ground colour pigment", and Comfort that "the pigments of almost all the higher molluscs are insoluble in acid".

Shells were dissolved in a quantity of 0.5N hydrochloric acid calculated to give a neutral solution when all the calcium carbonate of the shell had been etched away, and the resulting solution filtered through Whatman No. 1 filterpaper. The filtrate was colourless, but some colour remained on the filterpaper, which was refluxed with an organic solvent (ethanol). A marked yellow coloration soon appeared in the ethanol, while the colour of the filterpaper depended on the colour of the

shell used, yellow shells giving a colourless filterpaper, pink shells a pink one, and brown shells a filterpaper of rather indeterminate dark hue. The pink colour of the filterpaper is not due simply to retention of flakes of insoluble pigment, as it can be seen to be dyed pink under the microscope. The colour could not be removed from the filterpaper by heating with a variety of organic solvents (including phenol and acetic acid).

iii) Spectrophotometry.

Single shells were treated with 10 ml. of 95% acetic acid for one hour, and the resulting solution centrifuged at 900G for 30 minutes to remove flakes of band pigment and suspended calcium acetate. The solutions were examined in a Unicam SP 800 spectrophotometer. Fig.27 shows eight typical spectrophotometer curves for yellow and pink shells from a colony near Penzance, Cornwall. The curves for yellow shell pigments show a marked inflexion near 430 mμ, which is absent from the spectrophotometer curves for pink shell pigment. There is a great deal of individual variation in the absorbance pattern of both shell colours over the whole wavelength range examined.

The absorbance spectra of solutions resulting from refluxing in ethanol filterpapers through which shells dissolved in hydrochloric acid had been filtered did not differ with the colour of the shell used. These solutions were therefore examined no further.

iv) Chromatography.

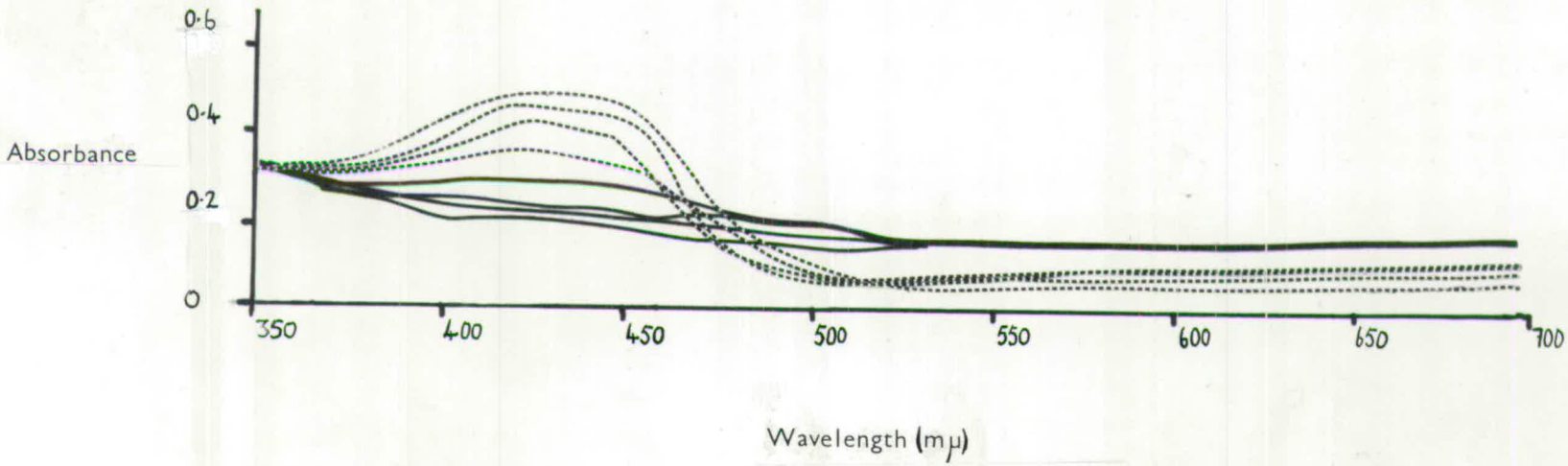
The differential absorption of pigment onto filterpaper after the shell has been dissolved in hydrochloric acid suggests that it may be possible to separate the two colour pigments by chromatography. Ascending-fluid adsorption chromatography of solutions of different coloured shells in hydrochloric acid was carried out on Whatman no. 3 chromatography paper, using hot ethanol as a solvent. Yellow shells gave one fast-moving spot ($R_f = 0.9$), while pink shells gave two, the slower-moving of which was pink ($R_f = 0.15$), the other ($R_f = 0.9$) being yellow. Both spots

Figure 27.

Fig. 27. Absorbance Spectra for Pink and Yellow C. nemoralis.

--------- Yellow Shells.

———— Pink Shells.


Absorbance
0·6
0·4
0·2
0
350
400
450
500
550
600
650
700
Wavelength (mμ)

(which are often very faint) were present in each of 20 pink shells from a sample collected on Montrose Dunes which would be expected from the observed phenotype frequencies to contain about 50% homozygous pinks. This result is obviously analagous to that given by refluxing filterpapers obtained from filtering HCl - treated shells in ethanol.

The results of these and other chromatographic experiments are described in more detail by Jones (1966).

Discussion.

i) Detection of Heterozygotes.

Attempts were made to identify traces of the recessive gene's pigment in heterozygous shells by attempting to distinguish two spectral or chromatographic classes within the pink morph which might be ascribed to homozygous and heterozygous individuals.

There is a great deal of variation in the spectrophotometer curves of pink and yellow shells both within and between samples. The sensitivity of this method to the presence of yellow pigment in pink-yellow mixtures was tested by adding small amounts of yellow pigment in acetic acid to pigment extracted from pink shells. Addition of more than 5% (by volume) of yellow pigment caused a noticeable displacement of the absorption spectrum of pink pigment. In many pink shells which are known to be heterozygous because of their yellow tip, the yellow pigment covers only the topmost whorl, which represents much less than 5% of the total surface area of the shell.

Examination of the spectrophotometer curves shows no tendency for the curves of pink shells from samples expected to contain both homozygous and heterozygous pinks to separate into two distinct classes which can be ascribed to the two genotypes, although some pinks do show a slight increase in absorbance in the 430 mμ region. The absorbances were transformed into two terms, one of which (the "specific chromaticity index") is independent of concentration and allows comparison of pink spectra at

the points where they are most different from yellow, and another (the CIE trichromatic specification) which utilises the whole absorption spectrum to give a specification of the shell's colour.

a) The Specific Chromaticity Index.

Examination of complete spectra is laborious and suffers from the disadvantage that differences in concentration tend to obscure any differences in spectral absorption. Many shells were examined by a simpler method - the comparison of absorbances at different wavelengths.

Absorbance contains a concentration term:-

$$\text{Absorbance} = \log_{10}\frac{F_o}{F} = E_\lambda cL$$

where F_o = intensity of incident light

F = intensity of transmitted light

E_λ = molecular extinction coefficient

c = concentration

L = path length.

Choosing absorbances at points of maximum difference between the curves for pink and yellow pigment, we have:-

$$\frac{abs_{360}}{abs_{430}} = \frac{E_{360}\cdot c.L}{E_{430}\cdot c.L} = \frac{E_{360}}{E_{430}} = S.$$

S, which I have called the "specific chromaticity index" is characteristic of the pigment used, is independent of concentration, and requires very little computation.

Examination of the specific chromaticity indices of a large number of pink shells from samples from Tean, Tresco and Penzance (which would, on the assumption of Hardy-Weinberg conditions, be expected to contain about 20%, 20%, and 60% heterozygotes respectively) revealed no consistent differences in this parameter either within or between samples which could be ascribed to differences between homozygous and heterozygous pink shells.

b) The CIE System.

The CIE (Commission Internationale de l'Eclairage) system is an accurate method of colour specification which is widely used in the study of the physics and chemistry of colour. The definition of visible light as "that part of the electromagnetic spectrum which excites the eye" involves physiological and psychological terms which show considerable individual variation. The CIE system attempts to overcome this variation by providing a reproducible standard for the specification of colour.

Any colour can be reproduced by mixing different proportions of the primary colours red, blue, and green. The CIE has adopted red (X), green (Y) and blue (Z) reference stimuli based on a "standard observer". The colour quality C of any colour c is recorded by its "unit trichromatic equation":-

$$C = xX + yY + zZ$$

where x, y and z are the trichromatic coefficients. On the CIE system, $x + y + z = 1$, so that colour quality becomes a function of two variables only, and can be represented on a chromaticity diagram.

The trichromatic specification of a colour can be calculated from the absorbance curve by summating the trichromatic equations of the spectral components using tables provided by Wright (1964). This method can separate some colours which are indistinguishable to the eye, so that any element of yellowness in heterozygous pink shells may be noticeable on a CIE chart.

The CIE specifications of a number of pink shells from three different collection localities were examined. There is no apparent tendency for shells collected at one locality to separate into two classes on a CIE chart which might represent homozygous and heterozygous individuals, although both genotypes are expected to be present in all the samples examined. There are some differences in CIE specification between localities; it is possible that refinement of this technique of measuring shell colour

combined with breeding experiments will reveal new alleles at the colour locus similar to the "dark", "pale" and "faint" allelic variants within the major colour classes already described by Cain et al (1968). Specification of shell colour by the CIE method could also be valuable for standardisation of colour morphs, particularly as shells fade fairly rapidly.

Several improvements will have to be made to the techniques described in this chapter before absolute measurement of shell colour (rather than comparison of shells of different colours) is possible. The most important of these involves the use of a standard white material as a reference at each wavelength when measuring spectra; as this was not possible with the apparatus available, the trichromaticity specifications so far obtained can only be used to compare the spectra of different shells and do not represent an accurate measure of the shell's real colour.

c) Chromatography.

The results of these experiments do not give any indication that it is possible to distinguish heterozygotes by chromatography. The fast-moving yellow spot found when acid extracts of pink shells are subjected to adsorption chromatography is unlikely to represent yellow pigment extracted from pink/yellow heterozygotes as it occurred in every pink shell tested. Partition chromatography also gave negative results (Jones 1966).

ii) Shell Pigmentation and Solar Heating.

It is well known that dark-coloured objects heat up more than light-coloured when exposed to the sun. The relevance of this to the effects of an animal's pigmentation on its thermal relations with the environment will be discussed at some length in the General Discussion of this thesis, with particular reference to the probable effects of climate on gene distribution in Cepaea.

The heat input of an object in sunlight can be predicted from information on its spectral characters combined with a knowledge of the energy distribution of the sun's radiation. The spectrophotometric analysis of Cepaea shell pigments described above provides some information on the absorption of radiation by shells of different colours. Solar energy at different wavelengths on the earth's surface can be calculated from tables of solar spectral irradiance above the atmosphere combined with a measure of the attenuation of the sun's rays by the atmosphere in the region under investigation. The "normal optical thickness" (τ) of the atmosphere (Deirmendjian & Sekera 1954) is a measure of its monochromatic attenuation coefficient (which depends on the density and refractive index of the air at different heights above sea level). Norris (1967) has combined this parameter with data on the spectrum of solar radiation to give a measure of absolute global radiation at different heights under standard conditions of time, season and angle of irradiation. The tables which he provides refer to solar energy reaching the earth at a latitude of 34°N (which traverses the Mediterranean). There are only minor differences between these values and those found within the European range of C. nemoralis.

Integration of the absorbance curves of Cepaea shell pigments with this curve of solar energy provides a measure of the amount of heating of Cepaea of different shell colours in sunlight. This calculation omits the effects of heating by reflected radiation, by infra-red radiation from the environment, and by direct conduction (see Gates 1962), and cannot therefore be used to predict the absolute amount of heating of different coloured shells. These sources of energy are normally less important than are the direct thermal effects of the sun's rays, and in any event an animal's thermal response to long-wave radiation does not depend to any great extent on its colour. Data from the analysis described above will therefore indicate the relative heat input of different coloured

C. nemoralis exposed to the sun fairly accurately.

Calculation of solar heating using this method for each of ten pink and ten yellow shells from a sample collected near Pensance gave a mean value of energy absorption from sunshine of 0.2221 cal/cm^2/min for pinks and 0.1741 cal/cm^2/min for yellows. Although this result must be regarded as preliminary, as the instrument available allowed measurement of absorption only up to a wavelength of 800 mμ instead of the standard 1500 mμ, and as insufficient attention was paid to differences in the concentration of the pigment solutions examined, it seem likely that pink shells will absorb more solar energy than do yellows. This may help to explain some of the patterns of distribution of the shell colour genes in natural populations of C. nemoralis both on the microgeographical and on the large scale (see General Discussion).

iii) Biochemistry of the Shell Pigment.

It is possible to speculate on the biochemical nature of the ground pigments. They are not immediately soluble in water, nor in organic solvents such as ether. They are therefore unlikely to be flavins, carotenoids, or chromolipoids. There is no Soret band in the ultraviolet absorption spectrum. This is true even when the shell has been digested away with HCl, in contrast to some bird egg shells where UV fluorescence does not appear until after this treatment (Fox and Vevers 1960). The pigments are therefore probably not porphyrins.

The pigments resist hot concentrated sodium hydroxide solution for a considerable time, and are not precipitated by dilute hydrochloric acid - this suggests that the ground pigment is not a melanin, as do Comfort's experiments in which melanin inhibitors had no effect on the shell colour. Emberton's (1964) positive result with the argentaffin reaction (which is a test for melanins, although positive results may be obtained with other substances) casts some doubt on this, however. The violet hue of some

shells included in the "brown" class is a colour which has not previously been attributed to melanins.

Indigoids are indole pigments which are often brightly coloured (dibromoindigotin, found in the marine mollusc Nucella lapidarius, for example, is purple). Simple indigoids are soluble in acetic acid and some other organic solvents. Cepaea shell pigments are soluble in some organic solvents after the shells have been treated with acids (which may release pigment molecules from a complex with the structural material of the shell). Indigoids are not highly labile when treated with dilute alkalis. (Fox & Vevers 1960).

The ground colour pigments of C. nemoralis have affinities with melanins and with indigoids. The final decision as to which class they belong must await further investigation.

GENERAL DISCUSSION.

There is now a considerable body of evidence suggesting that some dark-coloured shell phenotypes in *Cepaea* may be at a selective advantage over light-coloured shells in relatively cold places. This was first proposed by Cain & Currey (1963a) to explain the distribution of dark brown shells in *C. nemoralis* on the Marlborough Downs, and there have now been several other attempts to associate morph frequency with climate in this species (see below, and General Introduction). In this thesis I have described a rather clear association between light shell colours in *C. nemoralis* and warm conditions in a southern peripheral population of this species (Chapter 1), and also over the whole of the species' range (Chapter 2). In Yugoslav *C. vindobonensis* populations, fully pigmented shells appear to be favoured over shells with reduced pigmentation in areas where cold air accumulates (Chapter 3), and this may be reflected in a large-scale association of morph frequency with climate in this species (Chapter 4). Studies on the shell colour pigments themselves have shown that pink pigment probably absorbs more solar energy than does the yellow (Chapter 5); this would be expected to give pink shells an advantage over yellows in cold conditions.

In this General Discussion I shall attempt first of all to discuss the nature of the selective agent which may act on the genes determining the intensity of shell pigmentation, and then to speculate on the response of these genes to selection by the environment and to their possible interaction with other elements of the gene complex.

i) The Nature of the Selective Agent.

Organisms can gain heat (apart from metabolic heat) from their environment by conduction from the air and substrate, by incoming solar radiation (either direct or diffuse) and by infra-red radiation from the atmosphere, the ground and the surrounding vegetation. Heat may be lost

by conduction, by convection, by radiation and by evaporative cooling. (Gates 1962). The physics of the thermal relations of animals with their environment is well reviewed by Birkebak (1966) and by Porter & Gates (1969).

It is well known that dark-coloured objects heat up more than light-coloured when exposed to the sun; black cards, for example, may reach a temperature 40°C above that of white cards when placed in direct sunlight (Schropp 1931). Many experiments have shown that the dark forms of various animals heat up more rapidly and attain a higher equilibrium temperature than do light individuals of the same species when exposed to solar radiation.

Hill & Taylor (1933) found that the body temperature of black locusts in sunlight is up to 3.5°C higher than that of green locusts under the same conditions. Experiments with insects painted black or white show that black individuals may have a 20%-50% advantage of energy absorption from sunlight when compared to white (Digby 1955). Direct measurement of energy absorption in Colias butterflies has demonstrated that insects whose wings contain dark melanin pigment absorb approximately 0.62 cal/min/cm^2 of energy from sunshine, while light unpigmented individuals absorb only 0.39 cal/min/cm^2 (Watt 1968).

The effects of colour on energy absorption from sunlight have also been studied in other animals. In the fiddler crab, Uca, dark-coloured crabs attain a body temperature 2°C higher than that of light-coloured within five minutes of exposure to the sun (Wilkens & Fingerman 1965). Direct observation of the energy absorption of mammalian skin shows that white cows reflect 20%-40% more of the solar heat load than do red (Riemerschmid & Elder 1945), and that white pigs may absorb only half as much solar energy as do black (Kelly et al. 1954). Norris (1967) in an exhaustive analysis of energy flux in lizards has found that a desert iguana (Dipsosaurus dorsalis) will show a 23% decrease of heat input in

sunshine when skin colour changes from dark to light as a result of melanophore contraction. This a particularly convincing illustration of the effect of the colour of the integument on heat input, as it refers to the same individual under different natural conditions of skin pigmentation.

Such differences in energy absorption are known to have a considerable effect on the physiology of different coloured animals in sunlight. Watt (1968, 1969), working on Colias, has shown by behavioural studies combined with direct observation of body temperature that an initially cold and torpid dark-coloured insect reaches a temperature suitable for activity considerably more rapidly than a light-coloured one when exposed to the sun as it has a rate of heating approximately 1°C/minute greater than that of the light-coloured. As the body temperature rises above 38°C, heat-avoiding behaviour sets in; light-coloured insects can therefore remain active for longer than dark-coloured when exposed to bright sunshine on a hot day. Vertebrates of different colours also show different physiological responses to sunshine. White zebra finches exposed to an artificial "sun" show a decrease in oxygen consumption (which is, of course, an indication of a decreased metabolic rate) of 22.9% when their heat economy has been altered by dyeing them black (Hamilton & Heppner 1967). Porter & Gates (1969) using their calculations of the "climate space" which can be tolerated by various animals predict that, if there is no wind, a black pig will find it difficult to endure full sun if the air temperature is greater than about 10°C, while a white pig could endure full sun at air temperatures up to 25°C.

Colour of the body surface clearly has a major effect on energy absorption from sunlight. It has sometimes been assumed (see, for example, Kettlewell 1961) that, as dark-coloured animals gain much more heat by radiation from the sun, they will therefore lose more heat by radiative cooling at night. A little thought will show that this is not so. The

Wien Displacement Law states that the wavelength of radiation from a surface depends on its absolute temperature. This is about 280°K for invertebrates, resulting in a radiation peak of 8-10μ . The Kirchoff law relates the intensity of emission from an object to its fractional absorption of radiation at the same wavelength. A body's absorptivity of visible light (which will, of course, determine its colour) at about 400-700 mμ therefore bears no relationship to its loss of heat by emission of radiation which has a much longer wavelength. The problem of radiative heat loss from surfaces shielded from a heat source is treated in detail by Birkebak (1966), who concludes that, in general, radiation from animal bodies approximates to that from a perfect radiator irrespective of the colour of the integument. There is some experimental evidence which supports this conclusion. Photography of human subjects using heat-sensitive film shows that there is no difference in emissivity between whites and blacks (Barnes 1963). Similarly, dark and light Colias shielded from the sun show no difference in their rate of cooling or in their activity, and white and black zebra finches in the shade do not differ in their oxygen consumption (Watt 1968, Hamilton & Heppner 1967).

