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Climatic Selection in Cepaea nemoralis (L.) in the Pyrenees

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STUDIES ON *CEPAEA*
VII. CLIMATIC SELECTION IN *CEPAEA NEMORALIS* (L.) IN THE PYRENEES

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[Plates 34 and 35]

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In order to investigate the effects of climate on the shell colour and banding polymorphism of *Cepaea nemoralis*, surveys were carried out, in 1962 and 1963, in two extensive valley complexes in the Pyrenees; populations were sampled over a wide altitudinal range, such that considerable differences in the climatic environment were apparent, both within and between the valley complexes. The valleys selected for study were that of the Garonne in the central Pyrenees and on the north side of the watershed, and that of the Segre and its major tributary, the Valira, nearer the Mediterranean and on the southern side.

The unbanded phenotype exhibits a parallel frequency distribution in colonies sampled near the rivers in both regions. It is at higher frequencies at high altitudes, and also in the lower parts of the valleys sampled, intermediate altitudes having populations which are predominantly five-banded. There is, however, a marked difference between the two regions in the extent of the changes between the intermediate-altitude banding zones and the lower and upper zones; unbanded reaches much higher frequencies regularly in the upper zones of the Garonne compared with those in the Segre-Valira, whereas it is the latter region which exhibits really high frequencies in the lower zone.

The distribution of frequencies of the yellow morph in the Garonne resembles that of unbanded; only intermediate-altitude populations have appreciable frequencies of pink, other populations having high or very high frequencies of yellow. In the Segre-Valira, there are some parallels in frequency distribution, but yellow is at a high overall frequency almost everywhere.

The species is polymorphic for lip colour in the Pyrenees, and the results agree with Lamotte's for other Pyrenean valleys; the white-lipped morph is rare or infrequent in the foothills, and reaches high frequencies in the higher parts of the mountains.

The relative constancy of morph frequencies over considerable distances, and their regular distribution between valleys and between the two regions (for example) show that selection is operating. It is argued that the colour and banding zones are area effects as there is no evidence for variation with habitat in districts where this can be tested by comparing open habitat samples with samples taken from woods, despite the occurrence of visual predation; and certain morph frequencies characterize quite clearly geographical areas rather than habitats.

The broad correlation between morph frequencies—particularly banding morph frequencies—and altitude in the upper parts of the valleys suggested that some climatic aspects might be acting selectively. Comparison of samples made from hill slopes with those made by the rivers shows that the former tend to have less extreme morph frequencies; thus, at similar altitudes, hillside populations have lower frequencies of unbanded and of white-lip, and tend to have lower frequencies of yellow. This indicates that the factors favouring these morphs at higher altitudes do not act at the same strength on the hill slopes as in the valleys. It seems likely, from the accepted generalization that hill slopes are usually more temperate than valley bottoms, that cold air and concomitant low temperatures favour unbanded, yellow, and white-lip. Consideration of aspect of the valleys, and of certain colonies exceptional for banding frequencies concur with this: north-facing valleys and occluded situations tend to have populations with higher frequencies of unbanded than south-facing ones and sunny open localities. A comparison of morph frequencies in the Garonne and Segre-Valira regions with their climates also supports this interpretation for colour and banding.

Similarly, the increase in frequencies of unbanded and of yellow at lower altitudes in the Garonne, and the very marked rise in frequency of unbanded in the Segre-Valira suggests that these two morphs are also favoured in conditions which tend to be warm and dry. The extent of the changes agrees, for the lower Segre-Valira, unlike the lower surveyed reaches of the Garonne, is essentially mediterranean in climate, and the frequency of unbanded is overall much higher there.

Other field evidence, both from the Pyrenees and elsewhere, is in broad agreement with yellow and unbanded being favoured in more extreme climatic conditions, and most of the artificial resistance experiments performed with *Cepaea* accord in that these two morphs survive better when subjected to severe temperatures.

The results are discussed with relevance to morph frequency distributions elsewhere; it is suggested that area effects in unbanded and yellow may occur when climate becomes sufficiently extreme, and some evidence is presented that this may be so on high country in the English counties of Staffordshire and Cumberland. It is also suggested that if the strength of visual selection is relaxed in open country, as recent work indicates, then area effects in pink and five-banded may occur in mild conditions; some evidence is produced in support of this idea.

The clines in banding in the lower valleys are stepped; banding morph frequencies change apparently suddenly from one relatively stable frequency to another in both regions, without relation to topographical features which might cause climatic disjunction in the vicinity of the step. It is tentatively suggested that co-adaptive selection may interact with climatic selection in the intermediate and lower zones, to produce sharp steps in frequency with stability despite change in altitude and climate on either side.

I. Introduction

The kind of selection known to influence the balance of the shell colour and banding polymorphism of *Cepaea nemoralis* that has been identified with reasonable certainty is visual selection by predators (Cain & Sheppard 1950, 1954; Sheppard 1951; Currey, Arnold & Carter 1964; Arnold 1966). The discovery of area effects (Cain & Currey 1963*a*) opened up the possibility that other selective factors affecting the polymorphism might more easily be identified, for Cain & Currey concluded that area effects are caused by physiological selection acting on pleiotropic effects of the colour and banding genes and overriding the action of selection due to visual predators.

Subsequent investigations on area effects and the factors causing them have concentrated on describing the distribution of morph frequencies in different regions in England partly in an attempt to elucidate the action of different climates on the polymorphism, and also on attempting to find associations between topography and morph frequency, for it seemed reasonable to consider that climatic differences between areas could be causing different area effects (Cain & Currey 1963*a*, *b*; Carter 1965; Arnold 1966).

No selective agent causing an area effect has hitherto been discovered, however, although there is some evidence that certain climatic conditions may be responsible for area effects in brown (Cain & Currey 1963*a*; Carter 1965).

Since it was desirable to discover how climate might affect the polymorphism, two intensive surveys were carried out in high mountainous country where a wide range of climatic conditions could be encountered. This paper presents evidence that area effects may at least in some circumstances be caused by climate, and conclusions are made on the action of climate as a selective agent.

II. Choice and description of regions

(1) *Choice*

I chose to work in the Pyrenees, for *C. nemoralis* is abundant and widespread in distribution, and with an altitudinal range from the lowland plains to at least 1440 m (Lamotte 1951). The rock formations are largely calcareous schists and limestones, and it seemed from Lamotte's data that populations could be sampled to the altitudinal limit of the species. Further, the pronounced climatic differences between the north and south sides of the range could allow the comparison of observations in distant and climatically different regions.

Two valley systems were selected for the surveys; their positions are shown in figure 1. The valley of the Garonne, on the north side of the watershed and in the central and highest part of the Pyrenees, was surveyed between St Gaudens in the foothills and the source of the river in the Spanish Valle de Aran. The Segre-Valira region is on the southern side and lies nearer the Mediterranean; samples were made between a small town called Pons on the River Segre and the headwaters in Andorra of a major tributary of the Segre, the River Valira. Each region consists of an upper valley complex of a main valley with its tributary valleys (the Valle de Aran and Andorra) and a lower main valley leading out of the mountains. Figures 2 and 3 illustrate the parts of each region surveyed, and the positions of the samples. Samples were made over an altitudinal range of about 1500 m in both regions, and gross differences in environmental conditions, ranging from mediterranean to subalpine in type, were evident both within and between the sampling regions.

(2) *The Garonne region*

Between St Gaudens and Montréjeau (the west–east northern section of the river, figure 2), the Garonne fringes the northern limit of the Pyrenees, and runs in a wide plain through the foothills. Its valley enters limestone mountains near Montréjeau, and continues southwards into the mountains with the river in a cultivated plain seldom less than 1 km wide as far as the junction of the Luchon valley (figure 2) near St Béat. There, the rock changes from limestone to calcareous schist. The mountain slopes are covered in dense oak (*Quercus petraea* (Mattuschka) Liebl. and *Q. pubescens* Willd.) forest with poplar, alder, and ash (*Populus* sp., *Alnus* sp., and *Fraxinus excelsior* L.) in the plain. South of St Béat, the valley narrows, and it remains narrow until the Valle de Aran, where the Garonne flows in a broad glaciated valley running mainly east–west for 26 km, after which the main valley turns south as the valley of the Garona de Ruda. Nine important tributaries join the Garonne in its course through the Valle de Aran; they are usually narrow and steep-sided, and oriented in a north–south direction.