Several studies have also shown directly that radiative cooling is usually much less important than other methods of heat loss in animals. In homoiotherms (Porter & Gates 1969) and in poikilotherms which have a permeable integument (such as Ligia, the sandslater (Edney 1951)) cooling by evaporation is the most important factor in heat loss. In animals which do not have a permeable integument (such as insects (Church 1960a)) evaporative cooling plays a very small part in reducing heat load. Direct measurement of body temperature of snails in an environmental chamber has shown that evaporative cooling normally keeps the animal's temperature well below that of the environment when the body is extended, but that when water loss causes the snail to withdraw into its shell its

temperature approaches that of the air (Hogben & Kirk 1944). C. nemoralis rapidly withdraws into its shell unless the relative humidity is high, so that this species is usually inactive and sealed into its water-impermeable shell during the day (when it is exposed to solar heating)(Cameron 1970a). C. nemoralis is almost completely nocturnal in its activity even in humid conditions when the environmental temperature is high (Cameron 1970b). Evaporative cooling is therefore unlikely to be important in relieving solar heat load in Cepaea.

Convection seems to be the most important mechanism of heat loss in small poikilotherms. Measurement of the loss of heat from dead insects heated internally shows that over 70% of the heat generated must be lost by convection (Church 1960b). Investigation of the temperature of small blackened copper spheres suspended in sunlight also demonstrates that convection plays the most important part in heat loss from these objects (Parry 1951). Thermal losses by evaporation and convection are not, of course, affected by the colour of the surface which loses heat.

It seems clear that the amount of dark pigment in the shell of Cepaea is likely to have a marked effect on heat input in sunshine, and therefore upon the animal's physiology, but that the rate of heat loss will not depend on shell pigmentation. Snails with a light-coloured shell will therefore be favoured in situations where they are likely to be faced with a heavy heat load, while those with dark shells will be at an advantage in places where it is necessary to obtain maximum heat from the sun's rays. This may explain some of the patterns of gene distribution found in this genus. The cline of increasing frequency of yellow shells from the North to the South of C. nemoralis' range is probably due to the ability of snails with yellow shells to tolerate higher temperatures because of their relatively low absorption of solar radiation. Similar selective forces may act on the microgeographical scale. Dark brown and pink shells

are found preferentially in frosthollows in some C. nemoralis populations, and fully-pigmented shells of C. vindobonensis also seem to be commoner in frost hollows than are shells with reduced pigmentation. C. nemoralis and hortensis (and probably the other species of Cepaea also) are primarily nocturnal and crepuscular in their activity, but are active even in daylight under cold conditions (Cameron 1970b). Snails which are darkly pigmented will warm up more rapidly in the early morning sun, and this will enable them to reach a temperature suitable for feeding and other processes sooner than do light-coloured snails. This is likely to be particularly important after an inversion of temperature.

There is at present no direct evidence of differential heating of snails with different shell pigmentation similar to that provided by Watt for the pigment polymorphism of Colias. Emberton & Bradbury (1963) have found that pink and brown shells in C. nemoralis absorb more light than do yellow (although light absorption is also very dependent on shell thickness) and this accords with the observation of Watt that dark-winged Colias absorb light more efficiently than do light-winged. I have shown in chapter 5 that the spectral characters of the different shell colour pigments probably lead to pink shells absorbing more energy from sunlight than do yellows. There is also some indication that snails of different colours behave in a manner which may be related to their thermal characteristics, as does Colias. Under some conditions in the field yellow snails climb more than do pinks (Wolda 1965), and this may be a function of heat-seeking behaviour in yellows or heat-avoidance behaviour in pinks. Yellow snails placed in an artificial temperature gradient take up a resting position at a higher temperature than do pinks (Sedlmair 1956). Pink and brown C. nemoralis tend to shelter more under protecting ledges on an illuminated wall than do yellows (Gregg, pers. comm.); this is the pattern of behaviour which would be expected if pinks and browns are

more susceptible to the effects of radiant heating than are yellows. Experiments on the direct measurement of thermal uptake and response to radiation of the different shell morphs in Cepaea are likely to provide very valuable results.

Although some gene distributions in Cepaea accord with the hypothesis that dark-coloured shells are favoured in localities where it is necessary to absorb the maximum heat from the environment and light-coloured where heat load is likely to be excessive, this clearly cannot provide a complete explanation for the distribution of genes in area effects. Area effects are frequently found in topographically uniform regions where there is less obvious possibility of microclimatic differences between areas, and it is impossible to associate the frequency of some phenotypes with environmental selection even where there are clear climatic differences, either on the small or on the large scale.

I shall now discuss the manner in which different genes in Cepaea may respond to environmental factors, and the way in which this response may effect their frequencies in natural populations.

ii) The Response of Colour and Banding to Environmental Selection.

In this thesis we have seen that it is possible to associate the frequency of the genes controlling shell colour in C. nemoralis with climate in a Yugoslav peripheral population and also throughout this species' range. The microgeographical distribution of pink shells (which are most common in a frost hollow) in this peripheral population may also show an association with extremes of low temperature. A comparison of genetically rather isolated populations in Yugoslavia living in similar environments shows that they tend to have similar frequencies of the shell colour genes. The distribution of genes controlling the intensity of band pigmentation in C. vindobonensis has a very clear association with microclimate in Yugoslavia, and this may be reflected in the large-scale distribution of gene frequencies in this species. In none of the populations described in this thesis has it

been possible to associate the frequency of the genes controlling the number of bands on the shell in either C. nemoralis or C. vindobonensis with climate. Five-banded Cepaea have considerably more dark melanin pigment than do unbanded shells. Banded and unbanded shells also differ in their light transmission properties, both in the bands and in the inter-band regions (Emberton & Bradbury 1963). It therefore seems unlikely that a shell's thermal characteristics are unaffected by the number of bands which it possesses, as the differences in pigment intensity between banding morphs is often as great as that between colour morphs. It is, however, possible that the frequencies of the genes controlling the number of shell bands are usually determined primarily by selective factors other than climate, and that these may involve the "genetic environment" of the population.

There is a considerable body of evidence (together with some apparently contradictory evidence) from other research on Cepaea which also supports a hypothesis that the shell colour genes in general show a greater response to environmental selection than do the genes controlling the number of bands on the shell. This will now be discussed, as will the possibility that area effects for the number of bands on the shell may be primarily a function of the interaction of the banding genes with other elements of the population's gene complex while those for shell colour are more dependent on environmental selection.

a) Association of Morph Frequency with Topography.

Several surveys of natural populations of C. nemoralis have demonstrated an association of the frequency of the colour morphs with topography (and therefore presumably with microclimate), while the frequencies of the genes controlling the number of bands on the shell have no apparent association with this variable. The best-known of these is that of Cain & Currey (1963a) on the Marlborough Downs, where, as they themselves point out, the frequency

of dark brown shells, but not that of any of the banding morphs, is apparently associated with the ponding of cold air in frost hollows. Downlands adjacent to the Marlborough Downs also have a higher frequency of pink and brown shells in valley bottoms where cold air is likely to accumulate, although none of the banding morphs are unusually common in such regions (Carter 1968). Sand-dune populations show a very marked similar association between the frequency of dark brown and complex topography (which probably causes accumulation of cold air) (Cain 1968).

British and Irish dunes also tend to have higher frequencies of five-banded shells than do inland habitats, although there are no striking and generally occurring local correlations of the frequency of shell banding morphs with duneland topography similar to those found at the colour locus. Cain (1968) suggests that this pattern of variation is due to a general climatic similarity among dunes favouring five-banded shells. In view of the overall lack of an association of the frequency of this phenotype with climate described in chapter 2 this is perhaps rather unlikely. Dunes usually have a background of marram and other grasses, and five-banded is probably the most cryptic morph in this habitat. Visual selection by thrushes is known to occur on some dunes (Clarke & Murray 1962); the high frequencies of pink and five-banded on dunes may therefore be due primarily to visual rather than to climatic selection. This possibility is mentioned by Cain (1968).

Guerrucci-Henrion (1966) has shown that the frequency of yellow shells (but not of unbanded, midbanded, and trifasciate shells) in populations of C. nemoralis living in Brittany is negatively related to the sampling site's distance from the sea. She suggests that this is due to a negative relationship between the frequency of yellow and rainfall.

The major exception to this general finding that in those regions where it is possible to associate morph frequency with topography or climate

it is the colour morphs rather than the banding morphs which appear to be related to this factor is Arnold's work in the Pyrenees (Arnold 1968, 1969). In two separate Pyrenean valley-systems he found that the frequency of unbanded shells is usually much higher on the floors of the highest valleys than elsewhere. Arnold suggests that this pattern of distribution is due to unbanded shells' greater resistance to the cold conditions caused by the ponding of cold air in the steep-sided upper valleys. Unbanded shells are also at a relatively high frequency in the lowest parts of the valleys. In these regions they are commoner on the hillsides than in the valley bottoms; this trend is opposite in direction to that found in the upper valleys. Arnold interprets these morph distributions as being due to unbanded snails' greater resistance to the hot and dry conditions found on the lower hillsides as well as to the cold conditions found in the upper valley bottoms. None of the colour morphs show such obvious regularities in their distribution.

Arnold's findings are apparently an important exception to the hypothesis that colour morph frequencies are usually more responsive to environmental selection than are banding.

In collaboration with Mr. A.J. Irving, I have examined C. nemoralis populations in the Ter valley in the Eastern Spanish Pyrenees. Although the data are not yet extensive enough for a complete analysis, certain trends are obvious. Unbanded shells are most common in the intermediate parts of the species' range of height (where they often make up 100% of the snails collected), and are almost absent from the samples in the highest valleys, both on the hillsides and on the floors of the valleys. Pink shells are rare, (overall frequency = 3.8%) and there are few apparent regularities in their distribution. They are slightly more common in the lowest samples.

The distribution of morph frequencies in the Ter valley is therefore

very different from that in the valleys studied by Arnold. The distribution of unbanded shells is, indeed, the inverse of that found in Arnold's valley systems, so that the pattern of distribution of this morph found by Arnold is not of general occurrence in the Pyrenees.

ii) Selection by Predators.

In several regions, differential predation by thrushes acting against the more conspicuous shells is known to affect morph frequencies in C. nemoralis populations. In the Oxford area, where this pattern of morph distribution was first described, there is no evidence that samples match their backgrounds significantly better for colour than for banding (Currey et.al. 1964). The colour of the shell does not therefore appear to make an intrinsically greater contribution to its degree of crypsis than does its banding pattern. Differences in relative conspicuousness between shells of a colour which does not match their background and shells of an inappropriate banding pattern cannot in any case explain the situations described by a number of authors where, in some regions, both colour and banding morph frequencies appear to respond to differential selection by predators, whereas in other areas with similar contrasts in background, the frequency of the colour genes varies in the direction expected on the hypothesis of visual selection, while that of the banding genes is apparently independent of the colour of the background and depends on a systematic or regional effect.

Populations on the Marlborough Downs and on the nearby Lambourn Downs show strong area effects for both colour and banding. (Cain & Currey 1963a) In a number of woodland localities on the Downs visual selection appears to affect gene frequencies at the colour locus, but nowhere does selection by predators have a detectable effect on the frequencies of the banding genes. A similar pattern of morph distribution is found in some places on the South Downs (Arnold 1966) and on the Yorkshire Wolds (Harvey, pers. comm.).

Carter (1968), working on the Berkshire Downs in an extensive region over which area effects gradually give way to the patterns of morph distribution known to be due to visual selection found that the frequency of the colour genes begins to respond to differential selection by predators before that of the banding genes. There is thus a region of transition between the Marlborough Downs and Oxford which is characterised by a "visual selection" pattern of distribution of the shell colour genes, but an "area effect" distribution of the genes controlling the number of bands on the shell. It therefore appears that the systematic effects which maintain the frequency of the banding genes independent of background are more resistant to the directional action of visual selection than are those maintaining area effects for shell colour.

Populations of C. nemoralis in Touraine (France) show this type of response to environmental selection very clearly. (Arnold 1970) Over a large and ecologically diverse region banding morph frequencies are rather constant and independent of background, while the frequency of the colour morphs alters with background in the direction expected on the hypothesis of visual selection. Populations in Touraine therefore match their background for colour in a manner similar to that found in the Oxford region, while their pattern of banding morph distribution resembles that found on the Marlborough Downs. Once again, the colour genes appear to be responding to detectable environmental selection, while it is difficult to associate the selective force affecting the frequency of banding genes with an environmental variable.

Possible Causes of Area Effects.

From the results discussed in this thesis it appears that it is generally rather easier to associate the frequency of shell colour morphs with environmental selective forces in C. nemoralis than the frequency of shell banding morphs, although in some populations it is not possible to identify any environmental variables which may have a selective effect on these genes. It is difficult to carry out breeding experiments with Cepaea which might allow investigation of interaction of major genes with other elements of the gene complex, or to examine chromosomes directly for any evidence of such interactions between elements of the genetic material. There is, however, a great deal of evidence from research on other organisms which suggests that the frequencies of some genes or groups of genes may respond to environmental selection, while that of other genes is more dependent on their association with elements of the population's whole gene-complex. Such differential responses to environmental selection may help to explain some of the observed patterns of gene distribution in Cepaea.

Drosophila population cages founded with a high frequency of deleterious

mutants often show a rapid decrease in frequency and final elimination of the mutant which can be ascribed to its disadvantageous properties (see, for example, Wallace 1963 for recessive and Merrell 1965 for dominant mutants). In other cases, however, genes which are known to have deleterious effects when homozygous may persist in population cages for a considerable time (L'Heritier & Teissier 1937). Several experiments have shown that this is often due to interaction of these genes with other elements of the population's gene complex.

Frydenberg (1963, 1964) and Chung (1967) have analysed such a pattern of persistence of the recessive lethal sb^{W} in D. melanogaster. The mutant persisted for far longer than expected on theoretical grounds in some of the cages examined, although it was ultimately eliminated from all cages. Cytological examination showed that this was due to linkage of the mutant to a heterotic inversion in those cages in which sb^{W} did not follow the theoretical curve of elimination. Another investigation of D. melanogaster cages founded with high frequencies of various mutants showed that the selective values of the different mutant genotypes (and thus their persistence in the cages) depends to a very considerable degree on the genetic background of the founder population (Polivanov 1964). In some cases, interactions with the population's genetic background may lead to an apparently stable equilibrium of deleterious mutants in cages (Chigusa & Mukai 1964).

Experimental populations of other organisms also demonstrate the importance of genetic interactions in controlling the frequency, of at least some genes. Some Tribolium mutants are gradually eliminated from cages when in competition with wild-type beetles (McDonald & Peer 1960). In one case, however, two linked mutants which are rapidly eliminated when present singly persist for many generations when present together in the repulsion phase (Dawson 1970).

It is more difficult to study the relative importance of genetic interactions and environmental selection in natural populations than in the laboratory. As well as a number of well-known cases of supergenes,

(in which genes having synergistic effects evolve tight linkage and may even become associated together on an inversion) there are several instances of natural populations in which the frequencies of some genes or groups of genes appears to depend primarily on their response to environmental selection, while that of others is associated with their interaction with elements of the population's gene complex. D. robusta presents a particularly striking example of this pattern of variation (Carson 1958a, Levitan 1958). Many inversions show clines which can be correlated with climate, while the frequency of other inversions is primarily associated with the chromosome structure of the population. Levitan (1958) discusses many similar examples of non-random associations of inversions in Dipteran populations; others are described by Levitan & Salzano (1959) and Brncic (1961). The most intensively analysed case of an association between inversion polymorphisms is that of the Australian grasshopper Moraba scurra. (Lewontin & White 1960). There are strong interactions between the frequencies of certain inversions on different chromosomes. Although the general patterns of association are similar between populations there is great geographical variation in the relative frequency of particular pairs of gene arrangements which probably reflect differences in the adaptive value of the interaction between them. In one colony at least there appears to be no interaction effect between two inversions which elsewhere have highly correlated frequencies (White et al 1963). Interaction between an individual locus and an inversion has recently been found in a natural D. melanogaster population (Kojima et al 1970).

There have been several theoretical investigations of the origin and effects of such non-allelic correlations or "linkage disequilibria". Lewontin & Kojima (1960) showed that there will be a stable linkage disequilibrium if there is considerable epistasis or close linkage between

two genes, while Lewontin (1964b) found that selection for an optimum phenotype could lead to disequilibrium even between genes on separate chromosomes. Genes far apart on a chromosome can be held in disequilibrium by genes segregating between them (Lewontin 1964a, b), and recent work suggests that under certain conditions there may be strong correlations between loci along a whole chromosome even when the selective value of individual gene substitutions is small (Franklin & Lewontin 1970). Stable associations between loci may also arise as a result of finite population size (Hill & Robertson 1968); this is likely to be particularly important in immobile organisms which have a relatively small effective population size, such as Cepaea.

It may be possible to explain some of the observed patterns of gene distribution in Cepaea from a knowledge of the association of the frequency of some genes with environmental factors, and an understanding of how genes may interact in natural populations. There is little doubt that some local variations in gene frequency in Cepaea are greatly affected by microclimate. Several examples of this have already been discussed, as has the mechanism whereby such selection may act. It is equally clear, however, that climatic selection cannot provide a complete explanation of area effects in Cepaea. In many places it is impossible to associate the frequency of either shell colour or banding with microclimate, and in topographically very uniform regions it is in any case perhaps rather unlikely that microclimate could vary sufficiently to exert consistent selective effects on snail populations. Where it has been possible to associate morph frequency with environment, it has usually been the case that the shell colour genes show a greater response to environmental selection than do those controlling the number of bands on the shell.

These patterns of gene frequency distribution may be explicable in terms of differential integration of shell colour and banding genes into

the genetic background of the population. All four species of Cepaea show polymorphism for the number of bands on the shell, but only nemoralis and hortensis (which are much more closely related to each other than they are to vindobonensis or sylvatica (Perrot & Perrot 1938)) are polymorphic for shell colour. Banding polymorphism is also much more widespread than colour polymorphism throughout the Helicidae (Taylor 1914). Dowdeswell & McWhirter (1967) have described a rather similar situation in the butterfly Maniola, in which the gene systems influencing wing-spotting transcend the limits of the species in this genus; they refer to these genes as "palaeogenes". Many other interacting genes in Maniola's gene complex have evolved in conjunction with the spotting palaeogenes. The interaction between inversions in Moraba scurra is also known to have a very ancient origin, as similar disequilibria occur in the 15- and 17-chromosome races of this species, which have been separated for several million generations (Lewontin & White 1960). The frequency of the spotting genes in natural populations of Maniola appear to change in large quantum steps between a limited number of different stabilisations. Dowdeswell & McWhirter suggest that this type of gene frequency distribution may be expected to apply to palaeogenes in general.

The wide taxonomic distribution of some of the genes controlling the number of bands on the shell in Helicid snails suggests that they originated long before the colour genes, and can therefore be considered to be palaeogenes. As in Maniola, these genes may show stronger epistatic interactions with other elements of the population's gene pool than do the shell colour genes. The frequency of the shell banding genes in natural populations of Cepaea may therefore be expected to depend more on the strength and direction of these interactions than on environmental selection, while that of the colour genes shows fewer correlations with other loci in the population and is thus more responsive to the effects of

selection by the environment. Differential response to environmental selection similar to that described above for experimental and natural populations of several organisms may therefore help to explain some aspects of area effects in Cepaea.

Several area effects for shell colour in regions with local variations in topography and microclimate are clearly greatly influenced by environmental selection; it is possible to deduce one possible mechanism of this selection from our knowledge of the thermal relations of different coloured animals with their environment. The distribution of shell colour genes in area effects in topographically uniform places may, however, be primarily a function of their interaction with other genes in the population which overrides the small effects of local variations in microclimate. Epistatic interactions giving rise to stable disequilibria involving the genes controlling the number of bands on the shell are likely to be more powerful than those involving colour genes; local geographical variations in the frequency of shell banding phenotypes are therefore associated with complexes of genes which are more resistant to the disruptive effects of environmental selection, and can be maintained independent of the environment even in regions with considerable local differences in microclimate.

It is to be expected that the adaptive values of these gene interactions, the degree of linkage and the genes involved in the interacting complexes will vary from population to population as in Moraba scurra (where the degree of association of inversions shows considerable geographical variation) and in a number of experimental populations of Drosophila (see above). In some places there will therefore be local correlations of banding morph frequency with environment, which may be due either to direct selective responses of the banding genes themselves in a genetic background in which there are no strong epistatic interactions, or to the banding genes being held in disequilibrium with other genes

which themselves show a response to environmental selection. It is difficult to decide between these alternatives on the basis of field observations alone.

The most convincing association of banding morph frequency with environment is found in C. nemoralis in the central Pyrenees, where unbanded shells are much commoner in the bottoms of the upper valleys than elsewhere. Arnold (1968) suggests that this pattern of distribution is due to the greater resistance of unbanded shells to cold conditions occurring during temperature inversions in the valleys. This might be a sufficient explanation of the distribution of the alleles at this locus in Pyrenean populations although, in contrast to the pattern of allele distribution at the colour locus on the Marlborough Downs and elsewhere, it is difficult to identify physiological factors which could favour the relatively light-coloured unbanded shells in frost hollows. It is interesting to note, however, that the distribution of unbanded shells in the Ter valley is almost exactly the inverse of that found in the valleys studied by Arnold (Irving & Jones, unpublished data). This suggests that the pattern of distribution of the genes controlling presence or absence of shell bands in Pyrenean C. nemoralis populations may be due to an association of this locus with other genes or groups of genes which are responding to climatic selection, and to variation in the direction of this disequilibrium from valley to valley. This pattern of linkage distribution is found in Drosophila robusta, in which the same two inversions show a very significant coupling association in some populations and an equally strong repulsion association elsewhere (Levitan 1961). Variation in the direction of linkage could also explain the pattern of gene distribution found in lower valleys in the Central Pyrenees (where unbandeds are less common in valley bottoms) without having to postulate, as did Arnold (1969), that unbandeds are resistant to hot as well as to cold conditions.

Possible modes of origin of gene interactions giving rise to area effects in Cepaea have been considered by several authors. Goodhart (1963) proposes a simple model of founding populations evolving divergent gene pools until they meet, which, as Cain & Currey (1963d) point out, is probably not a sufficient explanation for the origin of most area effects. Wright (1965) has analysed the probable results of random formation of favourable combinations of genes (one of which may control a shell character) on population structure in Cepaea, and concludes that the spread of such interacting gene systems through a continuous population could give rise to area effects. Models of the evolution of clines (Clarke 1966) in which interaction of modifiers with major genes leads to genetic divergence between adjacent populations also provides a feasible mechanism whereby epistasis could lead to abrupt changes in gene frequency.

In all these models, increased epistasis will lead to greater local differentiation of population structure which may be independent of the environment. Involvement of such second-order phenomena in controlling the distribution of genes in populations may mean that it will often be impossible to identify the factors affecting gene frequency by simple observation of their distribution in natural populations. It may therefore be necessary to use methods quite different from those attempted so far in order to elucidate the causes of area effects in Cepaea.

ABSTRACT OF THESIS

This thesis is mainly concerned with the effects of climate on the genetic structure of natural populations of Cepaea snails. The Introduction discusses previous research on this genus, and in particular the controversy on the causes of "area effects" (which are local genetic differentiations of population structure which do not appear to be due to selective predation) between those workers who emphasise environmental selection as the main cause of these patterns of gene distribution and those who place more importance on evolutionary divergence of a whole complex of genes as the mode of origin of area effects.

Chapter 1 describes the genetic structure of a southern peripheral population of C. nemoralis in Yugoslavia. The gene for yellow shell colour is at a high frequency in this population, but the frequency of most of the genes controlling the number of bands on the shell does not differ greatly from that found in British populations. One population of this species living in hedgerows along roadsides in the study area showed great differences in the frequency of the shell banding genes between genetically rather isolated populations living close together, but had rather similar frequencies of the shell colour genes in these closely adjacent populations. Chapter 2 extends this investigation of peripheral populations to include the associations of gene frequency with climate throughout C. nemoralis' range. Published and unpublished data from other workers and from my own collections involving a total of about 500,000 snails was utilised. There was a very significant positive association of the frequency of yellow shells with mean summer temperature, but no such association of banding morph frequency with any of the climatic variables tested.

Chapters 3 and 4 are concerned with the structure of natural populations of C. vindobonensis. This species is much less polymorphic than C. nemoralis, as there is no shell colour polymorphism and as banding polymorphism is

restricted to a few variants in the number of bands, in their degree of coalescence and in the intensity of band pigmentation. Yugoslav populations living in a limestone region with a topography which is known to give rise to marked nocturnal inversions of temperature were investigated. There is a striking tendency for shells with reduced intensity of band pigmentation to occur only in places where cold air does not accumulate at night. No such clear associations of morph frequency with topography were found for the other shell phenotypes. A much less detailed investigation of C. vindobonensis populations was carried out in Romania, in an area with rather uniform topography. There were marked local fluctuations in the frequency of all the shell phenotypes, which did not appear to be related to microclimate. The overall frequencies of all phenotypes differed from those found in Yugoslavia; as only two regions with different climates were compared it is not possible to decide whether these differences represent a selective response to climate similar to that found in C. nemoralis. It is, however, interesting to note that shells with reduced intensity of band pigmentation are less common in Yugoslavia than in Romania (which is much hotter in summer than is Yugoslavia). This reflects the tendency of this morph to be commoner in warm places in Yugoslavia.

An attempt to develop a method of detecting shell colour heterozygotes in C. nemoralis (which if successful would have rendered possible several new aspects of research with Cepaea) did not succeed. Investigation of the spectral characters of the pigment suggested that pink shells will absorb more solar energy than do yellows. (Chapter 5).

The General Discussion reviews the evidence available on the effect of the colour of the body surface in animals on their thermal relations with the environment. It seems very likely that dark-coloured Cepaea will heat up more when exposed to sunshine than do light-coloured. This may help to explain some of the patterns of gene distribution found in this

genus both on the small and on the large scale. Climatic selection is unlikely to provide a complete explanation of gene distribution as area effects occur even in very uniform regions where there is little opportunity for local climatic differences to arise. A review of the literature, as well as the results presented in this thesis suggests that in general it is more difficult to associate the frequencies of the genes controlling the number of bands on the shell with the action of environmental selection than it is the frequency of other genes (such as the shell colour genes in C. nemoralis). The relevance of this to the causes of area effects is discussed.

APPENDIX I.

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THE DISTRIBUTION OF *CEPAEA* IN SCOTLAND

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(*Read before the Society, 20 January 1968*)

During the past three years we have been studying the population genetics of the polymorphic land-snail *Cepaea nemoralis* (L.) at the northern limits of its range in Scotland. In the course of our work we have prepared maps of the Scottish distribution of *C. nemoralis* and of its close relative *Cepaea hortensis* (Müll.). These maps (see Figs. 1 and 2) have been compiled from a number of sources:

(1) We have examined complete runs of the following journals:

The Journal of Conchology.
The Proceedings of the Malacological Society of London.
The Proceedings of the Royal Physical Society of Edinburgh.
The Scottish Naturalist.
The Transactions of the Banffshire Field Club.
The Transactions of the Stirling Natural History and Archaeological Society.
The Transactions and Journal of Proceedings of the Dumfries and Galloway Antiquarian and Natural History Society.
The Transactions and Proceedings of the Natural History Society of Glasgow (*continued as* The Glasgow Naturalist).
The Transactions and Proceedings of the Perthshire Society of Natural Science.
The Zoologist.

(2) We have corresponded with several Scottish conchologists, and have examined the collections of *Cepaea* in the Royal Scottish Museum and at the Nature Conservancy's Edinburgh office.

(3) With the help of members of Edinburgh University Biological Society and York University Biology Society we have collected about 15,000 specimens of *Cepaea* in Forfar, Kincardine, Aberdeen South, Aberdeen North, Banff, Elgin, Easterness, Westerness, Main Argyll, Ebudes North, Ross West, Ross East, and Sutherland West.

It is probable that some of the earlier distribution records are inaccurate. Roebuck (1917), for example, has shown that Gordon's (1839) description of *C. nemoralis* at Burghead (Elgin) is in fact a mistaken identification of black-lipped *C. hortensis*. Because of such uncertainties, we have attempted to re-examine all the most northerly localities from which *C. nemoralis* has been recorded. Where necessary we have dissected out the mucous glands and darts of individual

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KEY TO TABLES.

Table 1.

Grid Ref. : All samples are in the 55/49 square of the Yugoslav National Grid unless otherwise stated.

5N: Banding pattern 12345 with non-punctate bands.

5P: " " 12345 with punctate "

3N: " " 00300 with non-punctate "

3P: " " 00300 " punctate "

0 : " " 00000.

EN: " " 00345 " non-punctate "

EP. " " 00345 " punctate "

Other N: Other banding patterns with non-punctate bands.

Other P: " " " " punctate "

Hyalo: Hyalozonate bands.

WL: White Lip.

Table 2.

G. S. No.: National Grid 10-kilometre square number.

Habitat: Unless otherwise specified all samples are from "open habitats".

Y: Yellow shell colour.

P: Pink shell colour.

B: Brown shell colour.

5: Banding pattern 12345 (including minor variants).

3: " " 00300.

0: " " 00000.

E: " " 00345.

Data from:

1. Cain 1968.

2. Cain & Currey 1963b.

3. Cain & Currey 1963c.

4. Cain & Sheppard 1950.

5. Cain & Sheppard 1952.

6. Cain & Sheppard 1954.

7. Cameron 1969.

8. Carter 1968.

9. Clarke 1962.

10. Clarke & Murray 1962.

11. Currey, Arnold & Carter 1964.

12. Currey & Cain 1968.

13. Day & Dowdeswell 1966.

14. Goodhart 1956.

15. Goodhart 1958.

16. Goodhart 1962.

17. Murray 1966.

18. Sheppard 1952.

19. Arnold 1966.

20. D.A. Briscoe, pers. comm.

21. A.J. Cain, pers. comm.

22. In coll. B.C. Clarke.

23. In coll. C. Diver.

24. In coll. Mrs. A.W. Ford.

25. In coll. J.J.D. Greenwood.

26. In coll. P. Harvey.

27. In coll. J.S. Jones.

28. In coll. Mrs. N.F. Macmillan.

29. In coll. C.R.D. Reynolds.

Table 4.

Polje Index: Distance between contours (metres); see page .

Height: Height above sea level (metres).

Hab: Habitat - H = Hedgerow.

RH = Rough Herbage.

S = Scrub.

BW = Beech Wood.

DW = Deciduous Wood.

TABLE I.

Morph Frequencies in Yugoslav populations of *Cepaea nemoralis*

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
VRATNIK		000813	140	16	40	7	13	1		7		33	3:5N;15:5P;1:3N 1:3P; 3:other P
MELNICE	1	032798	3	1		2							
	2	028796	8		5		1			1			1:5N
	3	016802	8	1	1			1		3			1:5P; 1:EP
	4	025796	14	1		7	6						
	5	028791	42	20		3	1	2		5	4	7	
	6	031783	12		1	2	3	2			1	2	1:O
	7	034782	4	1	1					1		1	
	8	036778	5		1							4	
VRZICI	1	040773	14	2	5	1						2	2:5P; 2:EP
	2	041769	30	5	13	2	3	3				4	
	3	044761	12	2	4					2		4	
CRNI KAL	1	056756	12	2	7					2		1	
	2	060753	26	10	1	5	2	1		5		1	1:5P

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
			5N	5P	3N	3P	O	EN	EP	otherN	otherP	
3/	067743	29	16	7		2			1		2	1:3P
4	057738	18	6	9	1	1	1					
ZUTA LOKVA 1	060803	24	12	7							5	
2	057803	30	12			1			5	9	1	2:EP
3	052802	19	7	2		1	1		2		5	
4	053811	21	8	4		6	1		2			
5	048805	26	5	3		1			9	3	5	
6	044801	27	9	1	1	1	1		7		4	3:5P
DOBRICA 1	085799	5	3	1							1	
2	089799	5	3	2								
KOSA BRLOSKA	101792	2		1					1			
RAPAJIN KLANAC L	064800	17	5	3	1	2	1		2	1	2	
2	075789	20	2	2	3	3	1	1	2	1	5	
3	077796	32	13	2	5	3			1	4	4	
4	082790	48	13	2	4	1	3		11	1	12	1 Other P
RAPAJIN DO L	080789	13	6		1		1	3	2			
2	080789	14	2	3	4	4			1			

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
				5N	5P	3N	3P	O	EN	EP	otherN	otherP	
	3	081788	46	14	4	7	1	3	1	7	3	6	
	4	081788	46	16	7		2	1	1	11	2	6	
	5	083788	2	1								1	
	6	085787	25	2		4	8			8		3	
	7	086787	12	2	1		5	3		1			
	8	087787	19	3	4	8	3				1		
	9	089786	38	15	5	8	1	2		2	2	2	1:5N
	10	089786	100	32	2	18	27	1		4	1	14	1:3N
RAPAJICI	1	091785	45	24	1	8	3	1	1	1		2	1:5N;2:3N; 1 Other P
	2	091785	26	10		6					6	3	1 other N
	3	091783	22	10	3					5		1	2:5P;1 otherP
	4	091783	24	14	2					2			1:5N; 5:5P
	5	091781	46	18	1	11	1			5	7		1:5N; 1:5P 1: other P
	6	091781	25	15	1	4				1	2		1:3N; 1EP
	7	093777	16	6	2					1			6:5N; 1:EP
	8	093777	30	7	2	8		1		2	1	1	3:5N;2:5P;2:3N 1: Other N

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
			5N	5P	3N	3P	O	EN	EP	otherN	otherP	
9	095776	45	21	3	6	2		1		2	3	2:5N;1:3N;1:3P 1:EP;2 OtherP
10	095776	52	19		12	1		1	2	7	5	4 5N;1:5P
11	097774	34	18					4	3	7		2:5N
12	099773	106	46	20		2			11		22	2:5N;3:5P
13	100772	49	5	15	5	3			3	1	9	2:5N;3:5P;1:3N 1:3P;1:otherP
14	100772	44	2	10	4	7		1	9	3	6	1:5P;1:EP
BRLOG STACIJA 1	102772	60	31	1				1	1		4	15:5N;4:5P;3:3N
2	103770	63	22	8				1	10	8	1	2:5N;7:5P;3:EP 1:other P
3	104768	28	21							1		6:5N
4	104768	37	8	6					8	5	6	1:5N;1:O;1:EN 1:other N
5	106766	56	38	1				9	3	4	1	
6	106766	22	13		2	1		2	2	1		1:5N
7	109762	36	9	7			1		1		4	3:5N;8:5P;1:EP 2:other P
8	109761	26	4	9					4		7	1:5N;1:5P
9	109760	3	3									

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
	16	109760	3	3									
	11	110758	5	1	1	1				1		1	
	12	110757	32	13	2	2				2		2	2:5N;4:5P;1:3P 1:EP;2:other N 1:other P
	13	111757	127	54	5				7	2	6	8	29:5N;13:5P; 1:EN;1:EP; 1: other P
	14	111756	70	37	9	3	1				4	3	5:5N;2:5P;2:3N 1:3P;2:EP;1: other P
	15	112756	1	1									
SRPSKO POLJE	L	126738	35	5	4	2	3	2		5	1	2	3:5N;4:5P;3:3P 1:other P
	2	125740	62	3	19				4	13	1	22	
	3	126736	24	5		12	3	2	1			1	
	4	123736	33	8	3	2					4	2	7:5N;3:5P;2:3N 1:3P;1:EN
	5	119735	27	9		2	1	4				3	4:5N;2:5P;1:3N 1:O
	6	115731	21	4	2	3	10	2					
	7	110728	18	9	4								4:5N;1:5P

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O	YELLOW EN	YELLOW EP	otherN	otherP	PINK and NOTES
	8	109731	41	15	3	8	1			2		2	3:5N;2:5P;5:3N 1?5 is HYALO
	9	095738	18	11	3		1					2	1:5P
	11	109735	89	9	23		5	2	1	18		31	
	12	111742	3	1		1						1	
	13	112736	38	4	19		1			1		12	1:5N
	14	113737	76	5	15	2	8			4		39	1:5P;2:3P
	15	115739	36	2	3	19	4					3	1:5N;2:5P;2:3P
	16	117739	60	22	11	1				4		7	13:5P;2:otherP
	17	118743	51	12	8	5	11			9	1	5	
	18	119744	22	4	5		4	2		4		3	
BJELJEVINE	1	108722	21	4	7			1		1		7	1:other P
	2	102719	35	7	4	6	5	2		1		9	1:5P
KOMPOLJE	1	116745	22	9	4	2	2	1		2		2	
	2	115751	16	14									1:5N;1:3P
	3	114755	14	5	3					2	1	3	
	4	114755	35	21		2			4		4	3	1:5N
	5	116753	22	9	3	4				1	1	1	2:5N;1:5P

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
			5N	5P	3N	3P	O	EN	EP	otherN	otherP	
6	116753	42	13		8	2		1	4	1	2	6:5N;3:3N;2:EN
7	118752	68	31	15		5		3	4	6	2	1:5P;1:EP
8	118752	31	11	5	1	3		1	5		5	
9	120751	28	6	1	3		1	3		4	1	8:5N;1:3N
10	120751	33	20	2				1	1	6	2	1:5N
11	121751	16	2	1	1	2	2			1	7	
12	121751	44	22	10	6	1		1	3	1		
13	123750	29	10	10		3			1		2	2:5N;1:5P
14	123750	18	7	7							4	
15	125748	41	26		10	1			2		1	1:5N
16	125748	69	26	8	2			3	19	5	3	2:5N;1:otherN
17	126746	6	3	3								
18	126746	5	4	1								
19	128745	17	6	1	5					2		1:5P;2:3N
20	128745	12	6	2	1					1		2:5P
21	130745	71	10	28	2	9	3		7	1	10	1:5P
22	130745	135	29	28	27	21	6		12	4	5	1:5N;2:5P

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
	23	132743	118	78	8	3	2			1	7	7	5:5N;5:5P; 1:other P
	24	133741	20	3	2	1				10		4	
	25	135739	77	47	16				1		3	2	4:5N;4:5P
	26	135739	12	10						1	1		
	27	136738	19	2	7					7		3	
	28	136738	3		1							2	
	29	134733	48	15	4	1	9		2	4	1	6	2:5N;1:5P; 1:3P;1:EP
	30	136736	29	4	3					10		12	
	31	138736	138	54	17	2	3		5	16	6	35	
	32	138736	78	34	12	1	1	2	1	8	9	10	
	33	139734	141	68	14					26	12	21	
	34	139734	75	28	10	4	1	3	2	10	4	13	
	35	141733	54	22	1	21	3	3		1	1	2	
	36	145730	3		1	1					1		
	37	145730	17	4		4			1	3	2	3	
OROVAC	1	146729	50	19		4		5	4	1	9	3	2:5N;1:5P;1:3N 1:O