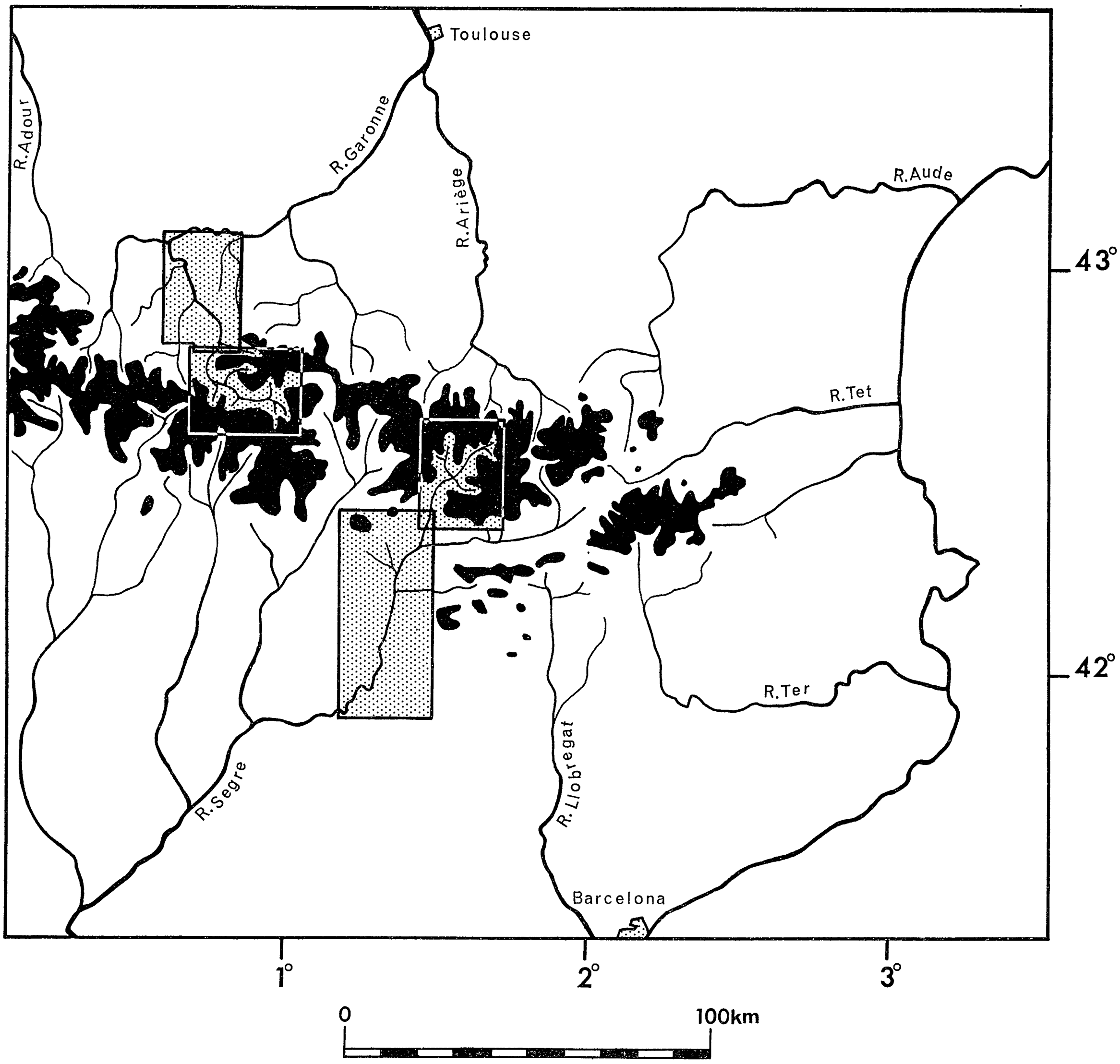

FIGURE 1. The eastern half of the Pyrenees, showing the regions selected for study. The Garonne is on the left, and the Segre-Valira region is on the right. Land over 2000 m is shown black.

There are no deciduous woods in the main valley of the Valle de Aran. Extensive spruce (*Picea abies* (L.)) forests are found on the western and southern slopes, and oak scrub is frequent. Hazel (*Corylus avellana* L.) is abundant in hedgerows, and it often forms

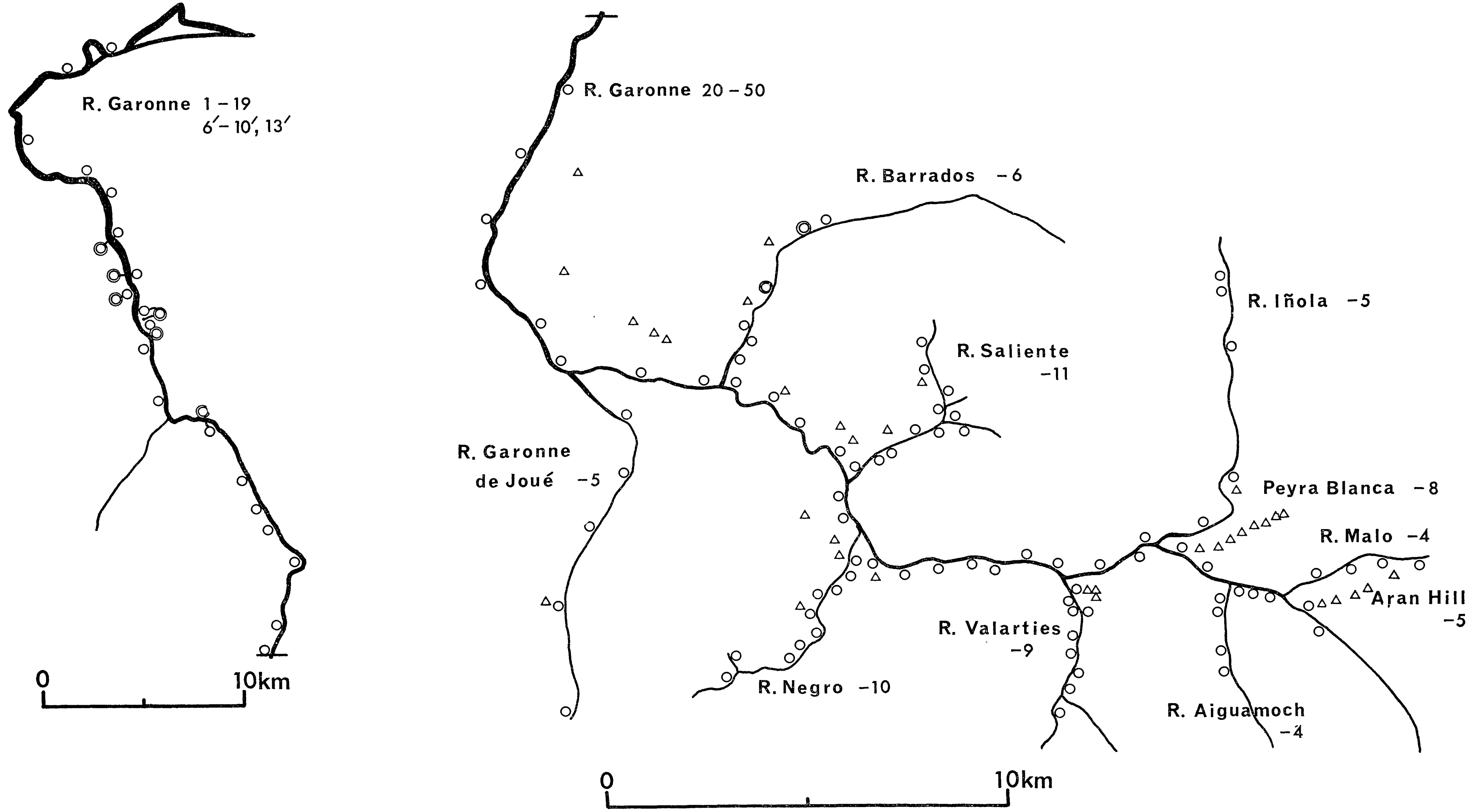

Figure 2. The Garonne region, with the lower Garonne on the left and the Valle de Aran on the right. Circles represent riverside samples, double circles wood samples, and triangles hillside samples. The samples are numbered in order of increasing altitude for each river.

extensive scrubby groves. The floor of the main valley is intensively cultivated, and there are many small villages both in the valley and on the mountain sides. The most frequent riverside trees are ash, sallows (*Salix* spp.), hawthorn (*Crataegus monogyna* Jacq.), and hazel. Above about 1200 m, birch (*Betula* sp.), rowan (*Sorbus aucuparia* L.), and Scots pine (*Pinus sylvestris* L.) become important in the flora. The tree line ends at about 2100 m.

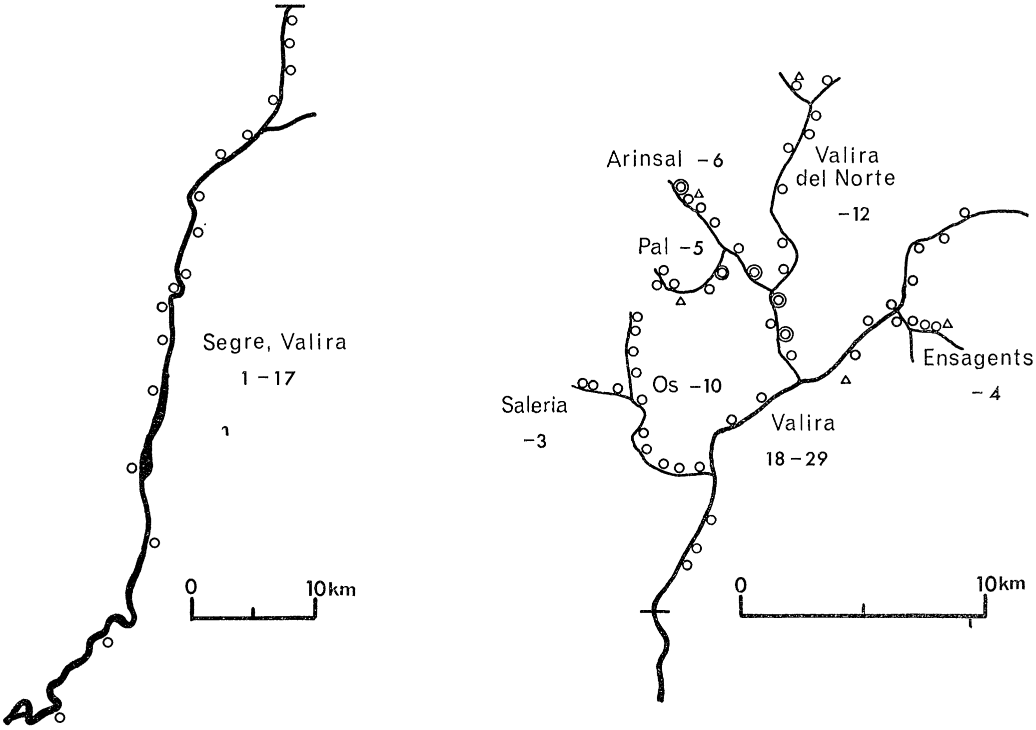

FIGURE 3. The Segre-Valira region, with the lower valley on the left and Andorra on the right. Symbols as in figure 2.