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW									PINK and Notes
				5N	5P	3N	3P	0	EN	EP	otherN	otherP	
	2	146729	15	2		1	1	1		3	2	4	1:5P
	3	147726	2		2								
	4	147726	37	1	7	1	3	1	3	17		4	
	5	147721	28	8	3	12	4	1					
	6	148724	32	17	2	2	3		3	3	1	1	
	7	150721	20	5		3	1	1		4	2	1	2:5P;1:EP
	8	150721	8	1		1	1			3		2	
	9	152719	19				7	5		5	1	1	
	10	157713	54	19	5	17	7	2				4	
	11	158711	4	3	1								
	12	160709	4				2	2					
	13	161709	7	6							1		
	14	164706	14	1						6		7	
	15	167705	10	6	2							2	
	16	166703	6				1	1		3		1	
	17	168701	3				1			1		1	
PODBRDJE	1	096784	22	3	1	2	1	4		3		8	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O EN	EP	otherN	otherP	PINK and NOTES
	2	103782	47	2	13		3		6	2	17	4:5P
	3	108779	78	37	3	10	7	3	2	4	12	
	4	111779	71	9	19		6	13	6		16	2:5P
	5	114779	60	8	15	1	5	3	2		20	5:5P;1:3N
	6											
KLANAC	1	128781	24	4			1	3			2	5:5N;1:5P;3:3N 3:3P;2:other P
	2	129783	18	7			4			3	1	1:5N;2:3N
	3	135785	47	19	6				3		14	4:5N;1:5P
	4	136783	80		6		2	1	44		27	
BRLOG	1	106771	135	63	10				1	1	9	36:5N;15:5P
	2	106773	13	5							1	5:5N;1:EP; 1:other P
	3	114775	53	35	6	9					3	
	4	128778	35	12	8	1	4		1		6	2:5P;1:3N
	5	132776	5	2	2						1	
PRICE	1	139778	17				1	3	13			
	2	144776	29	1	6				14	1	7	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
ZAKULJE	1	147775	22	2	1	3	2	7		3		4	
	2	150774	20			1	8	4		3		4	
	3	153773	8		1					7			
	4	157772	28	15	4					2	4	3	
	5	158771	14		7					3		4	
	6	163768	12	3	1	3		1			3	1	
	7	166766	46	27					5	2	12		
LALICI	1	174760	1								1		
	2	179762	36	5		2	4	3	10	9		2	1:5P
	3	178758	3	1					1	1			
	4	180756	19	2	4	1	5			2		5	
LONCARI	1	188753	6		1					2		3	
	2	191751	2	1		1							
	3	193750	10		3					4		3	
	4	197749	19	9				1	3	5		1	
	5	191756	1	1									
GLAVACE	1	204745	14	4	5					2		3	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
				5N	5P	3N	3P	O	EN	EP	otherN	otherP	
	2	208744	105	6	2	1	1		2	32		61	
	3	212741	66	2	4	2	1	2		35	3	17	
	4	216727	71	31	8	23	1	2				5	1:other P
	5	222741	19	2	1	11	4					1	
	6	217747	16	2	4	1	2	1		1		4	1:EP
	7	212748	4				2					2	
	8	216733	13	2			1			9		1	
	9	216729	11	2	2					6		1	
	10	216726	30	1				1		20	1	7	
	11	222734	25	2	3				1	6		13	
	12	226729	26	2	2	3	10			1		8	
POLJICE	1	171697	23		1	2	2	1		8		9	
	2	164697	35		3		9	16		3		4	
	3	162697	12	1	4		3	2		2			
	4	158696	42	6	10	3	5	5		10	1	2	
	5	154697	25	9	3	2	3	2		2	2	2	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
SVICA	1	145704	43	1	10	2	14	3		1		12	
	2	138698	32	6	15	1	2			1	2	5	
	3	138695	22	6	4	5	3	1				2	1:5P
BURIC KLANAC		145711	34	1	6		16			4		7	
GEROVO SELO	1	138689	40		8		5	6		6		15	
	2	136685	28		3	1	5	3		3		13	
	3	132684	12	1	3		2	2		2		1	1:3P
	4	132683	17	1	7		3					4	2:3P
GORICI	1	126681	2				1	1					
	2	122676	9		2	1	3	3					
	3	122673	35	21	2	1			1	5	4	1	
	4	118670	37	5	17			3		6		6	
	5	115669	45	10	7	2	9	7		3		7	1 Y5 is HYALO
	6	111669	2	1	1								
	7	111680	6	1	3	1							1:5N
POLJANE	1	101668	14	2	11					1			

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	YELLOW 5P	YELLOW 3N	YELLOW 3P	YELLOW O EN	YELLOW EP	otherN	otherP	PINK and NOTES
	2	097667	33	5	23				2		3	
	3	093667	13		11				1		1	
	4	103657	12	2	2	3	4		1			
	5	105655	2		1		1					
	6	096666	17		16						1	
KUTEREVO		112638	22		15			1	2		4	
LIPOVLJE	1	132676	56	19	22		2		4	1	8	
	2	135672	49	18	10	3	6	1	4	1	6	
	3	140668	12		8	1	1			1	1	
	4	142665	13	6		2	3			1	1	
VULADA NEDELJA	1	131698	11	3	2	1	4			1		
	2	126697	33	16	4	3	3		2	1	4	
	3	124676	18	7	3			2	2		4	
PONORI	1	121700	21	6		8	2	2	2		1	
	2	111696	19	1	4	4	4	2	3		1	
	3	107695	2		2							

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
GROZDANICI		102688	13	3		7	2			1			
PODUM	1	215722	19				4			15			
	2	216719	98		32		7	2		41		16	
	3	214718	126	3	9	4	48	1		31		30	
	4	218718	57	23	2	9	11	2		5	1	4	
	5	224719	52	4	2	13	9	1		14	2	7	1 Y5 and 5 Y3 are HYALO
	6	229719	1									1	
	7	228717	15	9	2					1	2	1	
	8	237715	15		11					1		3	
	9	246709	7	2	2							3	
	10	255707	12	4	1	1	1	1		1		3	
MARKOVICEVO SELO		207710	34	3		1	2	1	3	17	1	6	
	2	205706	55	3	3					29		20	
	3	202705	43	2	5					26		10	
STARO SELO	1	202714	30	22	1					4		3	
	2	196717	24	7	5					2		10	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O	YELLOW EN	EP	otherN	otherP	PINK and NOTES
	3	194720	25	4	7					4		10	
	4	190714	1							1			
SRELISTE	1	186702	107	57	8	33	2	3			1	3	
	2	189703	8	3	1	1				1		2	
OTOCAC	1	205691	9		3					6			
	2	200693	3	1								2	
OLTARI		234684	78	3	10				3	33	3	26	
INICI		261681	31		9		7			6		9	
SKARE	1	231727	21		2		1	1		6		11	
	2	237722	80	33	2	2	1			7	1	34	
	3	238720	25	4	1	1	2	3		7		7	
	4	243720	14	7					1	2		4	3 Y5s are HYALO
	5	246720	28	7	2					12		7	
	6	251722	32	2	1	3	2	3		8		13	
	7	256712	18	1	1							14	1:5P;1:EP
DONJI DOLJANI		266710	10		7							3	
ZALUZNICA		280688	3	1	1								1:5P

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
				5N	5P	3N	3P	O	EN	EP	otherN	otherP	
PODKOREN		282602	2		2								
KRS	1	253540	1		1								
	2	248540	4	2		1						1	
	3	242541	6	3	2					1			
KOSINJSKI ZAHOST		122542	48	2	3	23	14	2	2	2			
	2	223545	19	5	3		4					7	
GORNJI KOSINJ	1	224535	12	3	1					2		6	
KOSINJSKI BAKOVAC		165521	1	1									
MLAKVA	1	227522	12	3	4		2				1	2	
	2	232524	6			3				3			
	3	234520	14	9	4					1			
	4	235518	24	9	13							2	
	5	230509	9	1	2		4		1			1	
DONJI KOSINJ	1	211564	14	7	3		1			2	1		
	2	205570	8	3	2							3	
ZAMRSTEN		208541	30	1	4		5			7	2	2	2:5N;2:5P;4:EP 1:other P

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O	YELLOW EN	EP	otherN	otherP	PINK and NOTES
LIPOVO POLJE	1	195551	27	6	11	5	4					1	
	2	180560	37	22	5	1	1			1	3	4	
	3	152573	10			8				1		1	
PERUSIC	1	301470	50	3	11		2					33	1:5P
	2	295452	119	1	38	2	34	6		8		28	2:5P
JURISICI		292454	15		2					2		11	
BALENIJA		261443	12		4	2	5			1			
STOJEVICA DRAGA		242440	1									1	
GORNJI PAZARISTE		239430	39	1	11	6	20					1	
	2	229432	38	2			28			3		5	2 Y5s are HYALO
	3	226431	19				13			2		4	
PREDVAGANAC		211435	13	11							1		1:5N
ALEKSINICA		188444	1										1:5N
SOKOLICI		313454	12		5							7	
KONJSKO BRDO	1	327467	35	7	2		2	1		3		9	2:5N;2:5P; 7:other P
	2	332467	20		4					2		14	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O	YELLOW EN	EP	otherN	otherP	PINK and NOTES
MALO SELO MUSALUK		277426	2			1	1						
DUNJEVAC		274431	1				1						
BACINAC		252377	102	2	1	2	30	48		12		7	
MILKOVICA	23	237371	3	2							1		
KOVACEVICI		242347	36	2	1	2	19			3		9	
SV. PETAR		251354	74		18		13	3		9		31	
PRVTAN SELO		324423	6	6									
VUKOVMOST		332405	6	2	2		1	1					
LICKI OSIK	1	332404	44	6	8	18	11					1	
	2	324391	14	10	2							2	
PODSTRANA		323399	19	9			1					3	1:5N;3:5P;2:3N
GOSPIC		307356	33		3	1	22	3		2		2	
JASIKOVAC		303327	6		1		2			3			
OSTRA	1	260312	15		6		8	1					
	2	273315	78	3	4	6	58	1		3		3	
DUDELICI		262326	11			1	2	8					

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
NOVO SELO		245294	60		8	8	30	4				10	3 Y3s are HYALO
BRUSANI	1	240285	64	14	11	9	16	3				4	2:5P;5:3P 1 Y3 is HYALO
	2	228282	32	5	10	2	8						1:5N;2:5P;2:3N 23 P. 1 Y5, 1 Y3 and 1 P5 are HYAL
	3	208288	18		2	3	10	3					2 Y3s are HYALO
POCUCI		326318	39	15	1	10	3			2	8		
BILAJ		360315	22		12	1	3			2		4	
BARLETE		373321	22		8					3		11	
VREBAC	1	403331	13		8					1		4	
	2	402308	27	27									
RUCAJICE		345298	5				1			1		3	
LICKI NOVI		270305	4	1	1		1	1					
DIVOSELO		302278	2	1			1						
GRAĐVCI		406296	22	1	5	4	11	1					
RIBNIK		370272	60	21	13	10	7	1		5		3	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O EN	EP	otherN	otherP	PINK and NOTES
MEDAK	1	405238	89	9	48	5	21			1	5	
	2	415225	25	2	7	4	11		1			1 Y5 and 3 Y3s are HYALO
VEDRINE		409219	37	6	9	1	10	1			1	5:5P;2:3N;2:3P 2 Y5s are HYALO
PAPUCA		435219	58	13	14	1	4		14		12	8 Y5s and 1 Y3 are HYALO
RADUC		470170	33	9	21						2	L:3P
LICKO CERJE		555130	11	1		5	5					
SJIKAD KLANAC	1	613090	50	7	4	3	11	1	9		7	5:5N;1:3N;1:3P 1:EP
	2	622086	26	3	3	4	3		2		1	1:5N;1:5P;5:3P 1:eP;2:other P
PROKIKE	1	055812	24	1	3	4	9	5	2			
	2	056814	5	3	2							
	3	056816	28	9	6	4	2	2	2	2	1	
	4	059817	28	9	5	2	1	1	2	2	3	2:5P;1:3P
	5	055820	35	7	9	3	10			2	3	1:5N

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW									PINK and NOTES
				5N	5P	3N	3P	O	EN	EP	otherN	otherP	
SMILENCI	1	041829	20	2		11	3	3				1	
	2	057831	1	1									
	3	061833	7	2	1		3					1	
	4	067833	11	2	3		2	1		3			
	5	070834	9	1	1	1	2	2		1	1		
BRINJE	1	073833	18	4		2			2	4		6	
	2	083855	24				3			11		10	
	3	084835	29	1	2	1	1	1	1	13		8	1:5P
	4	091834	42	2		13	14	5		2	1	5	
	5	094835	1							1			
	6	112848	112	6	1	74	6	10	2	3	4		4:8N;2:3P
	7	111851	4	1		2						1	
BLAZANI	1	085832	3	1	1							1	
	2	090828	4	3	1								
	3	093832	16	1	5					1		9	
Sv. VID	1	101830	22	6						3		13	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	YELLOW (5N	5P	3N	3P	O	EN)	EP	otherN	otherP	PINK and NOTES
	2	106834	15	2	7	2	1			2		1	
	3	103829	28		3	2	12	6		3		1	1:3P
DRAZENOVICI	1	111836	12	6		2	1					3	
	2	116837	28	8		11	2	1		1		5	
VUCEJICI		121832	33	3	1	1	5	2		12	1	8	
RUMENOVICI		140829	21	5		3	5	1		3		2	1:5P;1:3P
PLASCICA	1	145829	18	3	1	1	5	1		1	1	5	
	2	153830	16		2	3	4	2				5	
LETINAC		171826	40	2	2			2		14		20	
DOMICI		099845	15	1		4	4	1		1		1	1:5N;1:5P
BORICI	1	096858	1									1	
	2	096861	16	6	6		1					1	1:5P;1:3P
BUKOVLJE	1	093865	3				3						
	2	086873	23	3		9	4	3		2		2	
	3	087878	10	2	1					1		6	
MALJKOVICI	1	079879	13	3			1			4		5	

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O	YELLOW EN	EP	otherN	otherP	PINK and NOTES
	2	076881	3	1								2	
KOLJEVICI	1	113853	19	1	2		4	5		2		5	
	2	121860	28	1		1	5	15		5		1	
KRIZPOLJE	2	128870	55		1	1	23	29				1	
	3	140878	19	1	3			1		10	1	3	
MALIKUT	1	132866	1	1									
	3	135861	2	1	1								
SPRAJCI		127876	3	1						1		1	
VELIKIKUT		143873	2	2									
PERKOVICI	1	149871	73	10	2	27	10	5		8	2	9	1 Y5 and 6 Y3s are HYALO
	2	147872	19	12		4				1	1	1	
	3	145873	67	8	2	14	17	13	1	5		7	1 Y5, 1 Y3, 1 y Other - HYALO 4 YO WL.
JELVICA	1	143892	15	6	3					2	1	2	1:5P
	2	138877	1				1						
	3	144893	51	7	11	6	9	5		5		8	

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	YELLOW 5N	5P	3N	3P	O	EN	EP	otherN	otherP	PINK and NOTES
4	143896	6	1				1				4	
DUMENCICI	152900	26	1	2		6	6		7		4	
BORIC	116924	2		1								1:5N

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	5N	5P	3N	3P	YELLOW O	YELLOW EN	EP	otherN	otherP	PINK and NOTES
JOSIPDOL	55/50 227038	26	4	5					10		7	
OGULIN	55/50 181118	67		12		10	15		16		14	
LJUBOSINA	55/50 128191	35		1		5	23				6	
GOMIRJE	55/50 098211	1		1								
BROD MORAVICE	54/50 980309	25	10	2	10	2					1	
BROD	54/50 885342	18	1		8	5	2					1:3N;1:EP
BOSANCI	55/50 207333	2					1		1			
GRABSK	55/50 298208	3	2								1	
BIHAC	640620	18	2	7		2	1		5		1	
LOHOVO	715555	2	1									1:3P
DONJI LAPAC	762382	4		1	1					2		
KOZJAN	449512	7	1	4		2						
TITOVO KORENICA	564550	8	5	3								

Throughout this table, wherever it is E V S, read E V S.

- Second thoughts - just blot out the "V" so that it becomes E - S

TABLE 2

Morph Frequencies in British Populations of Cepaea Nemoralis

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL	Y	F	B	S	3	O	E V S	NOTES	DATA FROM
NG 60		4	14	4	10	0	13	0	1	0		22
NG 61		1	1	0	1	0	0	0	1	0		22
NH 41		1	1	0	1	0	0	0	1	0		22, 27
NM 15	DUNE	29	1242	900	342	0	871	202	169	0		27
NM 26		2	36	17	19	0	36	0	0	0		27
NM 46	DUNE	31	1599	1108	491	0	1378	114	107	0		29
NM 48	DUNE	1	1	1	0	0	1	0	0	0		22
NM 57		1	5	5	0	0	4	0	0	1		22
NM 82		12	264	161	103	0	138	5	12	109		24
NM 83		8	186	170	16	0	154	0	28	4		27
NM 84		19	523	346	177	0	331	10	58	124		27
NM 94		32	793	383	410	0	429	4	105	255		24, 27
NN 04		3	43	16	27	0	24	0	12	7		24, 27
NN 15		4	57	38	14	5	40	6	1	10	Bs are pale	27

See Note

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL	Y	P	B	S	3	O	E.S	DATA FROM	NOTES
NN 53		1	28	15	13	0	35	0	3	0	23	
NN 86		3	56	41	15	0	45	0	11	0	27	
NO 42		2	318	129	189	0	225	0	93	0	25	
NO 59		1	44	33	11	0	44	0	0	0	27	
NO 66		1	87	0	87	0	87	0	0	0	27	
NO 75	DUNE	12	174	60	114	0	71	2	101	0	27	
NO 76	Dune	52	1705	97	1608	0	1377	119	209	0	27	
	DUNE	39	583	78	505	0	532	0	51	0	27	
NO 77		1	39	24	15	0	21	0	18	0	27	
NO 87		10	151	73	78	0	118	0	33	0	27	
NR 26	DUNE	1	15	14	1	0	4	5	6	0	28	
NR 27		1	1	0	1	0	1	0	0	0	28	
NR 34		3	23	13	10	0	18	4	1	0	28	
NR 39		2	84	41	42	1	76	8	0	0	6, 22	
NS 09		1	106	61	45	0	106	0	0	0	22	
NS 79		5	40	15	25	0	27	9	4	0	27	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	B/S	DATA FROM	NOTES
NS 85		2	36	15	21	0	28	7	1	0	24	
NS 88		1	3	2	1	0	2	0	1	0	27	
NT 15		1	1	1	0	0	0	0	1	0	22	
NT 25		1	2	0	2	0	1	1	0	0	22	
NT 26		15	223	90	133	0	198	6	5	14	22	
NT 27		1	1	1	0	0	1	0	0	0	22	
NT 36		4	45	14	31	0	34	0	4	7	22	
NT 48	DUNE	8	461	111	149	201	287	0	174	0	22,24	91 Bs are pale
NT 51		1	22	7	15	0	20	0	2	0	22	
NT 53		5	19	4	15	0	16	0	3	0	22	
NT 58	DUNE	4	250	68	99	83	132	0	118	0	27	
NT 67	DUNE	7	90	7	46	37	59	2	29	0	22,24	
NT 77	DUNE	20	1120	390	728	2	1058	60	1	1	24	
NU 04	DUNE	36	1424	387	1037	0	1171	0	246	7	24	
NU 13	DUNE	14	826	279	374	173	475	140	199	12	1,24	
NU 14	DUNE	11	376	68	308	0	372	0	4	0	19,24	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	B S	DATA FROM	NOTES
NU 20	DUNE	2	170	90	80	0	104	0	66	0	23,27	
NU 21	DUNE	2	201	87	112	2	176	0	21	4	1	
NU 23	DUNE	8	365	289	23	53	95	182	88	0	24	12 Bs are pale
NY o5	DUNE	1	24	9	15	0	20	0	4	0	1	
NY 92		1	14	8	6	0	14	0	0	0	23	
NZ 29	DUNE	2	546	303	243	0	519	0	27	0	1	
NZ 33		5	140	92	48	0	109	31	0	0	25	
NZ 37	DUNE	2	268	163	62	43	250	0	10	8	1	
NZ 81		1	67	17	50	0	67	0	0	0	23	
NZ 90		2	3	2	1	0	3	0	0	0	23	
SD 09	DUNE	5	344	101	243	0	318	0	20	6	22	
SD 20	DUNE	1	159	0	159	0	71	62	11	15	1	
SD 31	DUNE	3	233	7	226	0	187	46	0	0	1	
SD 86		7	419	419	0	0	135	24	259	1	22,27,23,25	
SD 96		17	486	402	84	0	441	4	39	2	22,25,27	
SD 97		1	24	21	3	0	23	0	0	1	22	
SE 33		8	1083	570	513	0	887	152	38	6	23	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	5	3	O	B 5	DATA FROM	NOTES
SE 77		1	45	8	37	0	21	10	14	0	23	
SH 34		4	1130	891	239	0	739	186	205	0	23	
SH 46	DUNE	4	477	178	239	60	311	99	62	5	1	
SH 52	DUNE	2	265	148	117	0	261	1	0	3	1	
SH 53	DUNE	2	136	48	88	0	95	24	0	17	1,23	
SJ 16		1	18	9	9	0	18	0	0	0	25	
SJ 18	DUNE	56	5094	3120	1754	220	3768	1060	254	12	1	
SJ 28	DUNE	2	185	110	75	0	148	34	2	1	1	
SJ 29	DUNE	1	241	113	128	0	237	2	2	0	1	
SJ 88		3	33	23	10	0	12	8	13	0	25	
SK 06		5	120	91	27	2	0	0	120	0	25	
SK o7	WOOD	4	14	6	8	0	0	7	7	0	23,25	Some Bs are pale
		91	6943	4329	1889	725	151	1476	5316	0	23,25	
SK 15	WOOD	31	618	390	63	165	7	48	563	0	25	Some Bs are pale

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	5	3	O	E	5	DATA FROM	NOTES
		72	3164	1730	261	1173	118	160	2886	0			
SK 16	WOOD	4	115	32	30	53	23	79	13	0		25	Some Bs are pale
		14	527	339	51	137	64	306	157	0			
SK 17	WOOD	16	171	137	27	7	10	132	29	0		25	Some Bs are pale
		202	7858	5592	1966	300	1355	4875	1628	0			
SK 25	WOOD	13	168	99	69	0	65	69	34	0		25	
		13	368	251	116	1	130	135	103	0			
SK 26		4	110	64	34	12	25	78	7	0		25	
SM 70		1	34	3	31	0	16	1	9	8		19	
SO 53		4	112	48	58	6	92	8	8	4		23	
SO 84	WOOD	3	34	5	25	4	18	8	5	3		25	
		6	73	23	40	10	42	15	10	6			
SO 85	WOOD	7	137	27	86	24	39	46	45	7		25	
		16	313	145	148	20	166	68	29	50			
SO 86		1	7	0	6	1	6	0	1	0		25	
SO 91	WOOD	2	71	11	46	14	9	41	21	0		23	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	B/S	DATA FROM	NOTES
		1	53	45	6	2	11	37	5	0		
SO 92		8	1650	1297	339	14	1423	128	12	87	23	
SO 93	WOOD	2	85	55	23	7	64	0	6	15	2	
		3	148	112	35	1	117	8	5	18		
SO 94	WOOD	5	44	5	29	10	9	16	13	6	25	
		3	29	16	9	4	15	6	3	5		
SO 95	WOOD	2	76	18	38	20	26	13	27	10	25	
SP 00	WOOD	1	50	4	42	4	10	30	10	0		
		3	108	70	38	0	55	44	7	2		
SP 01		1	6	1	4	1	4	2	0	0		
SP 02		1	18	9	9	0	8	9	1	0		
SP 03	WOOD	1	27	17	10	0	22	1	4	0	23	
		5	470	354	94	22	253	123	31	63		
SP 10		1	152	97	55	0	105	47	0	0	23	
SP 12	WOOD	1	27	6	21	0	6	9	3	9	2,23	
		1	93	52	41	0	74	7	1	11		

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E S	DATA FROM	NOTES
SP 13		2	128	80	48	0	92	9	2	25	2,23	
SP 20		1	48	28	7	13	18	15	15	0	2	
SP 21	WOOD	1	81	69	12	0	53	28	0	0	2	
SP 24	WOOD	2	101	36	49	16	36	28	33	4	11	
		1	45	21	19	5	20	7	33	4		
SP 25	WOOD	6	180	56	122	2	65	51	35	29	11	
		17	1163	576	527	60	709	281	109	64		
SP 30		1	80	52	20	8	45	8	25	2	6	
SP 35	WOOD	3	372	53	311	8	136	15	155	66	11	
		7	319	162	149	8	137	52	72	58		
SP 40	WOOD	13	4747	1132	3215	400	2316	743	1126	362	4,5,6,9	
		14	1572	1003	505	64	1074	123	299	76		
SP 41		5	290	230	59	1	158	62	54	16	6	
SP 42	WOOD	1	250	60	190	0	88	79	79	4	2,6	
		4	809	524	253	32	610	67	64	68		
SP 43		1	241	125	106	10	111	49	80	1	6	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E	5	DATA FROM	NOTES
SP 44		2	170	86	54	0	86	58	25	1		6	
SP 50	WOOD	3	224	37	164	23	123	46	53	2		2,4,5,6,9	
		6	628	317	300	11	483	82	43	20			
SP 51	WOOD	1	11	1	10	0	7	0	4	0		2,6,9	
		4	269	149	115	5	192	38	31	8			
SP 53		1	119	64	35	10	56	29	34	0			
SP 57		1	223	174	49	0	65	83	75	0		6	
SP 60		1	361	119	240	2	163	1	196	1		2	
SP 61	WOOD	4	369	16	350	3	154	128	84	3		2,6,9	
		1	19	8	11	0	6	8	5	0			
SP 70	WOOD	3	132	17	115	0	60	2	70	0		19	
		4	193	52	140	1	151	0	39	3			
SP 78		2	165	116	49	0	158	0	1	6		23	
SP 80	WOOD	4	591	142	449	0	296	8	275	12		19	
		4	230	134	96	0	179	20	19	12			
SP 91	WOOD	3	118	13	105	0	51	9	54	4		9,19	

See Nite

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	R S	DATA FROM	NOTES
SR 89	DUNE	1	48	14	34	0	33	8	0	7	1	
SS 10	DUNE	7	911	442	469	0	423	344	144	0	19	
		4	343	281	62	0	95	122	125	1		
SS 20		1	99	67	32	0	41	39	19	0	19	
SS 21		19	1300	671	629	0	186	462	652	0	19	
SS 22		3	135	94	41	0	16	18	100	1	19	
SS 43	DUNE	7	372	60	312	0	160	179	30	3	1	
SS 49	DUNE	4	240	33	178	29	188	8	43	1	1	
SS 74		5	90	20	70	0	22	54	13	1	23	
SS 78	DUNE	3	237	187	50	0	183	49	0	5	1	
SS 87	DUNE	2	438	69	368	1	422	13	3	0	1	
ST 25	DUNE	50	5629	3977	1321	331	4583	690	165	191	10	154 Bs pale; 15 hyalos
ST 41		2	170	17	123	30	121	42	7	0		
ST 45		1	53	22	31	0	48	4	0	1	2	
ST 57	WOOD	2	129	13	100	16	40	56	23	10	2	
ST 62	WOOD	3	87	7	65	15	16	13	57	1		

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E	S	DATA FROM	NOTES
		1	14	0	14	10	2	3	9	0			
ST 63	WOOD	4	77	8	44	25	28	9	37	3			
		1	11	1	2	8	3	0	8	0			
ST 71		1	1	0	1	0	1	0	0	0		23	
ST 73	WOOD	1	12	0	10	2	2	6	4	0			
ST 75	WOOD	1	4	0	4	0	0	3	1	0			
ST 76	WOOD	1	32	1	22	9	10	5	16	1			
ST 85		1	122	71	51	0	70	14	34	4		2	
ST 87	WOOD	3	143	4	78	61	21	32	90	0		2,9	
		1	6	0	6	0	1	4	1	0			
ST 90		3	277	146	113	18	267	7	0	3		23	
ST 95	WOOD	1	64	9	51	4	16	9	39	0		2	
		1	4	0	3	1	2	1	1	0			
ST 96		1	66	13	50	3	37	21	8	0		2	
SU 04	WOOD	1	4	3	0	1	2	0	2	0		3	
		2	29	5	24	0	23	6	0	0			

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E	DATA FROM	NOTES
SU 05	WOOD	14	782	417	361	4	167	569	44	2	2,3,4	
		43	1886	841	1043	2	392	1358	114	22		1 sinistral
SU 06	WOOD	4	292	33	83	176	54	93	145	0	2,9	
		11	213	64	89	60	131	24	56	2		
SU 07	WOOD	1	21	0	9	12	9	1	11	0	2	
SU 13	WOOD	6	420	16	278	126	1	237	181	1	23	
		2	105	5	63	37	1	52	52	0		
SU 15	WOOD	4	191	78	20	93	20	107	58	6	2,3	
		6	231	116	101	14	35	151	44	1		
SU 16	WOOD	2	136	19	67	50	12	83	41	0	2,4,6	
		6	271	93	111	67	82	38	148	3		
SU 17	WOOD	44	2819	928	916	975	50	926	1837	6	2,4,9,18	
		119	6380	3006	1316	2058	859	2008	3430	83		
SU 18	WOOD	1	114	45	44	25	56	9	44	5	4	
SU 19	WOOD	1	24	7	17	0	15	6	3	0	6	
SU 21		1	61	48	9	4	45	9	4	3	23	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E S	DATA FROM	NOTES
SU 24		2	250	13	180	57	46	150	54	0	6	
SU 25		2	56	13	35	8	1	30	25	0		
SU 26	WOOD	2	57	4	53	0	12	33	12	0	2,23	
SU 27	WOOD	7	452	347	105	0	418	11	19	4	2,9	
		21	979	707	272	0	834	66	50	29		
SU 28	WOOD	7	456	178	229	49	247	132	67	10	2,5,9	
		53	2602	1433	913	256	1437	627	452	86		
SU 37		3	169	105	64	0	120	46	1	2		
SU 38	WOOD	51	5566	3667	1700	199	1668	2887	935	76	2,9	
		72	4948	3887	900	161	1345	2654	863	86		
SU 39	WOOD	1	166	20	77	69	50	1	115	0	6,9	
		5	305	116	176	13	209	22	72	2		
SU 45		1	33	3	30	0	30	0	2	1	2	
SU 47	WOOD	1	102	31	70	1	95	6	1	0		
SU 48	WOOD	10	522	161	270	91	286	32	182	22	2,4	
		37	2071	1055	783	233	1160	289	507	165		

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E S	DATA FROM	NOTES
SU 49		8	602	350	217	35	368	49	173	12	4,5,9	
SU 57	WOOD	1	73	8	57	8	24	5	44	0	4	
		1	21	14	6	1	17	3	1	0		
SU 58	WOOD	14	871	91	684	96	228	254	345	44	4,6	
		35	2288	806	1202	280	1378	254	570	86		
SU 59	WOOD	2	437	193	170	84	155	13	265	4	6	
		4	544	297	197	40	421	38	80	5		
SU 67	WOOD	4	223	22	175	26	61	25	135	2	6	
		2	103	22	52	29	44	6	48	5		
SU 68	WOOD	1	11	0	11	0	2	6	3	0		
		7	364	121	149	94	107	114	131	12		
SU 69	WOOD	2	241	148	93	0	210	3	28	0	19,22	
		1	202	145	57	0	198	0	4	0		
SU 78	WOOD	2	26	1	25	0	13	0	7	6	9	
SU 79	WOOD	11	415	36	376	3	133	36	224	22	4,6,9,19	
		16	1280	564	714	2	971	84	142	83		

See Notes

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E	DATA FROM	NOTES
SU 99	WOOD	1	15	1	14	0	8	3	3	1	7	
SV 80		5	359	48	311	0	43	224	92	0	17	
SV 81		18	1957	281	1676	0	723	745	489	0	17	2 hyalos
SV 91		28	2578	644	1934	0	939	871	768	0	17	2 hyalos
SW 32		17	975	631	344	0	386	150	433	6	23,26	
SW 33		150	6101	4481	1619	1	1620	2285	2189	7	26	
SW 42		15	373	263	109	1	192	69	108	4	19,26	
SW 43		4	126	95	31	0	17	12	96	1	19	
SW 44		1	29	22	7	0	1	1	26	1	19	
SW 52		19	568	395	173	0	240	77	243	8	26	
SW 53		3	168	138	30	0	71	21	74	2	26	
SW 54	DUNE	7	511	286	225	0	331	26	77	77	1,19	1 hyalo
		2	88	63	25	0	15	17	55	1		
SW 61		11	429	347	75	7	183	49	196	1	23,26	
SW 62		8	379	274	105	0	185	79	112	3	26	
SW 64		5	149	122	27	0	115	15	8	11	19	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	EVS	DATA FROM	NOTES
SW 71		13	354	264	87	3	211	52	88	3	26	
SW 72		8	231	140	91	0	109	18	102	2	26	
SW 75	DUNE	1	19	18	1	0	3	0	13	3	1	
SW 76	DUNE	2	1074	1067	7	0	618	366	66	24	1,19	
SW 82		4	189	95	94	0	93	16	73	7	26	
SW 83		2	108	72	35	1	42	2	47	17	2,26	
SW 84		5	116	39	77	0	33	42	39	2	19,26	
SW 86		5	158	139	19	0	33	15	10	0	19	
SW 93		1	28	20	8	0	17	0	11	0	26	
SW 94		2	66	45	21	0	25	7	34	0	26	
SW 97	DUNE	2	94	36	49	9	63	7	22	2	19	
SX 04		2	192	184	8	0	60	113	18	1	2,26	
SX 08		6	338	249	89	0	101	122	112	3	19	
SX 09		2	168	122	46	0	11	30	127	0	19	
SX 19		8	518	385	133	0	99	238	178	3	19	
SX 45		1	1	0	1	0	0	0	1	0	23	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	EVS	DATA FROM	NOTES
SY 18		1	19	11	8	0	8	8	3	0	22	
SY 19		1	4	0	4	0	1	2	1	0	22	
SY 28		13	2895	1344	1256	295	1557	326	1003	9	23	31 hyalo
SY 29		7	313	101	185	27	184	64	65	0	23	
SY 39		5	45	13	24	8	17	16	12	0	23	
SY 66		6	495	401	94	0	457	0	38	0	13	
SY 67		2	33	23	10	0	32	1	0	0	23	
SY 68		5	470	78	364	28	326	89	48	7	23	
SY 69		1	3	1	2	0	3	0	0	0	23	
SY 78		2	20	17	3	0	14	6	0	0		
SY 88	WOOD	1	20	20	0	0	18	2	0	0		
		21	1200	924	145	131	658	441	76	45		3 hyalo
SY 98	WOOD	5	138	25	57	56	27	57	54	0	23	
		7	186	93	38	55	27	59	98	2		
SY 99		1	1	0	1	0	0	1	0	0	23	
SZ 08		2	58	5	48	5	37	16	5	0	23	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	ϕ	B.S	DATA FROM	NOTES
SZ 09	DUNE	1	11	1	10	0	2	7	2	0	23	
		2	42	0	42	0	39	3	0	0		
TA 08		2	130	94	36	0	130	0	0	0	23	
TA 17		1	9	7	2	0	9	0	0	0	23	
TA 27		6	424	256	168	0	247	0	177	0	23	
TA 41	DUNE	1	51	33	18	0	37	9	0	5	1	
TF 55	DUNE	9	446	187	221	38	377	10	55	4	1	
TF 56	DUNE	1	36	14	18	4	32	0	4	0	1	
TF 84	DUNE	2	586	537	9	40	512	57	13	4	1	
TG 33		2	87	50	37	0	48	31	7	1	23	
TL 08		1	159	72	87	0	108	19	25	7	1	
TL 23		1	22	7	15	0	19	3	0	0		
TL 27		1	16	4	9	3	13	0	3	0	23	
TL 35	WOOD	1	807	222	398	187	576	4	55	172	14	
TL 37		14	916	542	297	77	451	43	364	58	16	
TL 47		22	2659	1448	924	287	1525	114	691	329	16	8 hyalo

G.S. Np.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E/S	DATA FROM	NOTES
TL 52		1	34	13	21	0	31	0	3	0		
TL 56		1	474	266	191	17	347	15	24	88	15	
TL 57		1	27	25	2	0	23	2	0	2	5	
TL 74		8	206	112	89	5	171	11	17	7	23	
TM 09		1	172	108	64	0	172	0	0	0	6	
TM 47		9	1401	496	887	18	527	786	85	3	23	
TQ 04		1	2	0	2	0	1	1	0	0	23	
TQ 07		3	25	11	14	0	21	3	1	0	23	
TQ 08		2	2	0	1	1	1	0	1	0	23	
TQ 09	WOOD	12	365	35	328	2	196	46	38	85	7	
		8	106	35	70	1	80	8	12	6		
TQ 13		2	8	1	7	0	2	3	3	0	23	
TQ 18		11	1058	449	607	2	605	268	185	0	23	
TQ 19		1	9	3	6	0	7	2	0	0	23	
TQ 20		1	26	21	5	0	18	7	0	1	19	
TQ 21	WOOD	3	27	2	25	0	16	0	11	0	19	

G.S. No.	HABITAT	NO. OF SAMPLES	TOTAL SNAILS	Y	P	B	S	3	O	E/S	DATA FROM	NOTES
		4	67	48	19	0	55	9	0	3		
TQ 30		10	440	394	45	1	294	97	33	16	19,23	
TQ 31	WOOD	6	311	221	87	3	253	41	16	1	19	
		27	1336	1263	73	0	1072	172	83	9		
TQ 40	WOOD	2	79	8	71	0	44	35	0	0	19,23	
		27	1661	811	850	0	1208	319	130	4		
TQ 43		2	17	1	16	0	16	1	0	0	23	
TQ 45		3	7	2	3	2	4	0	3	0	23	
TQ 46		2	9	5	4	0	6	0	3	0	23	
TQ 47		3	38	20	18	0	30	3	4	1	23	
TQ 50		25	1248	845	399	4	996	142	72	38	19	271 hyalo
TQ 52		1	59	31	28	0	30	7	22	0	23	
TQ 55	WOOD	1	46	26	16	4	20	4	13	9		
TQ 56	WOOD	1	23	5	18	0	16	5	2	0	2,23	
		2	262	69	193	0	214	22	10	16		
TQ 65	WOOD	1	27	5	21	1	23	1	1	2		
TR 04	WOOD	1	75	72	2	1	66	1	7	1		

MB EVS should be = US throughout See Note on table 2

TABLE 3

Morph Frequencies in European Populations of Cepaea Nemoralis

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	[illegible]5
GREAT BRITAIN								
NG	15	4	11	0	13	0	2	0
NH	1	0	1	0	0	0	1	0
NM	4649	3091	1558	0	3342	335	479	493
NN	184	110	69	5	134	6	27	17
NO	3102	498	2604	0	2475	121	506	0
NR	123	68	55	0	99	17	7	0
NS	185	93	92	0	163	16	6	0
NT	2234	693	1309	232	1806	69	337	22
NU	3362	1200	1946	216	2393	322	624	23
NY	38	17	21	0	34	0	4	0
NZ	1024	577	404	43	948	31	37	8
SD	1665	950	715	0	1176	136	329	24
SE	1128	578	550	0	908	162	52	6
SH	2008	1265	683	60	1406	310	267	25

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	B S
SJ	5571	3375	1976	220	4183	1104	271	13
SK	20180	13062	5829	1289	1952	7368	10860	0
SM	34	3	31	0	16	1	9	8
SO	2832	1807	889	136	2037	394	190	211
SP	15832	6537	8574	721	8943	2423	3285	1181
SR	48	14	34	0	33	8	0	7
SS	4165	1924	2211	30	1737	1288	1098	12
ST	6901	4289	2233	379	5267	920	500	214
SU	40413	20281	14592	5540	14242	13502	11770	899
SV	4894	973	3921	0	1705	1840	1349	0
SW	12333	9052	3259	22	4602	3428	4121	182
SX	1195	922	273	0	266	496	426	7
SY	5842	3051	2191	600	3313	1067	1399	63
SZ	111	6	100	5	78	26	7	0
TA	614	390	224	0	423	9	177	5
TF	1068	738	248	82	921	67	72	8

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	E 5
TG	87	50	37	0	48	31	7	1
TL	5320	2711	2033	576	3264	211	1182	663
TM	1573	604	951	18	699	786	85	3
TQ	7258	4311	2926	21	5228	1196	643	191
TR	75	72	2	1	66	1	7	1
IRELAND								
B	318	282	36	0	184	4	112	18
C	4645	1509	3135	1	3793	151	580	121
D	225	151	78	0	106	38	76	9
F	49	40	9	0	24	7	18	0
G	11707	5195	4929	1583	7519	444	3505	239
H	45	37	5	3	33	3	9	0
J	83	46	36	1	33	37	13	0
L	232	150	82	0	81	56	95	0
M	646	197	449	0	570	39	35	2