Two of the tributary valleys, the Garonne de Joué and the Barrados, are well wooded, with spruce and beech (*Fagus sylvatica* L.) mixed or in pure stands. Two others (the Valarties and the Aiguamoch) have extensive spruce forests above 1400 m. The other tributary rivers pass through grass fields for most or all of the lengths collected, and the riversides have varying amounts of light cover from shrubs or trees. Above 1700 m, there is mountain grassland, often with juniper (*Juniperus* spp.), *Cistus*, *Vaccinium* spp., and heaths. Box (*Buxus sempervirens* L.) is sometimes frequent on the slopes of some of the tributary valleys.

The Valle de Aran is almost completely enclosed by mountains of schists and granite over 2500 m high, with Pico de Aneto, the highest in the Pyrenees, forming part of the massif making the south-west corner of the valley. The upper reaches of the valley are shown in figure 18, plate 34.

(3) *The Segre-Valira region*

Unlike the Garonne region, the Segre-Valira reaches to a climatic zone that is mediterranean in type. Olives grow south of Segre-Valira 6 (figure 3) and the general facies of the vegetation by the river is xerophytic south of that point. Evergreen oak (*Q. ilex* L.) and a species of *Pinus* are the dominant trees on the hill slopes, and lavender (*Lavandula* sp.), rosemary (*Rosmarinus officinalis* L.) and thorny papilionaceous scrub are abundant away from the immediate vicinity of the rivers. Such vegetation characterizes the first 40 km of the Segre valley north of Pons. The river runs in a wide plain for the first 20 km between sandstone hills, and then the valley narrows in limestone country for 30 km. A wide sandstone plain extending to the north of the confluence of the Valira with the Segre (figure 3) follows, after which the mountains of Andorra start. The vegetation there is broadly similar to that of the Valle de Aran, except that box is noticeably commoner. The rock formations are the same, and mountains over 2500 m high almost encircle the upper valley complex. The main valley of the Valira in Andorra contrasts with that of the Garonne in the Valle de Aran in that it is very steep sided, with cultivation much more restricted to the valley floor. The tributary valleys, radiating from the main valley, are narrow until a height of about 1200 m when they broaden into typical glaciated valleys.

III. METHODS

(1) *Collecting and habitats*

The upper valley complexes were surveyed in 1962, and the lower valleys in the following year. The Garonne region was worked first and more thoroughly in each year, and the Segre-Valira was used to some extent as a control to test conclusions from the Garonne. Samples were made at approximately 1 km intervals along the main river in the Valle de Aran, and at lesser intervals in the eight tributaries surveyed. Considerably fewer samples were taken from Andorra, and only 17 samples were collected over 60 km in the Segre-Valira lower valley.

Transects along the rivers formed the basis of the surveys, for they enabled large distances to be covered easily, and ensured as far as possible sampling with uniform change in climatic conditions. They were taken either very close to a river, or nearly level with it. The majority were taken from similar open habitats, which were scored according to the dominant vegetation type in the habitat. It was usually not possible to take samples from well-defined habitat-types (Cain & Sheppard 1954) for, except at high altitudes, the meadows by the rivers are herb-rich, and there is generally a tree or shrub component present. A habitat scored as rough herbage had, for example more than 50% broad-leaved vegetation, with long grass and perhaps trees like sallow and ash as the other components.

A few riverside samples were taken from exceptional habitats, namely, 'scrub' and woodland. Scrub is a category containing habitats with indeterminate background features where there is more than 5/10 cover from low woody vegetation, but where cover from trees is either absent or limited. For example, Garonne 32 and Malo 1 were taken from dense hazel scrub, and those scrub samples from the Saliente and Valarties are from dense sallow groves bordering the rivers.

Two riverside samples (Barrados 4 and 5) in the tributary valleys of the Valle de Aran were taken from deciduous woods with predominantly brown backgrounds fringing the river. In Andorra, five riverside samples were made from small woods in the tributary valleys. Valira del Norte 2, Arinsal 1, and Pal 1 were taken from open birch with hazel and box shrub layers; the habitat of Valira del Norte 4 was a young ash and poplar wood, with hazel, box and sallow; and Arinsal 6 was from the fringe of a pine and spruce forest, with juniper, box and heather present. All had brown backgrounds.

Six woodland samples, not part of the main survey, were made in the lower Garonne valley in order to test for variation of populations with habitat there. They were taken between 150 and 1000 m from the nearest riverside sample, with which they were paired. Three (Garonne 6′, 7′ and 8′) were from the oak and ash forests on the valley sides, and three from ash woods in the flood plain. All except one (Garonne 7′) had backgrounds more than half brownish with exposed earth and leaf litter.

A number of samples in both regions were taken from the mountain slopes in order to test whether the topographical positions of populations in relation to those near the river affected morph frequencies. These hillside samples were almost all taken between 50 and 300 m above the valley bottom. Altitudinal series of samples from open hill slopes were made at two points in the Valle de Aran, from a high bluff called Peyra Blanca, and from a mountainside that I have called Aran Hill, east of the Malo valley (figure 2). All the hillside samples came from habitats very similar to those near the river.

(2) *Scoring*

Samples were scored for condition (live, dead-whole, and broken-predated), for shell colour and banding, following the procedures adopted by Cain & Sheppard (1954), and for shell lip colour. In many populations, the latter was found to vary from completely white through violet and brown to the blackish brown characteristic of English populations. Only snails with no trace of dark pigment on the lip were scored as white-lipped, all others being assigned to the class dark-lipped. This is probably sound genetically for there is good evidence that the white-lipped condition is recessive to dark-lipped (Cook 1966; Cain, Sheppard & King 1968) and it is likely that the intermediate dark-lipped shells are heterozygous (Professor A. J. Cain, personal communication). Agreement of the frequencies of intermediate lip-colours in those samples tested from the surveys is fairly close to the expected frequencies of heterozygotes, calculated from the Hardy–Weinberg formula. Information on the samples is given in tables 3 and 4*; only adult snails are included. The gene-nomenclature system used is that agreed on at the conference on polymorphic snails held at York in January 1967 (Cain *et al.*, this volume, p. 395).

IV. RESULTS

(1) *The distribution of species*

C. nemoralis is widely distributed, and often abundant (even near the altitudinal edge of range), over most parts of the surveyed regions. It was found rare or absent in beechwoods in the Garonne de Joué and Barrados, and I never saw it in spruce forests (unlike *Cepaea hortensis* (Müll.)); it also appeared to be of sporadic occurrence in the lower Garonne hill slope forests. It was often very difficult to find in dry places in the lower Segre-Valira. The altitudes of all localities sampled, read from the maps used, are shown in tables 3 and 4, and it is noticeable that the altitudinal limit appears to vary considerably, for sampling was always continued up the valleys until no further *Cepaea* could be found. Altitudinal limits range between 1420 and 2100 m. The mean for nine rivers in the Valle

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* Tables 3 and 4 are at the end of this paper (p. 587).

de Aran is 1634 (±238) m, and 1738 (±89) m for seven rivers in Andorra. There is from this no evidence that the mean altitudinal limit between the regions is different. The variation in altitudinal limit in the Valle de Aran is striking, however, and inspection of table 3 shows that this appears to be greater in tributaries on the north side of the main valley (Barrados, Saliente, Iñola and Malo), than in ones on the south side, in which the highest sample, Garonne de Joué 5, was recorded at 1540 m.

The factors limiting the distribution of the species in the mountains may be several, and complex. It seems likely, however, that they may be directly related to altitude and climate, and the indication that the mean limit in Andorra may be greater (though not significantly so) than in the Valle de Aran, and the higher limit in the south-facing tributaries in the latter valley complex suggest that a cool climate is the restricting factor, the more mediterranean region and the warmer, more insolated, valleys having populations at higher altitudes.

C. hortensis is local in the Garonne. It was not found in riverside samples 1–13 in the lower valley, but within this district it was found in woods (Garonne 8′, 9′, 10′ and 13′), suggesting that its lower altitudinal range is limited by increasing insolation and warmth. Higher up the main valley it occurs in open habitats (Garonne 14–17, 20 and 48). It is more frequent in the tributary valleys, and was found absent only in the Malo and Iñola. It was on two occasions recorded at an altitude greater than the highest *C. nemoralis* record, in the Negro and Aiguamoch valleys. On the other hand, this species is often abundant and widespread in most of the Segre-Valira region. It is of regular occurrence in the main valley in the upper valley complex, and it is present in all the tributaries. In the lower valley, it was found as far south as Segre-Valira 8, being absent in the seven lowest localities sampled.

(2) *The distribution of phenotype frequencies in riverside samples*

(*a*) *Banding*

Unbanded, 00000, and five-banded, 12345, and minor variations, are the commonest banding morphs in both regions. Only 16 of the 145 samples from the Garonne, and eight (three of them from the Ensagents) of the 74 samples from the Segre-Valira have a frequency of banded morphs with at least the upper two bands absent (largely 00300 and 00345) in excess of the frequency of unbanded shells.

Morphs of formula 00345 (and minor variations) are at low frequency generally in the Garonne, and absent in many colonies (table 3); they are more frequent in the Segre-Valira, and of general distribution (table 4). No regularities in distribution are apparent.

Similarly, mid-banded, 00300, never reaches a high morph frequency in the Garonne, and gene-frequency calculations show that its gene frequency is seldom high (B^0 is epistatic to the expression of the mid-banded gene, M^3, Cain & Currey, 1963*a*). Its gene frequency is highest in populations in the lower main valley, and in the tributary valleys in the Garonne region, but the range of frequencies is great and differences between these districts and those at intermediate altitudes are not significant. There is no evidence for a correlation between the gene frequencies of unbanded and mid-banded. It is absent in the upper valley complex of the Segre-Valira; it occurs in only five samples in the

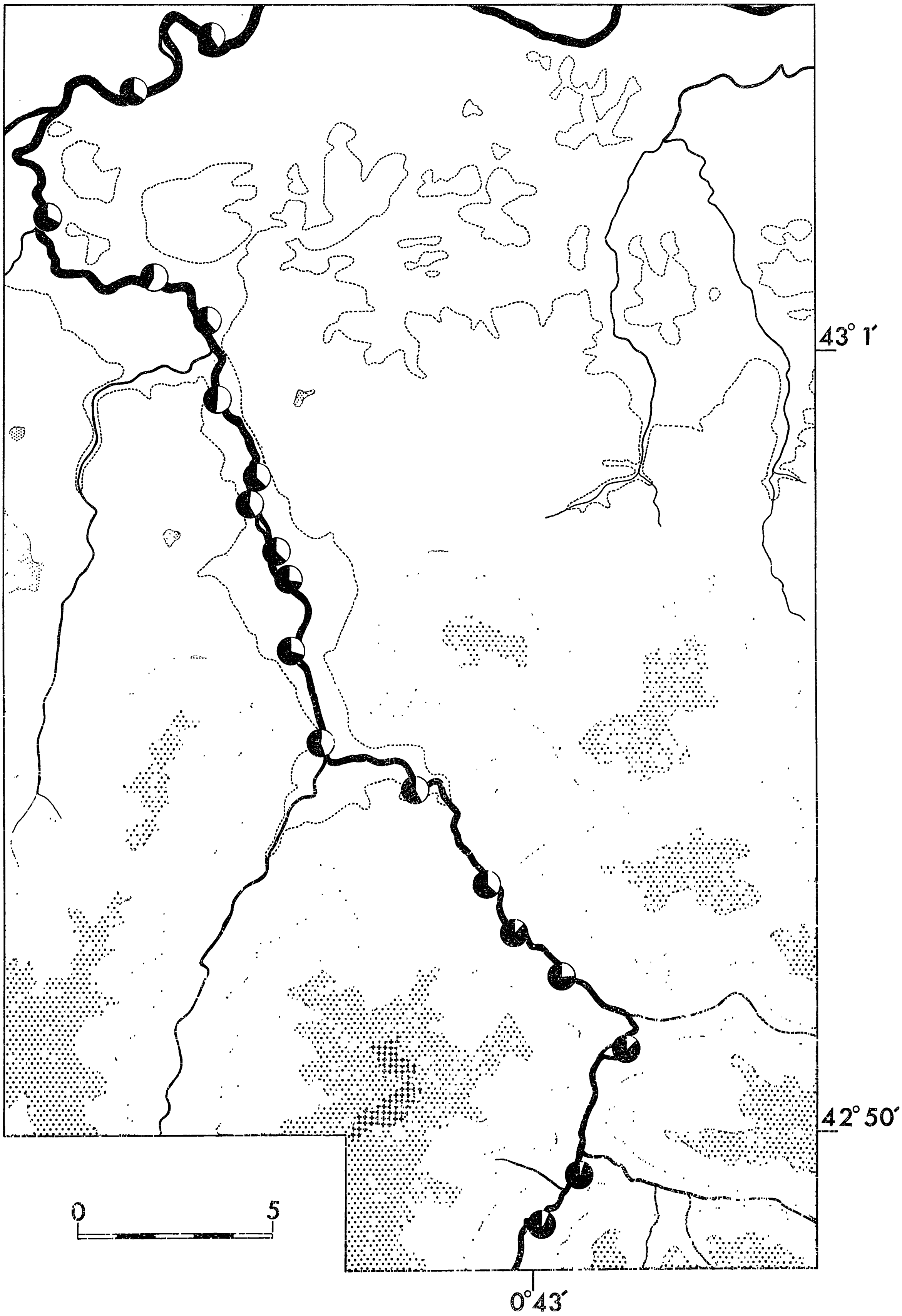

FIGURE 4. Frequencies of banded (black) and unbanded (white) in the lower Garonne samples. The paired wood samples are not included. The 500 m contour is shown by a dotted line, and stippling indicates land over 1000, 1500 and 2000 m. Kilometre scale.

region, all south of Segre-Valira 18, and reaches its highest gene frequency in the two lowest samples, Segre-Valira 1 and 2 (0·42 and 0·18 respectively).

Unbanded, on the other hand, shows a very clear distribution of morph frequencies in both regions. Figures 4 and 5 illustrate the distribution of frequencies of this morph in the lower Garonne and Valle de Aran respectively. Three frequency zones may be distinguished:

(i) A lower zone, Garonne riverside samples 1–14, in which all samples have frequencies greater than 25 % over the 32 km collected (figure 4).

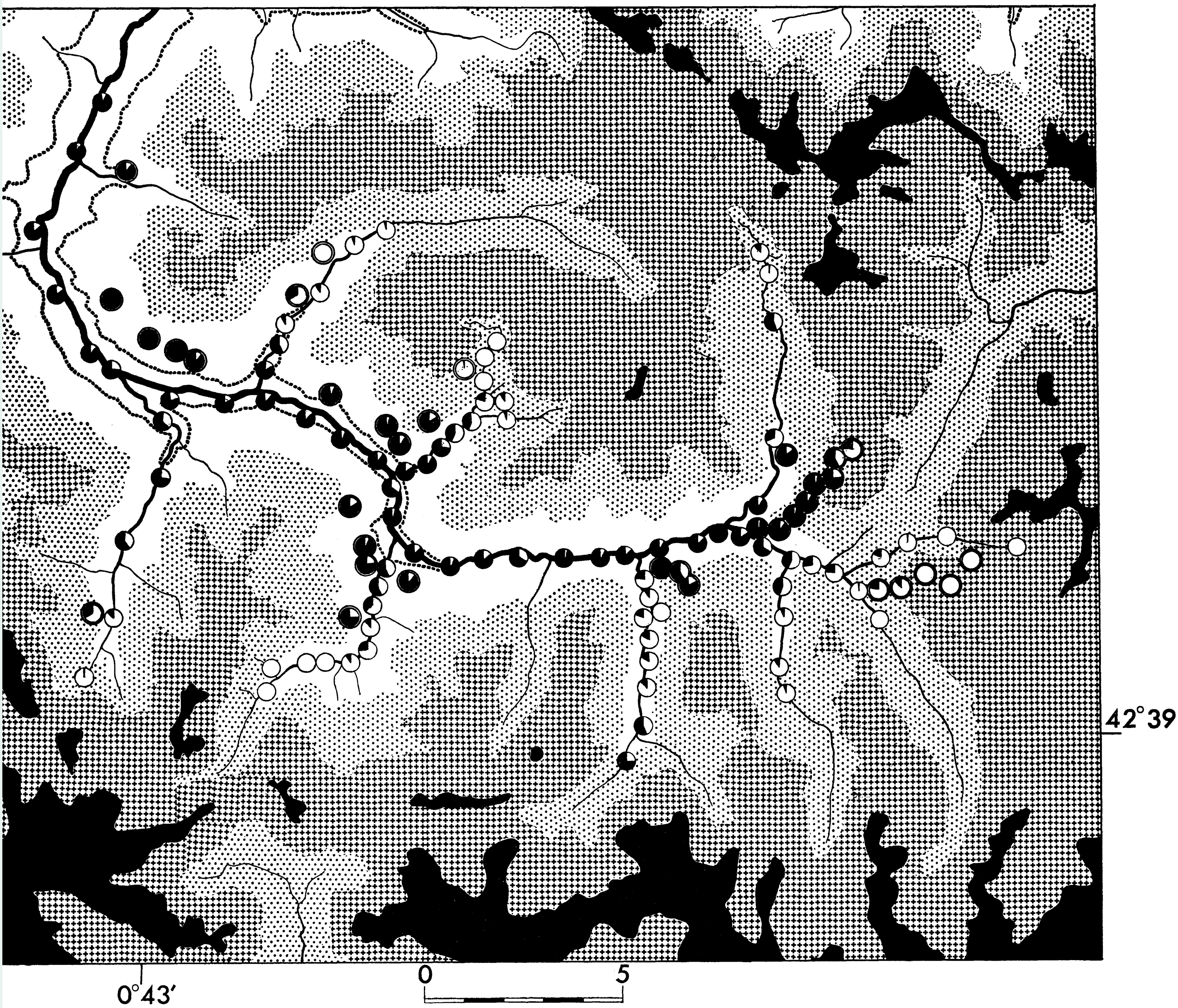

FIGURE 5. Frequencies of banded (black) and unbanded (white) in the Valle de Aran samples. Double circles represent hillside samples, the positions of most of which have been displaced in the diagram for clarity. The 1000 m contour is shown by a dotted line, and stippling indicates land over 1500, 2000 and 2500 m. Kilometre scale.

(ii) An intermediate zone, from Garonne 15 to Garonne 44 in the main valley, characterized by lower frequencies. Only three of the 29 samples in the zone have unbanded frequencies in excess of 25 %. This zone is approximately 28 km in length. The difference in frequencies between the two zones is significant (median test, $\chi_1^2 = 17{\cdot}19$, $P < 0{\cdot}001$).