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	E 5
N	59	32	26	1	38	8	12	1
O	156	76	68	12	87	12	38	19
Q	258	144	114	0	77	103	73	5
R	232	174	58	0	108	65	58	1
S	12	6	6	0	7	3	2	0
T	257	156	73	28	158	42	50	7
V	478	324	154	0	198	149	128	3
W	12	8	4	0	6	4	2	0
X	11	5	6	0	5	1	3	2
FRANCE								
PAS DE CALAIS	-	66%	34%	-	-	-	-	-
NORD	15449	-	-	-	8215	4255	2339	640
SOMME	28748	21273	7475	-	10545	4286	12005	1912
EST	6590	-	-	-	1335	666	3053	1536
NORMANDIE	5480	3726	1754	-	2051	928	2158	343

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	[illegible]5
REG. PARISIENNE	22249	15129	7120	-	11323	5509	3762	1655
BRETAGNE	26973	15601	11372	-	8462	10911	7417	183
MARNE	-	78%	22%	-	-	-	49%	-
LOIRE	-	52%	48%	-	-	-	17%	-
CHARENTE	-	-	-	-	-	-	19%	-
CENTRE	7659	5208	2451	-	2887	2256	1572	944
MASSIF CENTRAL	3571	3000	571	-	1777	982	565	247
ALPES	4091	3232	859	-	2319	331	1147	394
REG. MEDITERRANEAN	674	532	142	-	220	267	135	52
LOT	-	63%	-	-	-	-	-	-
CENTRAL PYRENEES	15906	11456	4450	0	9049	931	5023	903
AQUITAINE	35984	20511	15473	-	13483	4361	12645	5495
SPAIN								
SEGRE-VALIRA	2985	2722	263	0	1842	9	931	203
TER	3961	3842	119	0	1291	142	2487	41

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	E 5
GERMANY								
E. HOLSTEIN	4036	2220	1816	-	1615	1614	807	0
W. MECKLENBURG	16586	4976	11610	-	6634	1659	6634	1659
N. MECKLENBURG	58544	8782	49762	-	29272	17563	11709	0
E. MECKLENBURG	320	176	144	-	160	96	32	32
ODERBRUCH	122	49	73	-	49	12	49	12
MARK	9273	3709	5564	-	2782	2783	2782	927
BÖRDE	3814	2670	1144	-	1145	381	381	1907
N. SACHSEN	6512	3582	2930	-	650	1954	1954	1954
THÜRINGEN	11720	6446	5274	-	4688	1172	1172	4688
W. SACHSEN	2932	1613	1319	-	292	1173	586	881
E. SACHSEN	4458	1783	2675	-	1338	1337	1337	446
OBERFRANCKEN	683	478	205	-	136	68	137	342
MAINFRANCKEN	202	162	40	-	40	0	61	101
WESERTAL-WESTFALEN	669	368	301	-	385	42	134	108
WESTERWALD	1008	706	302	-	201	101	504	202

LOCALITY	TOTAL SNAILS	YELLOW	PINK	BROWN	12345	00300	00000	B/5
HANNOVER-W.HOLSTEIN	602	277	325	-	241	160	160	41
E. FRIESLAND	1655	662	993	-	496	381	662	166
EIFEL-W.PFALZ	26	14	12	-	5	3	8	10
N. OBERRHEIN	2200	1540	660	-	440	220	880	660
S. OBERRHEIN	5839	3212	2627	-	1751	584	1752	1752
WÜRTTEMBERG	131	118	13	-	13	28	26	66
SUDBAYERN	25	15	10	-	4	3	3	15
YUGOSLAVIA								
54/50	43	41	2	0	15	26	2	0
55/49	11021	10442	579	0	8224	2225	449	123
55/50	134	134	0	0	68	17	49	0

TABLE 4

Morph Frequencies in Yugoslav Populations of *Cepaea vindobonensis*: (a) Gacka Area

SAMPLE	NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
VRAINIK		000813	25	7	3	14			(FFF)FF	1	120	610	H
MELNICE	1	032798	27	24	3						150	570	H
	2	028796	25	22	2	1					110	580	H
	3	016802	98	65	29			2	L(L34)5	2	80	570	H
	4	025796	49	37	11			1			110	540	H
	5	028791	36	28	8						350	520	H
	6	0131783	94	79	7	3	1	2	FOFFF	2	120	500	H
									(FFF)FF	5			
	7	034782	150	55	18	72					160	500	H
	8	036778	71	33	3	34	1				60	510	H
VRZICI	1	040773	55	53		2					210	510	H
	2	041769	35	13	2	20					450	570	H
	3	044761	20	7		13					150	520	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
CRNI KAL	1	056756	79	13		64			FOFFF 2		120	490	H
	2	060753	39	24		14			FOFFF 1		800	480	H
	3	067743	26	24	2						560	470	H
	4	057738	27	26		1					160	560	H
ZUTA LOKVA	1	060803									360	480	H
	2	057803	87	21	9	51	5		(FF)FFF 1		420	480	H
	3	052802	36	6	1	27	2				190	480	RH
	4	053811	116	25		91					240	530	S
	5	048805	76	26		43	1		FOFFF 6		180	500	H
	6	044801	73	30	16	12	4	9	LLL45 1	FOFFF 1	100	520	RH
DOBRICA	1	085799	27	24	2				(LL3)45 1		820	470	S
	2	089799	24	20	4						430	470	H
KOSA BRLOSKA		101792	28	27	1						100	480	S
RAPAJIN KLANAC		064800	59	10	6	40	3				260	490	RH
	2	075789	42	29	10	2		1			110	460	H

See Note.

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	1(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	3	077796	97	61	34	1		1			200	440	H
	4	082790	43	23	16			3	LLL45 1		350	430	H
RAPAJIN DO	1	080789	4	2	2						200	430	H
	2	080789	3	2	1						"	"	H
	3	081788	8	5	3						230	430	H
	4	081788	9	2	7						"	"	H
	5	083788	1					1			420	430	H
	6	085787	10	7	3						340	440	H
	7	085787	11	9	1			1			"	"	H
	8	087787	20	17	3						880	430	H
	9	089786	75	66	8			1			1120	430	H
	10	089786	36	35	1						"	"	H
RAPAJICI	1	091785	9	8	1						760	430	H
	2	091785	4	3	1						"	"	H
	3	091783	48	31	16				LLO45 1		940	430	H
	4	091783	10	3	7						"	"	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	FOLJE INDEX	HEIGHT	HAB.
5	091781	71	43	28						380	430	H
6	091781	27	20	4			1	(LLL)45 2		"	"	H
7	093777	66	43	23						850	430	H
8	093777	205	160	33			8	L(L34)5 3	L(L3)(45) 1	"	"	H
9	095776	38	23	14				L(L3)(45) 1		1520	430	H
10	095776	103	80	19			2	(LL)345 2		"	"	H
11	097774	43	28	12			2	(LL)345 1		1300	430	H
12	099773	2		2						1460	430	H
13	100772	52	10	35				L(L34)5 5	L(L3)(45) 2	1350	430	H
14	100772	40	7	21			1	L(L34)5 10	(123)45 1	"	"	H
BELOG STACIJA	102772	31	8	16				L(L34)5 5	L(L345) 1			
								LL3(45) 1		1620	430	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
2	103770	63	34	23				LLL45 1	L(L34)5 5	1600	430	H
3	104768	42	15	20			3	L(L34)5 4		1180	430	RH
4	104768	49	16	24			1	L(L3)(45) 5	L(L34)5 3	"	"	H
5	106766	14	7	7						640	430	RH
6	106766	22	9	12			1			"	"	H
7	109762	6	2	4						240	430	H
8	109761	40	20	18				L(L34)5 2		"	"	H
9	109760	2	1	1						170	430	RH
10	109760	10	3	5				L(L34)5 2		"	"	RH
11	110758	7	3	3				L(L34)5 1		240	430	RH
12	110758	23	9	10				L(L34)5 4		"	"	H
13	111757	19	4	11				L(L34)5 4		460	430	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
14	111757	3	3							460	430	H
15	112756	21	8	11				L(L34)5 2		700	430	H
SRPSKO POLJE 1	126738	77	66	9				LLL45 1	(LL3)45 1	2240	420	H
2	125740	116	47	69						1810	420	H
3	126736	29	26	2			1			1390	420	H
4	123736	20	14	6						1860	420	H
5	119735	30	11	19						970	420	H
6	115731	38	28	10						480	420	H
7	110728	20	18	2						320	420	H
8	109731	30	21	9						560	420	H
9	995738	35	22	12	1					520	420	RH
10	101736	23	19	4						200	420	H
11	109735	40	14	26						300	420	H
12	111742	22	19		3					470	430	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	14	113737	61	29	31				L(L34)5 1		470	420	H
	15	115739	40	22	18						1050	420	H
	16	117739	11	7	4						850	420	H
	17	118743	98	66	24				(LL)345 2	(LL3)45 4 L(L34)5 1 L2345 1	880	420	H
	18	119744	47	22	21				LLL45 1	(LLL)45 3	3320	420	RH
BJELJEVINE	1	108722	27	19	8						610	430	H
	2	102719	31	24	7						250	440	RH
KOMPOLJE	1	116745	26	17	9						1200	420	BW
	2	115751	40	6	26				L(L34)5 8		840	420	H
	3	114755	7	1	4			2			620	430	RH
	4	114755	91	26	47			4	L(L34)5 14		"	"	H
	5	116753	35	11	14			3	L(L34)5 7		720	430	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	1(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
6	116753	39	10	23			1	L(L34)5 5		720	430	H
7	118752	170	51	77				L(L34)5 34 L(L345) 6 (LL3)(45) 2		2280	420	H
8	118752	32	4	10				L(L34)5 18		"	"	H
9	120751	21	3	8				1(L34)5 10		1820	420	H
10	120751	49	8	21				L(L34)5 15 1(L345) 2 LL3(45) 3		"	"	H
11	121751	69	55	10			3	1(L34)5 1		1910	420	H
12	121751	72	61	7			4			"	"	H
13	123750	98	43	46			2	L(L34)5 7		2400	420	H
15	125748	35	15	17			1	L(L34)5 2		1950	420	H
16	125748	103	32	50				L(L34)5 21		"	"	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
17	126746	45	14	25			1	L(L34)5 4 L(L345) 1		1830	420	H
18	126746	65	19	38				L(L34)5 6 1(L3)(45) 1 (LL3)45 1		"	"	H
19	128745	122	11	70			2	L(L34)5 39		2820	420	H
20	128745	159	44	99				L(L34)5 15 (LL3)45 1		"	"	RH
21	130745	85	42	31			1	L(L34)5 1 L(L3)(45) 5 (LL3)(45) 5		1070	420	H
22	130745	31	19	11				L(L34)5 1		"	"	H
23	132743	142	48	89				L(L34)5 2 (LL3)(45) 3		1270	420	H
24	133741	23	13	9				(LL34)5 1		1130	420	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	25	135739	175	155	20						2650	420	H
	26	135739	9	4	5						"	"	H
	27	136738	9	7	2						1390	420	H
	28	136738	3	3							"	"	H
	29	134733	68	64	4						1310	420	H
	30	136736	97	44	52				LO(34)5 1		1170	420	H
	31	138736	71	59				12			2500	420	H
	32	138736	74	60	6			7	(LL)345 1		"	"	H
	33	139734	31	27	3			1			880	420	H
	34	139734	83	69	2			12			"	"	H
	35	141733	5	2	3						1010	420	H
	36	145730	21	1	20						920	430	H
	37	145730	17	6	11						"	"	H
CROVAC	1	146729	29	8	16			3	L(L3)(45) 2		1070	440	H
	2	146729	35	5	28			1	L(L3)(45) 1		"	"	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	1(L3)45	FFFFF	F(FF)FF	L0345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
3	147726	2	1	1						1120	450	RH
4	147726	83	24	52			2	(LL3)45	5	"	"	RH
5	147721	22	19	3						220	440	H
6	148724	17	14	3						140	450	H
7	148724	2	1	1						"	"	RH
8	150721	101	77	14			9	LL045	1	240	450	H
9	150721	5	4	1						"	"	H
10	152719	27	16	7			4			340	460	H
11	154716	5	5							150	470	RH
12	155714	72	50	6			15	LL(34)5	1	260	470	H
13	157713	11	8	1		2				430	470	H
14	158711	4	2	1			1			380	470	H
15	158711	1		1						"	"	H
16	160709	24	22				2			480	470	H
17	161709	3	2				1			280	470	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	1(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	18	163707	9	7				2			270	470	H
	19	164706	31	16	10			5			200	470	H
	20	167705	1	1							500	460	SW
	21	166703	30	29	1						210	480	S
	22	168701	29	26	3						140	470	H
PODBRDJE	1	096784	146	69	60	17					1100	430	H
	2	102782	86	69	13			4			1720	430	H
	3	108779	81	65	9			4	L(L34)5 1 (LL)345 1 LL)45 1		1630	440	H
	4	111779	17	4	13						1740	450	H
	5	114779	55	34	14				L(L34)5 7		540	440	H
KLANAC	1	128781	81	27	36				L(L34)5 18		280	460	H
	2	129783	57	31	17	1			L(L34)5 8				H
	3	135785	26	24	1			1			1340	450	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	4	136783	60	55	5						1300	450	H
BELOG	1	106771	10	4	5				L(L34)5 1		760	440	H
	2	106773	32	28	4						220	440	H
	3	114775	21	19	2						660	460	H
	4	128778	23	19		4					300	480	H
	5	132776	21	18	3						660	490	H
PRICE	1	139778	35	23	7			5			1000	450	RH
	2	144776	54	42	5			7			900	450	RH
ZAKULJE	1	147775	43	41					(LL)345 2		900	450	H
	2	150774	81	74	5			1	LLL45 1		680	450	H
	3	153773	46	32	13			1			620	450	RH
	4	157772	23	4		19					80	460	H
	5	158771	16	8	3	4			(LLL)45 1		100	460	H
	6	163768	22	22							210	480	H
	7	166766	70	55		3		10	LL345 1	FOFFF 1	100	480	S

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
LALICI	1	171763	39	31		7			FOFFF	1	610	460	S
	2	174760	26	23				3			1000	460	S
	3	179762	27	5		18		3	FOFFF	1	200	500	S
	4	178758	22	5		16			FOFFF	1	980	460	S
	5	180756	27	21	1	5					970	460	H
LONCARI	1	188753	34	29	2	1		2			300	460	S
	2	191751	35	22		9		1	FOFFF	3	260	460	H
	3	193750	38	13	1	24					310	460	H
	4	197749	32	19	1	10		2			400	460	S
GLAVACE	1	204745	22	16	2	2		2			790	460	H
	2	208744	13	11	1	1					900	460	RH
	3	212741	35	30	4			1			1170	460	H
	4	216727	11	11							2520	470	H
	5	222741	34	31	2	1					110	470	BW
	6	217747	25	20	1	3		1			200	530	S
	7	212748	22	15	1	6					200	550	S

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	8	216733	133	120	4			9			1430	470	H
	9	216729	168	155	1			12			2340	470	H
	10	216726	35	33				2			2450	470	S
	11	222734	31	30	1						2760	460	H
	12	226729	72	69	1			2			2800	470	RH
POLJICE	1	171697	1	1							200	450	H
	2	164697	30	25	5						1240	460	H
	3	162697	36	31	5						1970	460	H
	4	158696	20	17	3						970	460	BW
	5	154697	82	70	9			3			180	460	S
	6	152696	49	40	7			1	LL3L5	1	180	450	H
SVICA	1	140697	2	1	1						300	470	RH
	2	145704	79	69	4			5	00345	1	280	490	S
	3	138698	68	59	9						380	450	H
	4	138695	25	23	2						740	450	H
BURIC KLANAC		145711	55	54	1						880	470	S

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
GEROVO SELO 1	138689	15	15							150	450	H
2	136685	46	40	5				(LL)345	1	50	500	H
3	132684	17	14	2				LLL45		80	520	H
4	132683	36	36							150	500	H
GORICI 1	126681	45	41	1			3			130	530	S
2	122676	42	34				8			380	500	S
3	122673	64	55	1			8			770	500	H
4	118670	32	29				3			520	490	H
5	115669	36	34	1			1			170	540	S
6	111669	12	12							110	570	S
7	111680	61	61							290	530	H
POLJANE 1	101668	65	5		57			FCFFF	3	80	630	H
2	097667	48	14		34					250	650	H
3	093667	22	3		19					220	660	S
4	092665	31	1		25			FCFFF	5	130	670	H

See Mbr

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	5	103657	12	2	10	10					140	620	H
	6	105655	11	11							140	620	H
	7	096666	9	9							180	600	H
KUTEREVO		112638	22	21		1					220	580	H
LIPOVLJE	1	132676	94	89	3			2			160	530	H
	2	135672	63	62	1						170	540	H
	3	140668	97	94	2			1			490	520	H
	4	142665	24	24							210	520	H
TISOVAC		150657	2	2							260	520	H!
MLADA NEDELJA		131698	80	77	2			1			160	480	S
	2	126697	114	105	9						190	480	H
	3	124676	40	33	7						790	460	S
PONORI	1	121693	17	14	2			1			80	450	S
	2	121700	138	130	8						290	480	H
	3	111696	60	57	3						410	480	H
	4	107695	2	2							490	470	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
GROZDANICI	1	097691	82	79	2				(LL)345 1		180	430	RH
	2	102688	20	19	1						170	450	H
	3	093695	11	11							90	450	H
PODUM	1	215722	67	63	1			3			2510	460	H
	2	216719	119	98	3	5		9	(FFF)(FF) 1	00345 2	2110	460	H
									LL045 1				
	3	214718	19	16	2			1			1500	460	H
	4	218718	93	82	2			8	00345 1		2280	460	H
	5	224719	21	20	1						240	470	H
	6	229719	43	28	1			14			1910	470	RH
	7	228717	65	63	1						1940	470	H
	8	237715	39	34	4			1	(LL)345 1		380	480	H
	9	242713	46	43	2	1					480	490	H
	10	246709	42	33	8	1					1450	490	H
	11	255707	38	38							1160	500	RH
	12	259696	7	7							1920	510	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	13	257692	3	3							1260	510	H
MARKOVICEVO SELO		207710	62	56	2			2	LLL45 1		2010	460	H
									(LL)345 1				
	2	205706	95	78	8	9					1060	460	H
	3	202705	67	44	10	10	1		LL045 1	LL305 1	970	460	H
STARO SELO	1	202714	106	101	2			3			1680	450	H
	2	196717	44	40		2			(LL)345 1		820	460	H
									LO045 1				
	3	194720	39	27	3	8			FOFFF 1		800	460	H
	4	195721	7	3	1	3					820	480	H
	5	190714	8	8							700	460	H
SRELISTE	1	186702	21	17	3			1			2260	460	H
	2	189703	22	22							690	460	H
OTOCAC	1	205691	3	3							620	450	RH
	2	200693	7	7							580	460	H
SV. MARKO		244687	11	10					(LL)345 1		1400	490	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
INICI		261681	16	15	1						1150	490	H
SKARE	1	231727	35	30	2			3			2500	480	H
	2	237722	49	47				1	(LL)345 1		320	480	H
	3	238720	41	18		17		4	LLL45 1	FoFFF 1	240	480	H
	4	243720	5	5							460	480	H
	5	246720	13	3		10					620	490	H
	6	251722	85	80	5						960	500	H
	7	256712	4	4							1200	510	H
DONJI DOLJANI		266710	46	39	7						1250	520	H
ZALUZNICA	1	280688	1	1							780	520	RH
	2	270700	1	1							620	570	H
VRHOVINE		314673	28			26	2				100	670	RH
PROKIKE	1	055812	29	9	1	19					440	530	S
	2	056814	29	8		21					140	520	H
	3	056816	50	11	10	26	3				470	510	H
	4	059817	31	11	3	16	1				340	510	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	5	055820	21	4		17					410	490	H
SMILENCI	1	041829	40	39					LLO45 1		210	550	H
	2	057831	26	17	5	4					160	520	H
	3	061833	93	73	7	9	2	2			260	520	S
	4	067833	34	29	2	3					130	530	S
	5	070834	25	19	5	1					200	520	S
BRINJE	1	073833	31	25	3			3			100	490	H
	2	083855	21	19				2			550	460	H
	3	084835	47	44				3			460	460	H
	4	091834	32	29	2			1			780	460	H
	5	094835	10	8	1			1			580	460	H
	6	112848	52	30	4	14	1	2	LLO45 1		390	490	H
	7	111851	42	35	2			3	(123)45 1	LLO45 1	100	520	RH
BLAZANI	1	085832	1	1							800	460	H
	2	090828	22	22							730	460	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	PCLJE INDEX	HEIGHT	HAB.
	3	093832	28	27	1						1050	460	H
SV. VID	1	101830	21	20	1						1330	460	H
	2	106834	45	44					(LL345) 1		2900	460	H
	3	103829	22	21	1						1170	460	H
DRAZENOVICI	1	111836	22	18	4						340	470	H
	2	116837	23	23							750	470	H
VUCETICI		121832	33	29	4						920	470	H
RUMENOVICI		140829	4	2	1	1					70	530	H
PLASCICA	1	145829	26	12	3	11					50	560	H
	2	153830	24	9	1	14					200	580	H
LETINAC		171826	21	17	3			1			70	610	H
DOMICI	1	101842	21	19	2						520	480	H
	2	099845	30	30							220	540	H
BORICI	2	096861	41	31	1	7			LL045 1	(LLL)45 1	40	630	H
BUKOVLJE	1	093865	31	29	1	1					50	630	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	2	086873	21	19	1					(LL)345 1	540	600	RH
	3	087878	21	21							760	580	H
MALJKOVICI	1	079879	22	22							940	590	H
	2	076881	27	27							1640	590	H
KOLJEVCI	1	113853	49	48						LLL45 1	50	560	S
	2	121860	108	108							210	560	S
KRIZPOLJE	1	127868	26	25						LL3L5 1	960	560	H
	2	128870	34	32				1		(LL)345 1	2260	550	H
	3	140878	49	24		14		6		FOFFF 5	270	570	H
MALIKUT	1	132866	21	21							760	550	H
	2	133860	14	14							800	560	H
	3	135861	12	11	1						840	560	H
SPRAJCI		127876	27	27							1660	550	H
DRAZENOVICI		160868	4	3	1						480	560	H
PERKOVICI	1	149871	38	26	3	8	1				620	540	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
	2	147872	27	24		2		1			440	560	H
	3	145873	26	21	1	3			LLO45 1		270	550	H
JELVICA	1	143892	57	2		55					160	560	H
	2	138877	21	11		7		2	FOFFF 1		110	570	H
	3	144893	36	15		18		1	FOFFF 1		220	570	BU
	4	143896	22	4		18					100	580	S
DUMENCICI		152900	25	6	1	14	2	1	FOFFF 1		90	530	S
CRNAC		135907	35	3	1	31					40	560	S
BORIC		116924	23			23					30	500	S