(iii) Upper zones, in which frequencies exceed 25 %, and in which they are often very high (figure 5). A cline to fixation or near fixation of B^0 takes place in Garonne 45–50. The majority of the samples from the tributaries may be included in the upper zones, for in most of them, unbanded rapidly reaches a high morph frequency after a short distance from the main valley in which it takes intermediate morph frequencies. B^5 may be absent in parts of two of the tributaries—the top three samples in the Saliente taken over 1½ km, and the top four in the Negro, over 2 km, consist only of unbanded shells. The highest samples of four of the nine valleys surveyed in the Valle de Aran are completely unbanded, and of the other five, four have top samples with more than 80 % unbanded shells. The exception will be discussed below. There is, therefore, a broad relation between the frequency of unbanded and altitude in the upper valley complex of the Garonne.

A parallel distribution is found in the Segre-Valira.

(i) The lower zone (figure 6), Segre-Valira 1 to 6, has frequencies of unbanded very much higher than those in the lower zone of the Garonne region. All six have frequencies greater than 70 % over 40 km.

(ii) The intermediate zone is comprised by most of the rest of the region, and frequencies are below 30 % in the majority of samples (figures 6 and 7).

(iii) An upper zone, where frequencies are in excess of 30 % is usually, although not always, found at the heads of the Andorran valleys (figure 7). Thus, neither the valleys of the Valira nor Pal exhibit upper zones (although in the latter valley, the top sample, Pal 5, has 20 % unbanded shells, whereas the two riverside samples below it have none). All the other valleys have some samples in which unbanded predominates, always, with one exception, above 1500 m. The exception—Valira del Norte 2—is unbanded at 1150 m, and will be considered later.

(*b*) *Ground colour*

The brown morph was not encountered. The majority of the yellows, especially at higher altitudes, were dark yellow. All kinds of pink were found, the commonest being pale pink; many of the latter looked at first inspection like faint pinks, for over parts of the shell—particularly in those pinks of banding formula 12345—the pigment was often very diluted.

Zonation of colour morph frequencies follows closely that of the banding morph frequencies in the Garonne. There is a lower zone of high yellow frequency (figure 8), an intermediate zone in the main Garonne valley in which pink may reach moderate frequencies, and an upper zone in the higher reaches of the Garonne and in the tributary valleys in the Valle de Aran with high and very high frequencies of yellow (figure 9). The difference between the lower and intermediate zone frequencies is significant (median test, $\chi_1^2 = 8{\cdot}68$, $P < 0{\cdot}01$). Although the colour frequency zones correspond well with the banding zones, the changes in frequencies of both colour and banding taking place

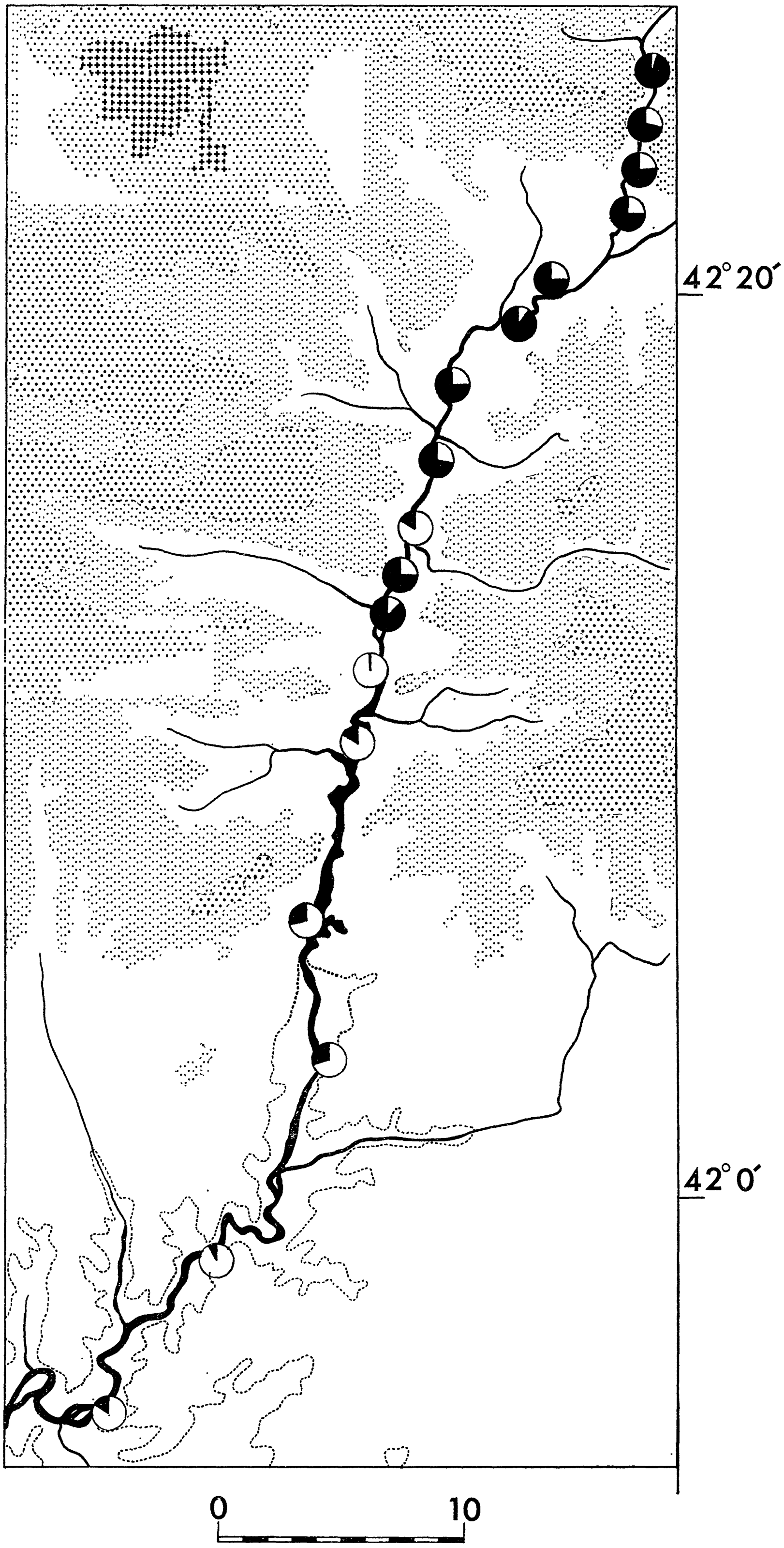

FIGURE 6. Frequencies of banded (black) and unbanded (white) in the lower Segre-Valira samples. Contours and scale as in figure 4.

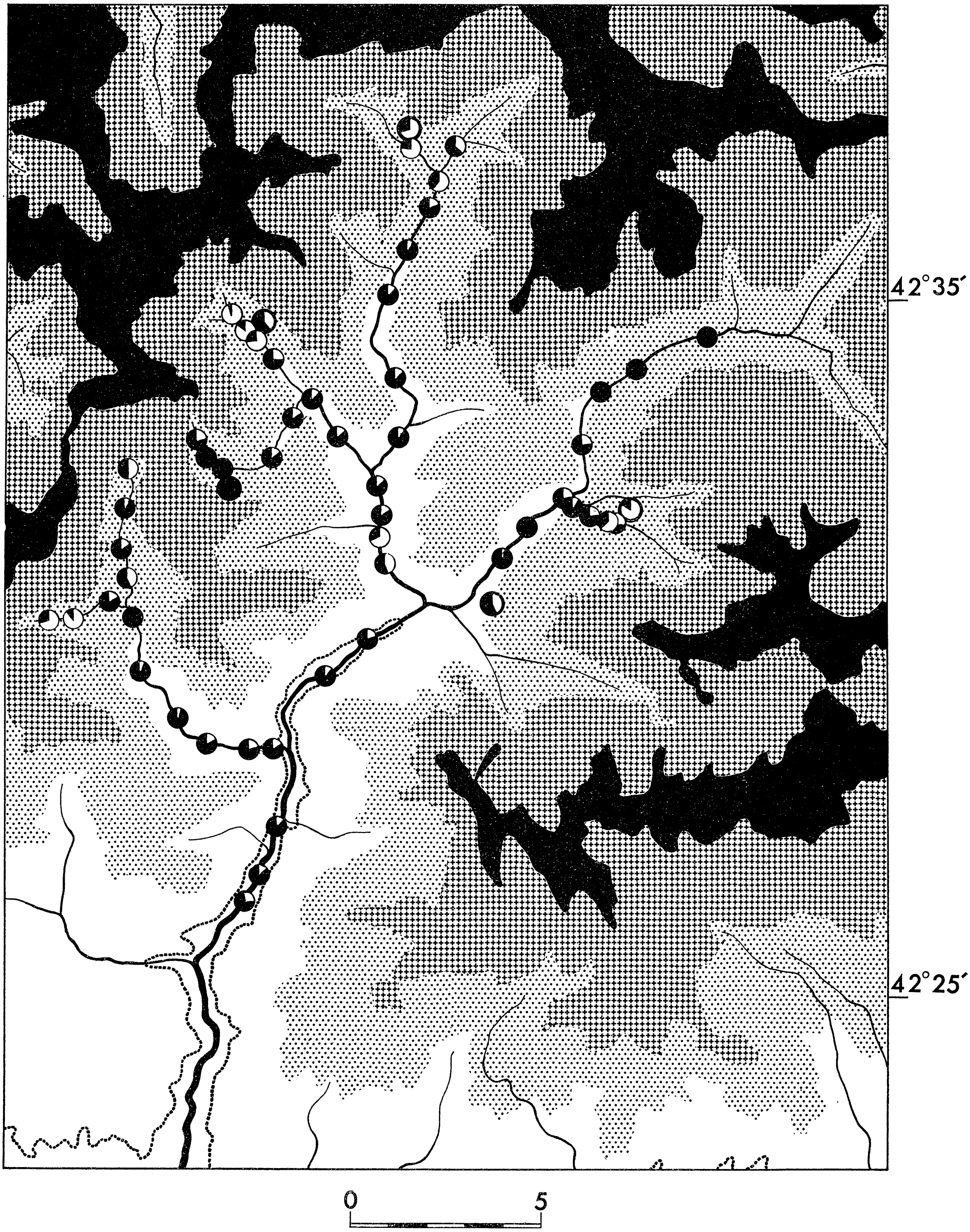

FIGURE 7. Frequencies of banded (black) and unbanded (white) in samples from Andorra. Symbols, contours, and scale as in figure 5.