4(b) Lika Area

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	L0345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
KLOBUCARE		260620	2	2							200	560	S
JANJCE		284560	1			1					210	580	S
PARIPOVICI		287566	10	1		9					120	550	S
KRS	1	253540	6		2	3	1				210	560	S
	2	248540	22	8	1	13					240	560	S
	3	242541	48	30		18					660	560	H
KOSINJSKI ZAMOST	1	224542	21	17	1			3			540	500	H
	2	223545	20	11	2	7					220	500	S
GORNJI KOSINJ		224535	27	21	4			2			320	500	S
	2	220528	10	9				1			380	500	H
	3	213522	1	1							600	500	H
	4	204520	2	2							680	500	H
KOSINJSKI BAKOVAC	1	118512	1			1					130	500	H
	2	165521	23			23					170	510	H

See Note.

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	L0345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
MLAKVA	1	227522	32	25	3	1		3			740	500	BW
	2	232524	39	18		11		4	FOFFF	6	430	510	H
	3	234520	10	7		2		1			400	510	H
	4	235518	8	6	2						250	520	H
	5	230509	2	2							380	510	H
DONJI KOSINJ	1	211564	48	39	6	1	1	1			460	500	S
	2	205570	25	15	2	8					700	500	H
ZAMRSTEN	1	208541	20	5		14	1				500	500	RH
	2	204549	7	7							570	500	H
LIPOVO POLJE	1	195551	25	15	6	3			12345	1	660	500	S
	2	180560	35	14	4	17					680	510	S
	3	152573	19	16		2		1			580	500	S
STUDENCI	1	283513	36	9	7	18	1		(FFF)FF	1	410	590	H
	2	280520	3					3			420	590	H
	3	264531	9			9					280	580	S
PERUSIC	1	301470	21	20	1					4	550	590	H

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	1(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
2	295452	4	3		1					900	590	S
JURISICI	292454	21	15	5	1					1240	580	H
KANIZA 1	281453	43	9	1	30	1		FOFFF 2		120	590	H
2	276454	6	1		4	1				140	590	H
BALENIJA 1	261443	22	10		9		3			100	590	H
2	263444	1	1							210	590	S
STOJEVICA DRAGA 1	248449	1	1							520	580	H
2	242440	34	29	3			2			1070	570	H
BUDZAK	239441	1	1							800	570	H
GORNJI PAZARISTE 1	239430	36	24	10				(LL3)45 2		910	570	H
PREDVAGANAC	211435	29	22	5	1			(FF)FFF 1		2150	570	H
ALEKSINICA 1	192443	13	13							1420	580	H
2	188444	10	5	2	3					1120	580	H
KOJSKO BRDO 1	327467	68	52	7	6	1	1	(LL)345 1		930	570	H
2	332467	1	1							250	580	H
DUNJEVAC	274431	21	21							160	580	S

SAMPLE NUMBER	GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
BREZOVO POLJE	249401	41	33	3			1	(LL)345 1 LL045 1	(LL)45 1 00345 1	1440	570	H
MILKOVICA	237371	7	6	1						110	570	H
SV. PETAR	251354	45	29	14			2			2180	560	H
LICKI OSIK 1	332404	4	3				1			2500	560	S
2	324391	15	9				6			3990	560	S
3	316386	10		2	8					620	570	H
PODSTRANA	323399	1	1							4450	570	H
GOSPIC	307356	8	8							1500	570	H
JASIKOVAC	303327	7	6	1						920	570	H
KANIZA GOSPIC	270329	21	8		7		5	FOFFF 1		180	570	H
OSTRA 1	260312	96	78	18						2390	560	H
2	273315	13	12				1			490	510	H
NOVO SELO 1	248308	2	2							510	570	H
POCUCI	326318	120	105	4			11			1480	580	H
BILAJ 1	340304	14	7	1			6			3900	570	H
2	360315	14	9	1			4			520	580	H

SAMPLE NUMBER		GRID R REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	LO345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
BARLETE		373321	21	15	3			3			1380	510	H
VREBAC	1	396320	87	78				7	LL305	2	620	580	H
	2	403331	13	9	2			2			1880	580	H
	3	432350	4			4					160	610	S
	4	402308	61	58	3						1320	580	H
RUDAJICE		345298	1	1							1400	570	H
LICKI NOVI		270305	1		1						2170	570	H
DIVOSELO		302278	7	3	4						1920	550	H
PAVLICE	1	347249	1	1							3070	570	H
	2	348259	44	16		27		1			3400	570	H
GRAOVCI	1	406296	115	113	2						5030	580	H
	2	401279	10	8				2			4320	580	H
RIBNIK		370272	112	97	14			1			4750	570	H
PLANTAZA		392247	56	43	4			9			1880	580	H
MEDAK	1	405238	88	71	4			13			2840	570	H
	2	415225	12	6				5	FOFFF	1	220	590	H

SAMPLE NUMBER		GRID REF.	TOTAL SNAILS	LL345	L(L3)45	FFFFF	F(FF)FF	L0345	OTHER	OTHER	POLJE INDEX	HEIGHT	HAB.
VEDRINE		409219	1	1							3000	590	H
PAPUCA		435219	51	14		18		10	LLL45 L FFOFF 6	FOFFF 2	140	590	H
RADUC		470170	20	8		5		1	FOFFF 6		500	590	H
MILETICA		513156	16	2				13	(LL3)45 1		3400	580	H
CAVCICI		532143	3	2				1			3000	570	H
LICKO CERJE	1	554132	26	23	2				(LL3)45 1		1160	570	H
	2	555130	2	2							1300	570	H
RICICE	1	562126	30	28	2						700	570	H
	2	572119	22	19				3			1100	580	H
	3	598092	93	73	10	8	1	1			740	580	H
	4	603099	31	2	1	21	5		FOFFF 2		420	580	S
STIKAD KLANAC		613090	26	7	3	12		3	FOFFF 1		270	590	H
	2	622086	36	4		17		1	FOFFF 14		240	550	H
GRACAC		651070	8	2	3			3			300	550	H

TABLE 5.

Morph Frequencies in Romanian Populations of Cepaea vindobonensis.

SAMPLE NUMBER	TOTAL SNAILS	LL345	L(L3)45	FFFFF	L0345	Other	Other		HABITAT
DUMBRAVENI 1	32	8	1	4	19				RH
2	26	11		3	10	FOFFF 1	00345 1		H
NEGRU VODA 1	21	14		3	3	FOFFF 1			RH
2	21	15		2	4				RH
DURGANI 1	29	7		10	7	FOFFF 5			DW
2	27	18		7	2				H
CERNA VODA	24	20			3	00345 1			H
COCHIRLENI	26	18		5	2	12345 1			RH
RASOVA 1	3	2				(123)45 1			S
2	42	25	3	9	4	12345 1			S
LIPNITA 1	44	16		6	13	FOFFF 1	00345 8		DW
2	71	28		3	24	FOFFF 3	OOFFF 2	00345 10	DW
							(LL3)45 1		
BANEASA 1	37	7		1	23	00345 6			DW
2	107	44		3	47	FOFFF 2	OOFFF 1	00345 10	DW
VALULTRAIAN	1			1					DW

SAMPLE NUMBER	TOTAL SNAILS	LL345	L(L3)45	FFFFF	LO345	Other	Other	HABITAT
NEGURENI	82	32		10	29	FOFFF 7	00345 4	DW
ION CORVIN 1	85	34		13	19	FOFFF 13	00345 6	S
2	47	22			17	00345 8		S
ADAMCLISI 1	34	12		7	3	00345 12		H
2	51	14		7	14	FOFFF 9	00345 7	DW
VIISOARA	24	19		5				DW
NICULITEL 1	23	10		1	9	FOFFF 3		S
2	26	11		2	12	FOFFF 1		S
SLAVA RUSA 1	26	13		4	6	LOL45 1	00345 2	DW
2	29	17		1	7	FOFFF 3	00345 1	DW
3	24	3		6	11	FOFFF 4		DW
4	9	3		3	3			DW
BABADAG 1	50	20		4	22	FOFFF 4		S
2	24	6		5	8	FOFFF 3	00345 2	DW
3	28	5		1	15	FOFFF 5	00345 2	DW
4	21	12		1	5	FOFFF 3		DW

SAMPLE NUMBER	TOTAL SNAILS	LL345	L(L3)45	FFFFF	LO345	Other	Other		HABITAT
5	36	18		2	13	FOFFF 2	00345 1		DW
6	37	20			13	00345 4			S
7	24	12		1	10	00345 1			DW
8	22	11			9	00345 2			DW
9	29	16			13				S
10	22	9		3	6	FOFFF 3	00345 1		S
11	22	18		3	1				S
12	39	18	1	3	11	FOFFF 6			DW
13	70	40		10	11	FOFFF 7	00FFF 1	00345 1	S
HAGIENI 1	46	33			12	12345 1			S
2	27	22			3	12345 2			RH
3	75	45	2		22	1L345 1	12345 4	10345 1	H
4	48	23			20	FOFFF 1	1L345 1	00345 3	S
5	70	37			28	FOFFF 1	00345 4		DW
6	77	37			30	12345 2	10345 2	00345 6	S
7	65	29			28	10345 1	00345 7		S
BASARABI	42	17		23	1	FOFFF 1			DW
MURFATLAR	36	21	2	10	2	FOFFF 1			DW

Allison, A.C., 1956. The sickle-cell and haemoglobin C genes in some African populations. Ann. Human Genetics 21: 67-89.

Anonymous, 1944. Geographical Handbook Series. BR 493. Jugoslavia. Naval Intelligence Division, London.

Anuarul Meteorologic 1955. Bucharest: Institutul Meteorologic RSR.

Arlery, R., 1961. La duree d'insolation (1946-1960) en France. La Météorologie 64: 327-349.

Arnold, R.W., 1966. Factors affecting gene-frequencies in British and continental populations of Cepaea. Thesis for the degree of Doctor of Philosophy, Bodleian Library, Oxford.

Arnold, R., 1968. Studies on Cepaea. VII. Climatic selection in Cepaea nemoralis (L.).in the Pyrenees. Phil. Trans. B: 253: 549-593.

Arnold, R., 1969. The effects of selection by climate on the land-snail Cepaea nemoralis (L.). Evolution 23: 370-378.

Arnold, R., 1970. A comparison of populations of the polymorphic land snail Cepaea nemoralis (L.) living in a lowland district in France with those in a similar district in England. Genetics 64: 589-604.

Atlas de France N.D. Comité Nationale de Géographie; Emm. de Martonne, Secretary-general. Paris: Editions Geographiques de France.

Atlas Geografic Republic Socialista Romania 1965. Editura didactica si pedagogica, Bucharest 1965.

Barker, J.F., 1968. Polymorphism in West African snails. Heredity 23: 81-98.

Barnes, R.B., 1963. Thermography of the human body. Science 140: 870-877.

Bernot, F., 1957. Temperaturni obrat v. spodnjem delu Ljubljanske Kotline. Hidrometeoroloske Zavod L.R. Slovenije 1957. IO let Hidrometeoroloske sluzbe 15-28.

Birkebak, R.C., 1966. Heat transfer in biological systems. Int.Rev.Gen.Exp. Zool. 2: 269-344.

Booth, R.E., 1966a. 1931-60 average monthly, seasonal and annual maps of bright sunshine over the British Isles. Climatological Memorandum 42A,

Meteorological Office, London.

Booth, R.E., 1966b. 1931 - 60 monthly and annual maps of mean daily maximum and mean daily minimum temperature, and of average summer and winter temperature over Great Britain and Northern Ireland. Climatological Memorandum 43, Meteorological Office, London.

Brncic, D., 1961. Non random association of inversions in Drosophila pavani. Genetics 46: 401-406.

Cain, A.J., 1953. Visual selection by tone of Cepaea nemoralis (L.). J. Conch. 23, 333-336.

Cain, A.J., 1968. Studies on Cepaea V. Sand dune populations of Cepaea nemoralis (L.). Phil. Trans. (B) 253: 499-517.

Cain, A.J., Cameron, R.A.D., & Parkin, D.T., 1969. Ecology and variation of some helicid snails in Northern Scotland. Proc. malac. Soc. Lond. 38: 269-299.

Cain, A.J., & Currey, J.D., 1963a. Area effects in Cepaea. Phil. Trans. B 246: 1-81.

Cain, A.J., & Currey, J.D., 1963b. Differences in interactions between selective forces acting in the wild on certain pleiotropic genes of Cepaea. Nature, Lond. 197: 411-412.

Cain, A.J., & Currey, J.D., 1963c Area effects in Cepaea on the Larkhill Artillery Ranges, Salisbury Plain. J. Linn. Soc. Lond. (Zool.) 45: 1-15.

Cain, A.J. & Currey, J.D., 1963d. The causes of area effects. Heredity 18: 467-471.

Cain, A.J., & Currey, J.D., 1968. Studies on Cepaea III. Ecogenetics of a population of Cepaea nemoralis (L.). subject to strong area effects. Phil. Trans. B. 253: 447-482.

Cain, A.J., & King, J.M.B., & Sheppard, P.M., 1960. New data on the genetics of polymorphism in the snail Cepaea nemoralis (L.). Genetics 45: 393-411.

Cain, A.J., & Sheppard, P.M., 1950. Selection in the polymorphic land snail Cepaea nemoralis, Heredity, 4: 275-294.

Cain, A.J., & Sheppard, P.M., 1952. The effects of natural selection on body colour in the land snail Cepaea nemoralis. Heredity, 6: 217-231.

Cain, A.J., & Sheppard, P.M., 1954. Natural selection in Cepaea. Genetics 39: 89-116.

Cain, A.J., & Sheppard, P.M., 1957. Some breeding experiments with Cepaea nemoralis (L.). J. Genet. 55: 195-199.

Cain, A.J., Sheppard, P.M., & King, J.M.B., 1968. Studies on Cepaea. I. The genetics of some morphs and varieties of Cepaea nemoralis (L.). Phil. Trans. B: 383-396.

Cameron, R.A.D., 1969a. The distribution and variation of three species of land snail near Rickmansworth, Hertfordshire. Zool. J. Linn. Soc. Lond. 48: 83-111.

Cameron, R.A.D., 1969b. The distribution and variation of Cepaea nemoralis L. near Slievecarron, County Clare and County Galway, Eire. Proc. Malac. Soc. Lond. 38: 439-450.

Cameron, R.A.D., 1970. The survival, weight-loss and behaviour of three species of land snail in conditions of low humidity. J. Zool. 160: 143-157.

Cameron, R.A.D., 1970b. The effect of temperature on the activity of three species of Helicid snail (Mollusca: Gastropoda). J. Zool. 162: 303-315.

Carson, H.L., 1955. The genetic characteristics of marginal populations of Drosophila. Cold Spring Harbor Symp. Quant. Biol. 20: 276-287.

Carson, H.L., 1958a. The population genetics of Drosophila robusta. Advances in Genetics 9: 1-40.

Carson, H.L., 1958b. Response to selection under different conditions of recombination in Drosophila. Cold Spring Harbor Symp. Quant. Biol. 23: 291-306.

Carson, H.L., & Heed, W.B., 1964. Structural homozygosity in marginal populations of nearctic and neotropical species of Drosophila in Florida. Proc. Natl. Acad. Sci. U.S. 52: 427-430.

Carter, M.A., 1965. An investigation of the area effect in Cepaea. Thesis for the degree of D.Phil. at the Univ. of Oxford.

Carter, M.A., 1968a. Thrush predation of an experimental population of the snail Cepaea nemoralis (L.). Proc. Linnean Soc. Lond. 179: 241-249.

Carter, M.A., 1968b. Area effects and visual selection in Cepaea nemoralis (L.) and Cepaea hortensis. Phil. Trans. B 253: 397-446.

Chigusa, S., & Mukai, T., 1964. Linkage disequilibrium and heterosis in experimental populations of Drosophila melanogaster with particular reference to the "sepia" gene. Jap. J. Genetics 39: 289-305.

Chung, Y.J., 1967. Persistance of a mutant gene in Drosophila populations of different genetic backgrounds. Genetics 57: 957-967.

Church, N.S., 1960a. Heat loss and body temperature of flying insects. I. Heat loss by evaporation of water from the body. J. exp. biol. 37: 171-185.

Church, N.S., 1960b. Heat loss and body temperature of flying insects. II. Heat conduction within the body and its loss by radiation and convection. J. exp. biol. 37: 186-212.

Clarke, B., 1960. Divergent effects of natural selection on two closely-related polymorphic snails. Heredity 14: 423-443.

Clarke, B., 1962. Natural selection in mixed colonies of two polymorphic snails. Heredity 17: 319-345.

Clarke, B., 1966. The evolution of morph-ratio clines. Am Nat., 100: 389-402.

Clarke, B., 1968. Balanced polymorphism and regional differentiation in land snails. In "Evolution and Environment", Ed. E.C. Drake, 351-368. Yale University Press. New Haven & London, 1968.

Clarke, B., Diver, C., & Murray, J., 1968. Studies on Cepaea. VI. The spatial and temporal distribution of phenotypes in a colony of Cepaea nemoralis (L.) Phil. Trans. B. 253: 519-548.

Clarke, B., & Murray, J., 1962. Changes of gene-frequency in Cepaea nemoralis. Heredity, 17: 445-65.

Clarke, B., & Murray, J., 1962. Changes of gene frequency in Cepaea nemoralis (L.); the estimation of selective values. Heredity 17: 467-476.