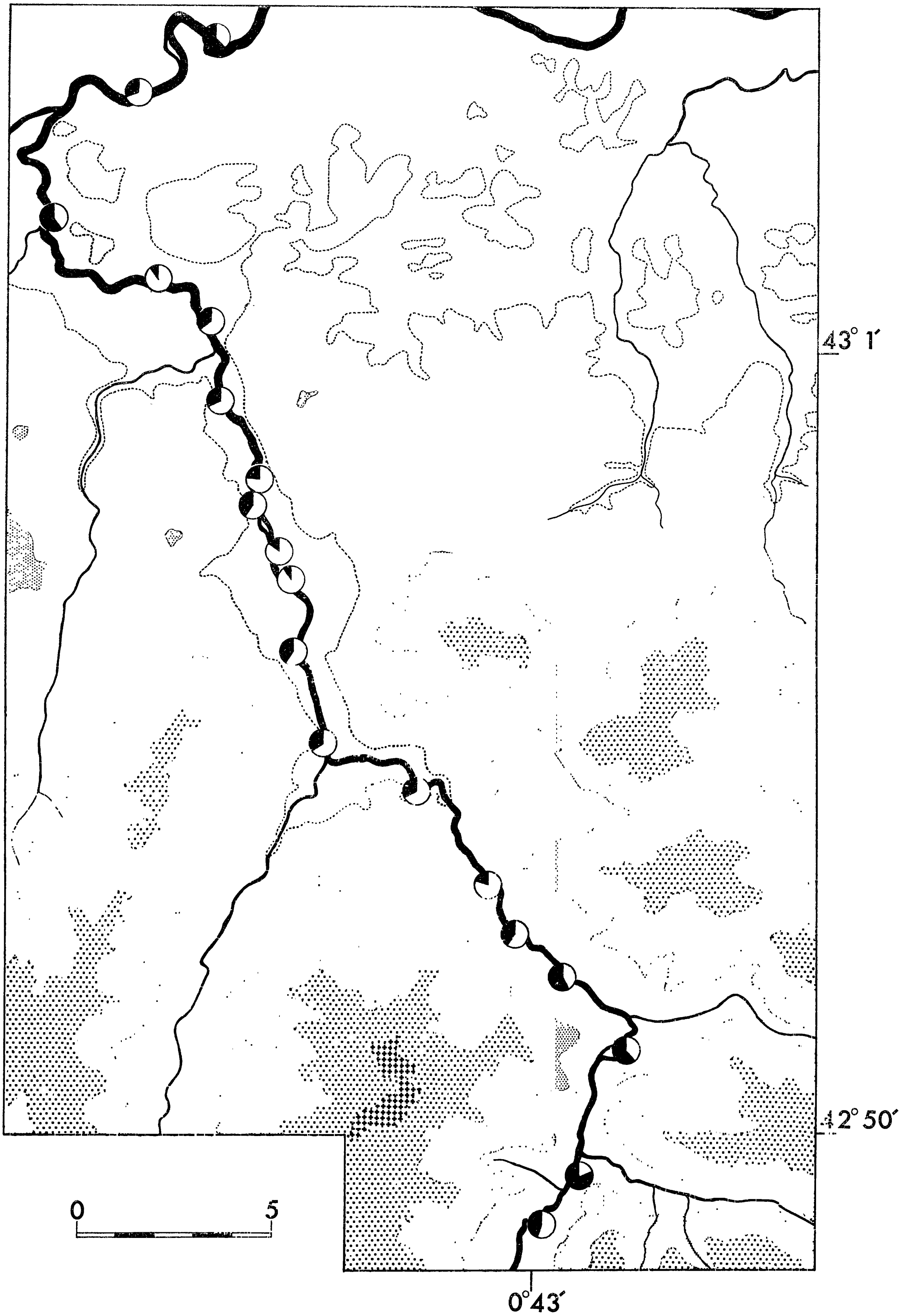

FIGURE 8. Frequencies of pink (black) and yellow (white) in the lower Garonne samples. Contours and scale as in figure 4.

at the same locality in the lower Garonne, there are a number of colonies which have anomalous frequencies; thus, both the Garonne de Joué and Barrados valleys have colonies at high altitudes (samples 4 and 5 respectively) which exhibit relatively high frequencies of pink; similarly, Valarties 8 has only 64·3 (±9·1) % yellow, although the

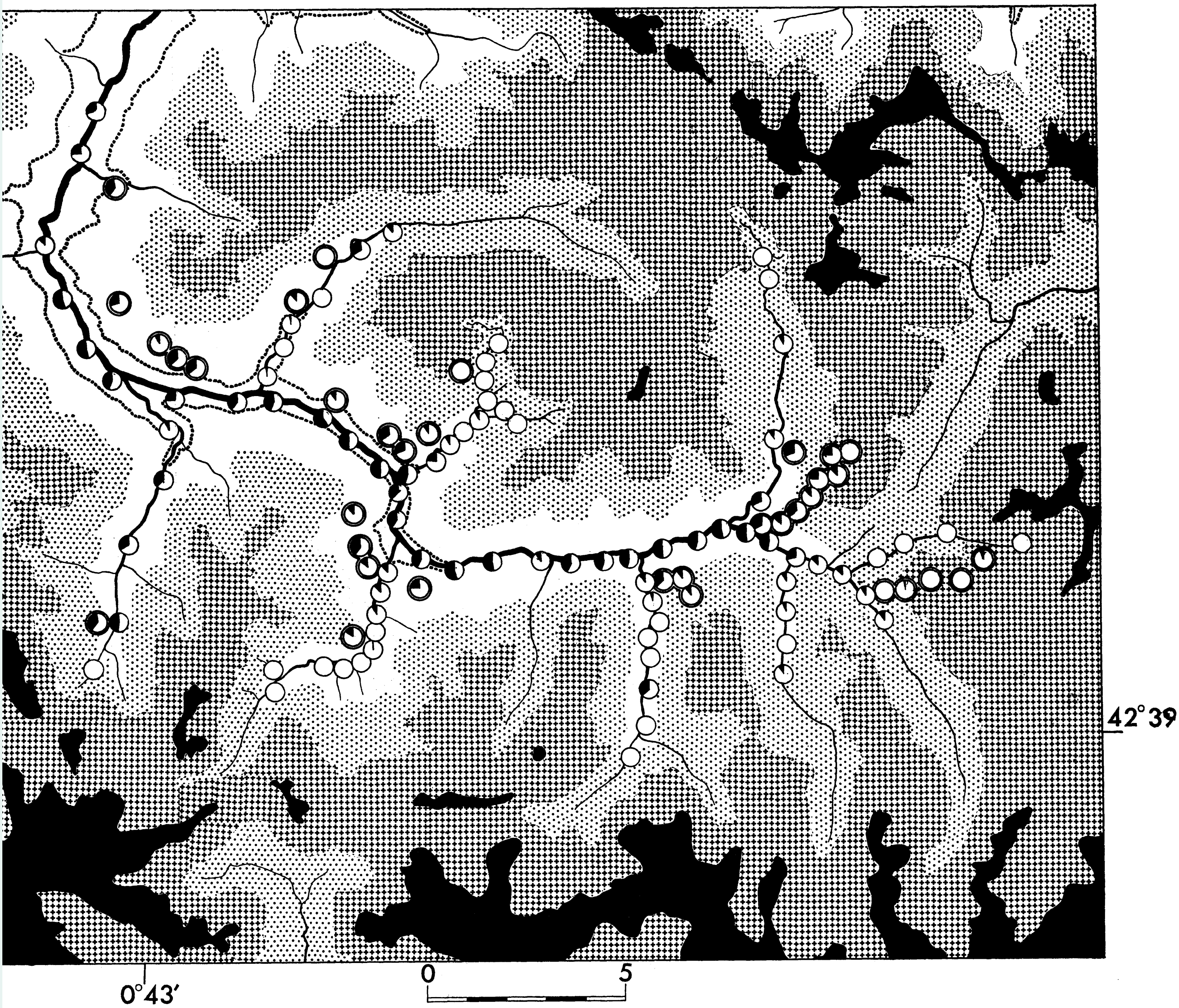

FIGURE 9. Frequencies of pink (black) and yellow (white) in the Valle de Aran samples. Symbols, contours, and scale as in figure 5.

three samples both below and above it contain only yellows. None of these exceptions are amenable to the kind of explanation which will reasonably account for unusual banding morph frequencies, to be discussed later.