Clarke, B., & Murray, J., 1969. Ecological genetics and speciation in land snails of the genus Partula. Biol. J. Linn. Soc. Lond., I: 31-42.

Comfort, A., 1951a. Observations on the shell pigments of land pulmonates. Proc. Malac. Soc. Lond., 29: 35-43.

Comfort, A., 1951b. The pigmentation of molluscan shells. Biol. Rev. Camb. Phil. Soc. 26: 285-301.

Cook, L.M., 1961. The edge effect in population genetics. Amer. Nat. 95: 295-307.

Cook, L.M., 1966. Notes on two colonies of Cepaea nemoralis (L.). polymorphic for white lip. J. Conch. 125-130.

Cook, L.M., 1967. The genetics of Cepaea nemoralis. Heredity 22: 397-410.

Cook, L.M., & Murray, J.J., 1966. New information on the inheritance of polymorphic characters in Cepaea hortensis. J. Heredity 57: 245-247

Cook, L.M., & Peake, J.F., 1960. A study of some populations of Cepaea nemoralis L. from the Dartry Mountains, Co.Sligo, Ireland. Proc. Malac. Soc. Lond. 34: 1-11.

Cook, L.M., & Peake, J.F., 1962. Populations of Cepaea nemoralis L. from sand dunes on the Mullaghmore Peninsula, Co.Sligo, Ireland; with a comparison with those from Annacoona, Dartry Mts., Co. Slig. Proc. Malac. Soc. Lond. 35: 7-13.

Currey, J.D., Arnold, R.W., & Carter, M.A., 1964. Further examples of variation of populations of Cepaea nemoralis with habitat. Evolution 18: 111-117.

Currey, J.D., & Cain, A.J., 1968. Studies on Cepaea IV. Climate and selection of banding morphs from the climatic optimum to the present day. Phil. Trans. B. 253: 483-498.

Cvijic, J., 1918. Hydrographie souterraine et evolution morphologique du karst. Rec. Inst. Geog. Alpine 6: 375-426.

Dawson, P.S., 1970. Linkage and the elimination of deleterious mutant genes from experimental populations. Genetica 41: 147-169.

Day, J.C.L., & Dowdeswell, W.H., 1968. Natural selection in Cepaea on Portland Bill. Heredity 23: 169-188.

Deirmendjian, D., & Sekera, Z., 1954. Global radiation resulting from multiple scattering in a Rayleigh atmosphere. Tellus 6: 382-398.

Digby, P.S.B., 1955. Factors affecting the temperature excess of insects in sunshine. J. Exp. Biol. 32: 279-298.

Diver, C., 1929. Fossil records of Mendelian mutants. Nature, Lond. 124: 183.

Diver, C., 1940. The problem of closely related species living in the same environment. In The New Systematics, ed. J. Huxley, London; Oxford University Press.

Dobzhansky, Th., 1933. Geographical variation in lady-beetles. Amer. Nat. 67: 97-126.

Dobzhansky, Th., 1962. Rigid versus flexible chromosomal polymorphism in Drosophila. Amer. Naturalist. 96: 321-328.

Dowdeswell, W.H., & McWhirter, K.G., 1967. Stability of spot distribution in Maniola jurtina throughout its range. Heredity 22: 187-210.

Downes, J.A., 1962. What is an arctic insect? Can. Entomol. 94: 143-162.

Downes, J.A., 1964. Arctic insects and their environment. Can. Entomol. 96: 279-307.

Edelstam, C., & Palmer, C., 1950. Homing behaviour in gastropodes. Oikos 2: 259-270.

Edney, E.B., 1951. The body temperature of woodlice. J. exp. biol. 28: 271-280.

Ehrlich, P.R., & Raven, P.H., 1969. Differentiation of populations.

Science 165: 1228-1232.

Emberton, L.R.B., 1964. D. Phil. Thesis, Oxford University.

Emberton, L.R.B., & Bradbury, S., 1963. Transmission of light through shells of Cepaea nemoralis (L.). Proc. Malac. Soc. Lond. 35: 211-219.

Epling, C., & Dobzhansky, Th., 1942. Microgeographic races in Linanthus parryae. Genetics, 27: 317-32.

Fisher, R.A., 1958. The genetical theory of natural selection. Second revised edition, Dover Books, New York.

Fisher, R.A., & Diver, C., 1934. Crossing-over in the land snail Cepaea nemoralis L. Nature 133: 834-835.

Fisher, R.A., & Ford, E.B., The spread of a gene in natural conditions in a colony of the moth, Panaxia dominula L. Heredity, 1: 143-174. (1947).

Fox, H.M., & Vevers, G., 1960. The nature of animal colours. Sidgwick & Jackson, London 1964.

Franklin, I., & Lewontin, R.C., 1970. Is the gene the unit of selection? Genetics 65: 707-734.

Frydenberg, O., 1963. Population studies of a lethal mutant in Drosophila melanogaster. I. Behaviour in populations with discrete generations. Hereditas 50: 89-116.

Frydenberg, O., 1964. Population studies of a lethal mutant in Drosophila melanogaster. II. Behaviour in populations with overlapping generations. Hereditas 51: 31-66.

Gates, D.M., 1962. Energy exchange in the biosphere. Biol. Monogr., Harper & Row; New York.

Goodhart, C.B., 1956. Genetic stability in populations of the polymorphic snail, Cepaea nemoralis (L.). Proc. Linn. Soc. Lond. Session 167: 50-67.

Goodhart, C.B., 1958. Genetic stability in the snail Cepaea nemoralis (L.): a further example. Proc. Linn. Soc. Lond. Session 169: 163-167.

Goodhart, C.B., 1962. Variation in a colony of the snail Cepaea nemoralis

(L.). J. Anim. Ecol. 31: 207-237.

Goodhart, C.B., 1963. 'Area effects' and non-adaptive variation between populations of Cepaea (Mollusca). Heredity 18, 459-465.

Guerrucci-Henrion, M-A., 1966. Recherches sur les populations naturelles de Cepaea nemoralis en Bretagne. Arch. Zool exp. gen. 107: 369-417.

Hamilton, W.J., III & Heppner, F., 1967. Radiant solar energy and the function of black homeotherm pigmentation: an hypothesis. Science 155: 196-197.

Helmcke, J.G., 1935. Untersuchungen über die Schalen- und Körperfarbung der Landschnecken. Zool. Jahrb. (Anat.) 60: 1-36.

Hidrometeoroloski Zavod N.R. Hrvatske. 1958. Klimatski Podaci za Gospic. Razdoblje 1946-1955.

Hill, L., & Taylor, H.J., 1933. Locusts in sunlight. Nature 132: 276.

Hill, W.B., & Robertson, A., 1968. Linkage disequilibrium in finite populations. Theoret. Appl. Genetics 38: 226-231.

Hogben, L., & Kirk, R.L., 1944. Studies on temperature regulation. I. The Pulmonata and Oligochaeta. Proc. Roy. Soc. B. 132: 239-252.

Hovanitz, W., 1941. Parallel ecogenotypical colour variation in butterflies. Ecology 22: 259-284.

Jones, J.S., 1966. "Two studies relating to the area effect in Cepaea" Thesis submitted for the degree of B.Sc. at the Univ. of Edinburgh.

Kelly, C.F., Bond, T.E., & Heitman, H., 1954. The role of thermal radiation in animal ecology. Ecology 35: 562-569.

Kendall, M.G., 1948. Rank correlation methods. London: Griffin.

Kettlewell, H.B.D., 1961a. Geographical melanism in the Lepidoptera of Shetland. Heredity 16: 393-402.

Kettlewell, H.B.D., 1961b. Selection experiments on melanism in Amathes glareosa Esp. (Lepidoptera). Heredity 16: 415-434.

Kojima, K-I., Gillespie, J., & Tobari, Y.N., 1970. A profile of Drosophila species' enzymes assayed by electrophoresis. I. Number of alleles, heterozygosities and linkage disequilibrium in glucose-metabolizing systems and some other enzymes. Biochem. Genetics 5: 627-637.

Komai, T., & Emura, S., 1955. Study of population genetics on the polymorphic land snail Bradybaena similaris. Evolution, 9: 400-18.

Labine, P.A., 1966. The population biology of the butterfly Euphydryas editha. IV. Sperm precedence - a preliminary report. Evolution 20: 580-586.

Lamotte, M., 1951. Recherches sur la structure genetique des populations naturelles de Cepaea nemoralis (L.). Bull. Biol. Suppl. 35: 1-238.

Lamotte, M., 1952. Le role des fluctuations fortuites dans la diversite des populations naturelles de Cepaea nemoralis (L.). Heredity, 6: 333-343.

Lamotte, M., 1954. Sur le determinisme genetique du polymorphism chez Cepaea nemoralis L. C.R. Acad. Sci., Paris, 239: 365-367.

Lamotte, M., 1959. Polymorphism of natural populations of Cepaea nemoralis. Cold Spr. Harb. Sym. Quant. Biol. 24: 65-84.

Lamotte, M., 1966. Les facteurs de la diversite du polymorphisme dans les populations naturelles de Cepaea nemoralis (L.). Lav. Soc. Malacologica Ital. 3: 33-72.

Lamotte, M., 1968. Influence de l'altitude sur la frequence du caracter "absence de bandes" dans les populations de Cepaea nemoralis (Mollusques, Helicidae) de Pyrenees francaises.

Levitan, M., 1958. Non-random associations of inversions. Cold Spring Harbor Symp. Quant. Biol. 23: 251-268.

Levitan, M., 1961. Proof of an adaptive linkage association. Science 134: 1617-1618.

Levitan, M., & Salzano, F.M., 1959. Studies of linkage in populations. III. An association of linked inversions in Drosophila guaramunu.

Heredity 13: 243-248.

Lewontin, R.C., 1964a. The interaction of selection and linkage. I. General considerations: heterotic models. Genetics 49: 49-67.

Lewontin, R.C., 1964b. The interaction of selection and linkage. II. Optimum models. Genetics 50: 757-782.

Lewontin, R.C., & Hubby, J.L., 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of Drosophila pseudoobscura. Genetics 54: 595-609.

Lewontin, R.C., & Kojima, K., 1960. The evolutionary dynamics of complex polymorphisms. Evolution 14: 458-472.

Lewontin, R.C., & White, M.J.D., 1960. Interaction between inversion polymorphisms of two chromosome pairs in the grasshopper Moraba scurra. Evolution 14: 116-129.

L'Heritier, P., & Teissier, G., 1937. Elimination des formes mutantes dans une population de Drosophiles. C.R. Soc. Biol. 124: 882-884.

Lomnicki, A., 1964. Some results of experimental introduction of new individuals into a natural population of the Roman snail, Helix pomatia L. Bull. Acad. Polon. Sci. Ser. Sci: Biol. 12: 301-304.

McDonald, D.J., & Peer, N.J., 1960 Natural selection in experimental populations of Tribolium. I. Preliminary experiments with population cages. Genetics 45: 1317-1333.

McFarquhar, A.M., & Robertson, F.W., 1963. The lack of evidence for coadaptation in crosses between geographical races of Drosophila subobscura Coll. Genet. Res., Camb. 4: 104-131.

Manwell, C., & Baker, C.M.A., 1970. Molecular biology and the origin of species: heterosis, protein polymorphism and animal breeding. Sidgwick & Jackson, London.

Mayr, E., 1963. Animal species and evolution. Harvard University, The

Belknap Press.

Mayr, E., & Rosen, C.E., 1956. Geographic variation and hybridization in populations of Bahama snails (Cerion). Am. Mus. Nat. Hist. Novitates, 1806: 1-48.

Merrell, D.J., 1965. Competition involving dominant mutants in experimental populations of Drosophila melanogaster. Genetics 52: 165-189.

Meteorological Office, Air Ministry, London 1956. Charts of mean decadal bright sunshine 1927-1936 for Europe (1928-1935 for several French stations). Prepared in the M.O. from observational material compiled by Mr. D.S. Hancock, The Roundels, Cranbrook, Kent.

Ministry of Housing & Local Government, 1967. 1/625,000 map of annual rainfall 1916-1950 prepared by the Ministry of Housing and Local Government from Meteorological Office statistics. Chessington, Surrey 1967.

Morris, D., 1954. The snail-eating behaviour of thrushes and blackbirds. British Birds 47: 33-49.

Mourant, A.E., 1954. The distribution of the human blood groups. Blackwell, Oxford.

Mukai, T., 1969. Maintenance of polygenic and isoallelic variation in populations. Proc. XII Intern. Congr. Genetics 3: 293-308.

Murray, J., 1963. The inheritance of some characters in Cepaea hortensis and Cepaea nemoralis (Gastropoda). Genetics 48: 605-15.

Murray, J.J., 1966. Cepaea nemoralis in the Isles of Scilly. Proc. Malac. Soc. Lond. 37: 167-181.

Nijenhuis, L.E., 1965. Blood groups and natural selection by the genetical environment. Genetica 36: 208-228.

Nolte, D.J., 1959a. The eye-pigmentary system of Drosophila. VII. The white locus. Heredity 13: 219-231.

Nolte, D.J., 1959b. The eye-pigmentary system of Drosophila. IX. Heterozygous effects of eye-colour genes. Heredity 13: 273-281.

Norris, K.S., 1967. Color adaptation in desert reptiles and its thermal relationships. In: Lizard Ecology, a Symposium. Ed. W.W. Milstead. University of Missouri Press, Columbia, Missouri. pp. 162-229.

Nuevo Atlas de España, 1961. Madrid: Aguilar.

Parry, D.A., 1951. Factors determining the temperature of terrestrial arthropods in sunlight. J. exp. biol. 28: 445-462.

Penzar, B., 1959. Razdioba godisnjik kolicina oborine u Gorskom Kotaru. II Savjetovanje Meteorologa F.N.R.J. za Planinsku Meteorologiju. Hidromet. Zavod. N.R. Hrvatske.

Perrot, J-L., & Perrot, M., 1938. Monographie des Helix du groupe Cepaea. Contribution a la notion d'espece. Bull. Biol. Fr. Belg. 72: 232-259.

Polivanov, S., 1964. Selection in experimental populations of Drosophila melanogaster with different genetic backgrounds. Genetics 50: 81-100.

Porter, W.M., & Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. Ecol. Monog. 39: 227-244.

Prakash, S., & Lewontin, R.C., 1967. A molecular approach to the study of genic heterozygosity in natural populations. III. Direct evidence of coadaptation in gene arrangements of Drosophila. Proc. Natl. Acad. Sci. U.S. , 59: 398-405.

Prout, T., 1965. The estimation of fitnesses from genotypic frequencies. Evolution 19: 546-551.

Prout, T., 1969. The estimation of fitnesses from population data. Genetics 63: 949-967.

Rapoport, E.H., 1969. Gloger's rule and pigmentation of Collembola. Evolution 23: 622-626.

Riemerschmid, G., & Elder, J.S., 1945. The absorptivity for solar radiation of different coloured hairy coats of cattle. Onderstepoort J. Vet. Sci. Animal Ind. 20: 223-234.

Schilder, F.A., & Schilder, M., 1957. Die Bänderschnecken. Eine Studie

zur Evolution der Tiere. Jena: Gustav Fischer Verlag.

Schropp, K., 1931. Temperatur techn Oberflachen unter die Einfluss die Sonnebestrahl. Gesundh.-Ing. 1931: 729-736.

Sedlmair, H., 1956. Verhaltens-, Resistenz- und Gehäuseunterschiede bei den polymorphen Bänderschnecken Cepaea hortensis (Mull.) und Cepaea nemoralis (L.). Biol. Zbl. 75: 281-313.

Sheppard, P.M., 1951a. Fluctuations in the selective value of certain phenotypes in the polymorphic land snail Cepaea nemoralis (L.). Heredity 5: 125-134.

Sheppard, P.M., 1952. Natural selection in two colonies of the polymorphic land snail Cepaea nemoralis. Heredity, 6: 233-238.

Sheppard, P.M., 1967. Natural Selection and Heredity. London: Hutchinson.

Societatea de Stiinte Naturale si Geografie din Republica Socialista Romania, 1966. Biblioteca Geografului 4. Dobrogea Maritima. Bucuresti 1966.

Taylor, J.W., 1914. Monograph of the land and freshwater Mollusca of the British Isles. 3. Leeds: Taylor.

Thran, P., & Broekhuizen, S., 1965. Agroclimatic atlas of Europe. Pudoc. Centre for Agricultural Publications and Documentation, Wageningen.

Turrill, W.B., 1929. The plant life of the Balkan Peninsula. Oxford University Press.

Vetukhiv, M., 1953. Viability of hybrids between local populations of D. pseudoobscura. Proc. Nat. Acad. Sci., 39: 30-34.

Vetukhiv, M., 1954. Integration of the genotype in local populations of three species of Drosophila. Evolution, 8: 241-251.

Vetukhiv, M., 1956. Fecundity of hybrids between geographic populations of D. pseudoobscura. Evolution, 10: 139-146.

Vetukhiv, M., 1957. Longevity of hybrids between geographic populations of D. pseudoobscura. Evolution, 11: 348-360.

Wallace, B., 1955. Inter-population hybrids in D. melanogaster. Evolution, 9: 302-316.

Wallace, B., 1958. The comparison of observed and calculated zygotic distributions. Evolution 12: 113-115.

Wallace, B., 1963. The elimination of an autosomal lethal from an experimental population of Drosophila melanogaster. Amer. Naturalist 97: 65-66.

Walton, J.N., 1969. Carrier detection in X-linked muscular dystrophy. J. Génet. humain 17: 497-510.

Watt, W.B., 1968. Adaptive significance of pigment polymorphism in Colias butterflies. I. Variation of melanin pigment in relation to thermoregulation; Evolution 22: 437-458.

Watt, W.B., 1969. Adaptive significance of pigment polymorphism in Colias butterflies. II. Thermoregulation and photoperiodically controlled melanin variation in Colias eurytheme. Proc. Natl. Acad. Sci. U.S. 63: 767-774.

White, M.J.D., Lewontin, R.C., & Andrew, L.E., 1963. Cytogenetics of the grasshopper Moraba scurra. VII. Geographic variation of adaptive properties of inversions. Evolution 17: 147-162.

Wilkens, J.L., & Fingerman, M., 1965. Heat tolerance and temperature relations of the Fiddler Crab, Uca pugilator, with reference to body coloration. Biol. Bull. 128: 133-141.

Wolda, H., 1963. Natural populations of the polymorphic landsnail Cepaea nemoralis (L.). Arch. Neerland. Zool. 15: 381-471.

Wolda, H., 1965a. The effect of drought on egg production in Cepaea nemoralis (L.). Arch. Neerland. Zool. 16: 387-399.

Wolda, H., 1965b. Some preliminary observations on the distribution of the various morphs within natural populations of the polymorphic landsnail Cepaea nemoralis (L.). Arch. Neerl. Zool. 16: 280-292.

Wolda, H., 1967. The effect of temperature on reproduction in some morphs of the landsnail Cepaea nemoralis. Evolution 21: 117-129.

Wolda, H., 1969a. Fine distribution of morph frequencies in the snail Cepaea nemoralis near Groningen. J. Anim. Ecol. 38: 305-327.

Wolda, H., 1969b. Stability of a steep cline in morph frequencies of the snail Cepaea nemoralis (L.). J. Anim. Ecol. 38: 623-635.

Wolda, H., 1969c. Genetics of polymorphism in the land snail Cepaea nemoralis. Genetica 40: 475-502.

Wright, S., 1931. Evolution in Mendelian populations. Genetics, 16: 97-159.

Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proc. VI int. Congr. Genet. 1: 356-366.

Wright, S., 1935. Evolution in populations in approximate equilibrium. J. Genet. 30: 257-266.

Wright, S., 1940. Breeding structure of populations in relation to speciation. Amer. Nat. 74: 232-248.

Wright, S., 1955. Classification of the factors of evolution. Cold Spr. Harb. Sym. Quant. Biol. 20: 16-24D.

Wright, S., 1956. Modes of selection. Amer. Nat. 90: 5-24.

Wright, S., 1965. Factor interaction and linkage in evolution. Proc. Roy. Soc. B 162: 80-104.

Wright, W.D., 1964. The measurement of colour. 3rd. edition. Hilger & Watts, London 1964.