Pink is at low frequency almost everywhere in the Segre-Valira region (figures 10 and 11). It tends to be more frequent in the middle parts of the Segre-Valira main valley

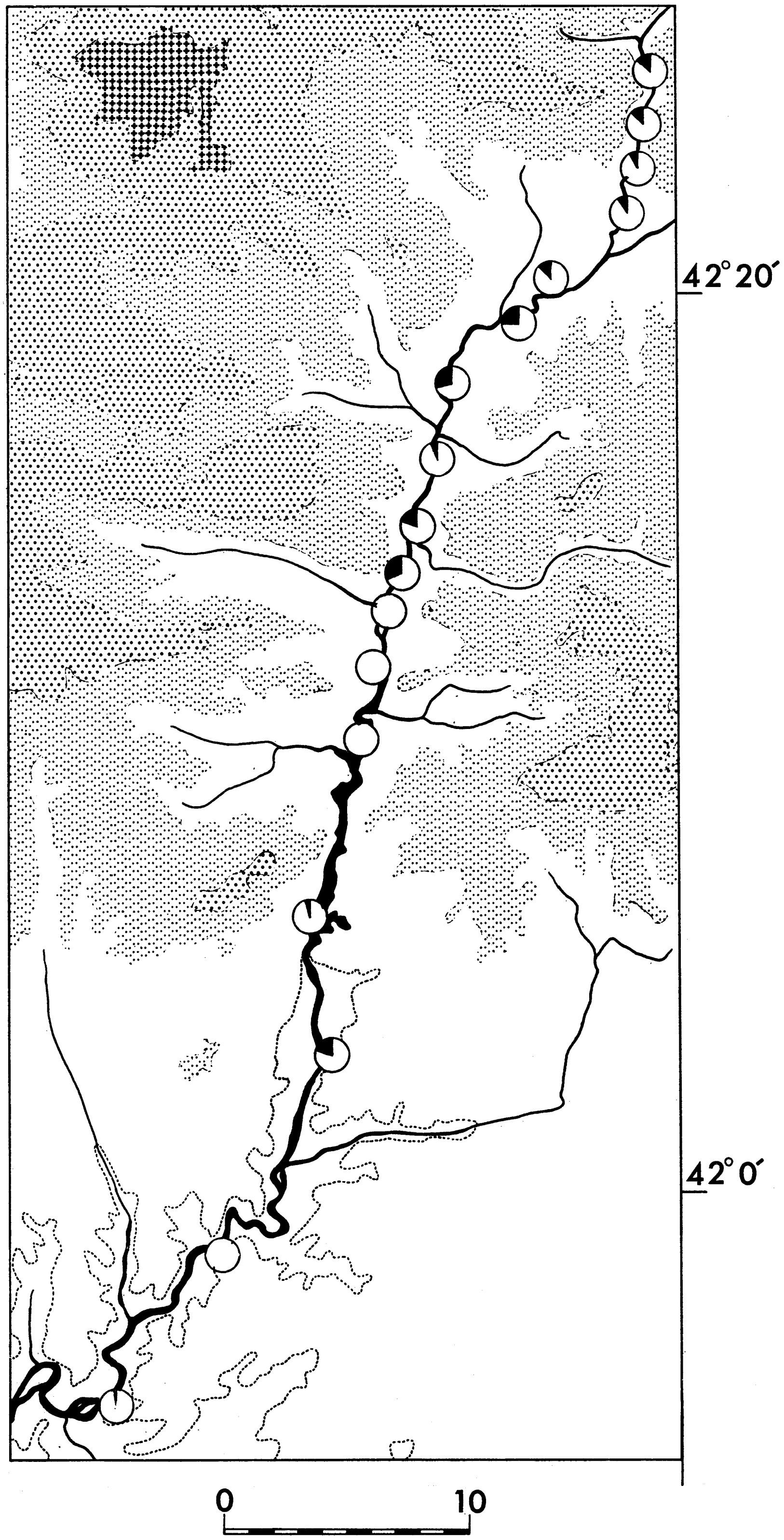

FIGURE 10. Frequencies of pink (black) and yellow (white) in the lower Ségre-Valira samples. Contours and scale as in figure 4.

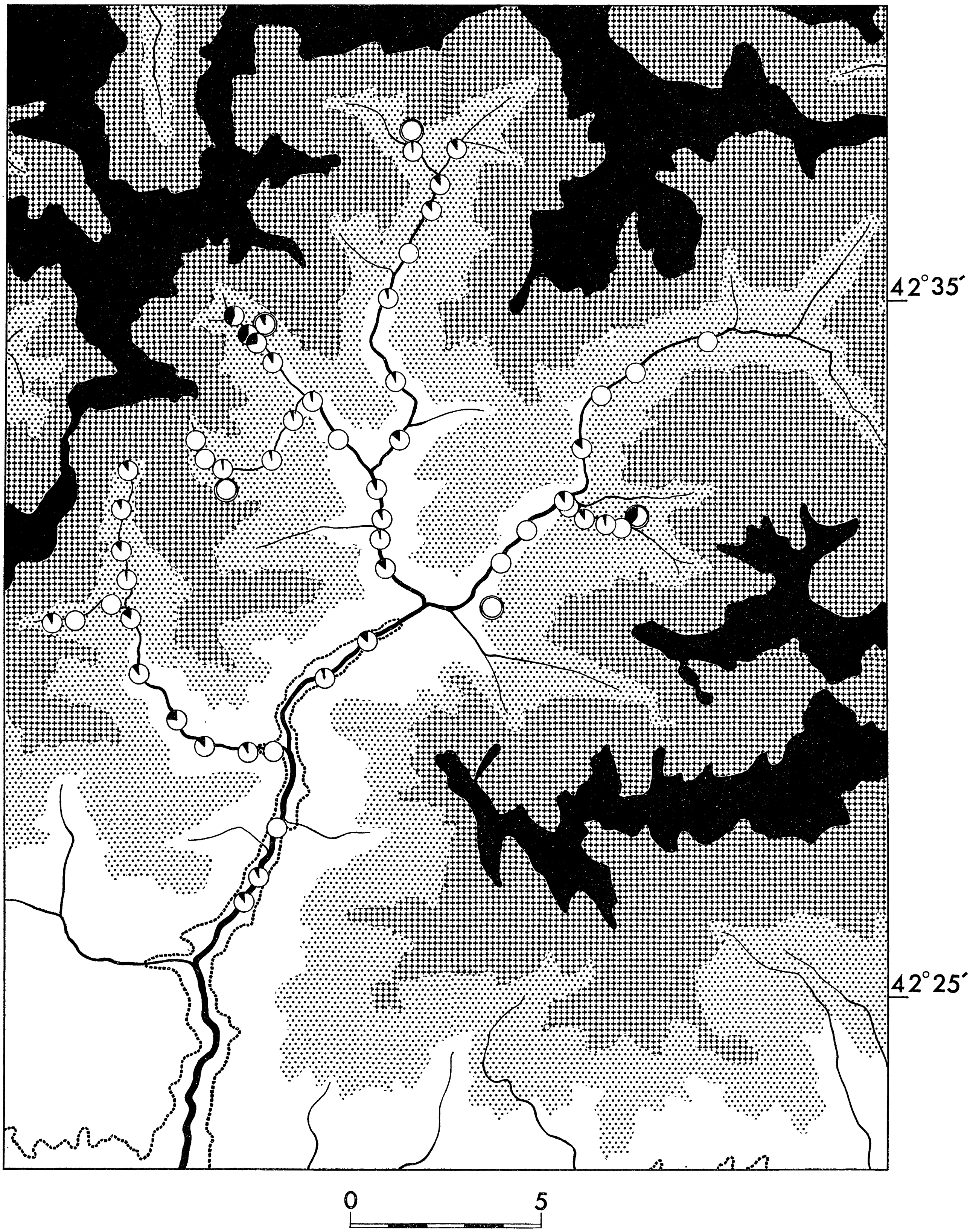

FIGURE 11. Frequencies of pink (black) and yellow (white) in samples from Andorra. Symbols, contours, and scale as in figure 5.

though, as in the Garonne main valley. Ten of the twenty-nine riverside samples from the Segre-Valira are monomorphic for yellow, and of these, four are among the lowest seven samples, and five in the highest seven. A median test on the lowest and highest fourteen samples combined compared with the middle fourteen samples shows that the former have significantly higher frequencies of yellow ($\chi_1^2 = 7{\cdot}00$, $P < 0{\cdot}01$). Yellow is usually at high frequency in the tributaries, but, as in the Garonne, there are anomalous colonies. The two highest samples in the Arinsal valley (Arinsal 5 and 6) have the highest frequencies of pink in the region, with less than 60% yellow shells; and the colony with the next highest frequency of pink in the region is a hillside sample at 1800 m in the Ensagents valley. Although similarities between the distributions of colour morph frequencies may be seen in the two regions, they are by no means as marked as those for banding.

(*c*) *Lip colour*

The locus *P*, which determines the pigmentation of the bands and lip, is linked to the ground colour (*C*) and banding (*B*) loci (Cain *et al.* 1968). There is in nearly all samples from the Pyrenees strong linkage disequilibrium, such that the majority of the yellows are white-lipped and the majority of the pinks dark-lipped. Calculation of the cross-product ratio:

$$\frac{\text{yellow dark-lip}}{\text{yellow white-lip}} \times \frac{\text{pink white-lip}}{\text{pink dark-lip}}$$

for all samples for which it is possible to determine whether the ratio is greater or less than one (in some samples one ground colour or lip colour class is absent) indicates an excess of the classes yellow white-lip and pink dark-lip in 100 of the 105 Garonne samples and 39 of the 45 Segre-Valira samples (the probabilities of obtaining these results by chance are in both cases less than 0·001). There are also associations between lip colour and banding. In the Garonne, 82 of the 110 samples amenable to this analysis indicate an excess of banded dark-lipped and unbanded white-lipped shells ($P < 0{\cdot}001$), whereas Segre-Valira samples show the reverse association: 34 of the 52 workable samples have an excess of banded white-lipped shells and unbanded dark-lipped shells (for which $P < 0{\cdot}05$). Inspection of tables 3 and 4 shows that the primary association in the majority of samples is between ground colour and lip colour, and for this reason, the frequency of white-lip has been expressed as its frequency within yellow. This frequency is shown in figures 12 and 13 for colonies in the two regions.

Populations in both lower valleys have low frequencies of white-lip in yellow, with higher frequencies in the upper valley complexes. Populations appear to be monomorphic for it near the upper limits of the Barrados, Saliente, Negro and some of the valleys in Andorra. The Garonne de Joué is unusual in exhibiting low frequencies along most of its length, and it is probably of significance that it is the lowest surveyed tributary in the Garonne. Colonies in one district in the Segre-Valira may be monomorphic for white-lip itself: all of the twelve samples at the heads of the adjacent Valira and Ensagents valleys (Segre-Valira 23–29, Ensagents 1–4, and the Ensagents hillside sample) have no dark-lipped shells (both in yellow and pink).

These surveys corroborate the findings of Lamotte (1959) for two French Pyrenean

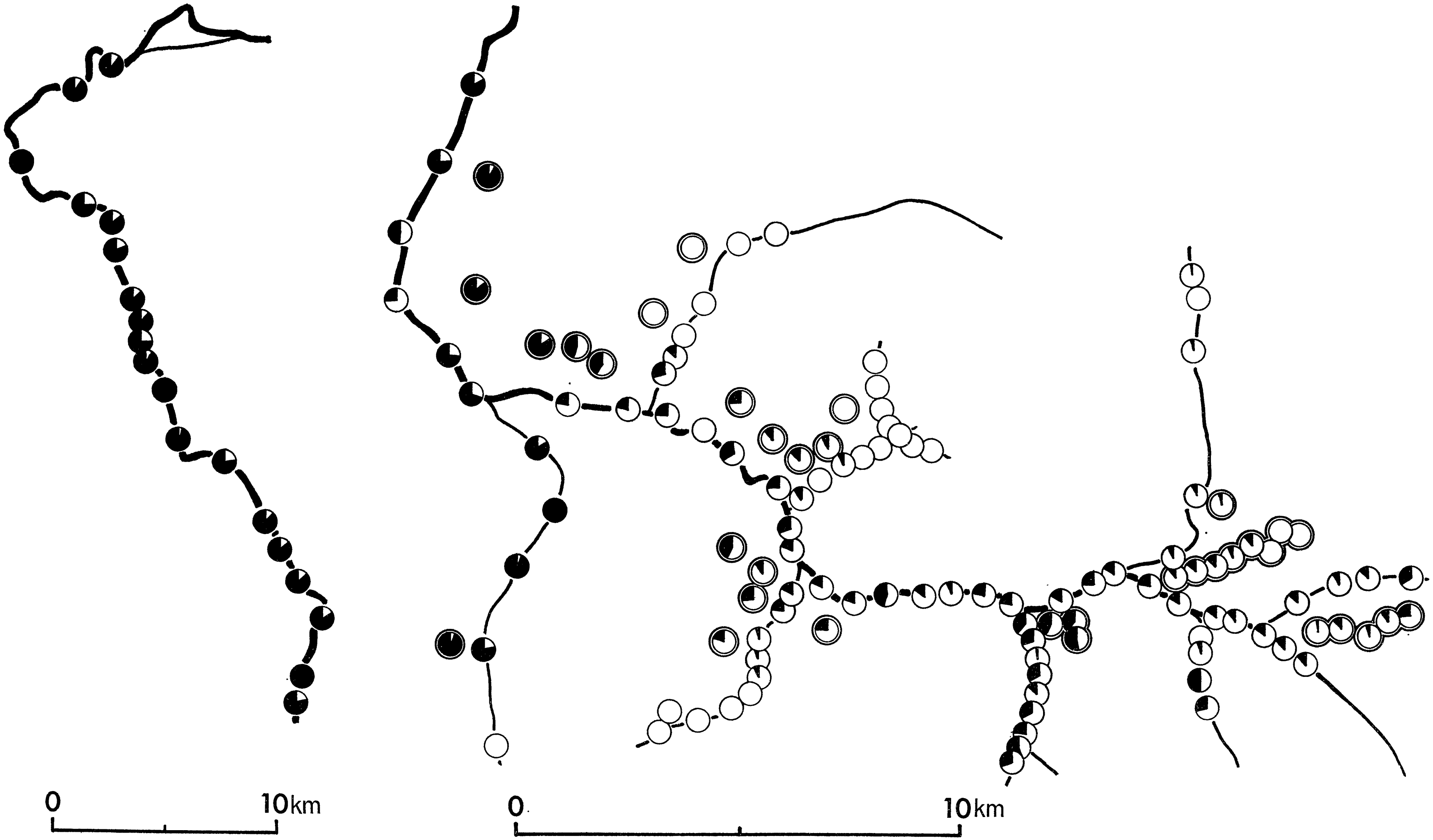

FIGURE 12. Frequencies of white-lip in yellow (white) and dark-lip in yellow (black) in all Garonne samples except the paired wood samples. Double circles represent hillside samples.

valleys. He states that white-lipped *C. nemoralis* are not present in the plains to the north of the Pyrenees, and shows that they appear in populations in the foothills to rise to frequencies of between 20 and 85% in the higher valleys. He illustrates the frequencies of white-lip in the valleys of the Adour and Neste d'Aure, to the west of the Garonne (figure 1 in this paper). These surveys further show that white-lip in yellow may regularly reach very high frequencies near the altitudinal edge of range of the species, if not fixation of the allele P^A, for C^Y also tends towards fixation there.

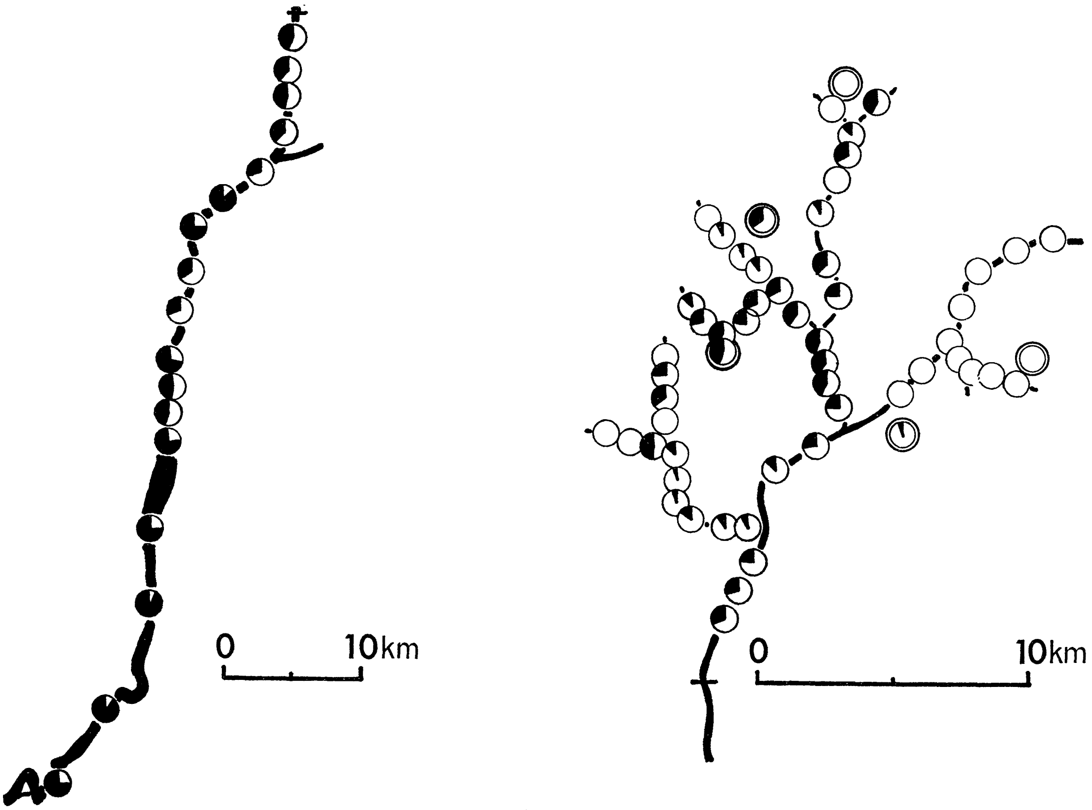

FIGURE 13. Frequencies of white-lip in yellow (white) and dark-lip in yellow (black) in all Segre-Valira samples. Double circles represent hillside samples.

(3) *The nature of the selective forces*

The relative constancy of morph frequencies within zones (illustrated in the scatter diagrams, figures 14 and 15) over large distances, the clines, the similar distribution of morph frequencies between valleys and the two regions, and the linkage disequilibria, are good evidence that selection is operating; random processes, whether in the past or near-present, can have played little or no part in determining the phenotypic composition of colonies.

Where morph frequencies do not correspond with those expected if visual selection were effective, and in situations where selection of some kind can be inferred, area effects are said to operate. Cain & Currey (1963*a*) defined them as 'the predominance of a few morphs irrespective of habitat and background characterizing areas vastly larger than that of a panmictic population'. The term embodies no implication as to the type of selection acting.

There was much evidence of predation on *Cepaea* at all altitudes except below Segre-Valira 17; for example, Garonne 9′, 27, 40 and 49 and Saliente 3 and 9 consist almost entirely of shells broken at thrush anvils. In the Segre-Valira, 25 of the samples show evidence of thrush predation. Many of the predated shells were freshly broken, and there was no epiphragm trace on most of them; there seems little reason to doubt therefore that predation had occurred in many cases while the snails were active, and consequently it had been selective. The breeding range of the song-thrush, one of the principal visual predators of adult *Cepaea*, extends as far as north Spain (Peterson, Mountfort & Hollom 1966). I recorded it on six occasions in the Valle de Aran at altitudes up to 2000 m, but it certainly was not a common species there; I did not record it in the lower Garonne, nor in the Segre-Valira region. Because of the presence of at least one visual predator and evidence of its predation, it is necessary to examine to what extent, if any, the morph frequencies found in the valleys could be controlled by visual selection, or whether they are controlled by area effect-type selection.

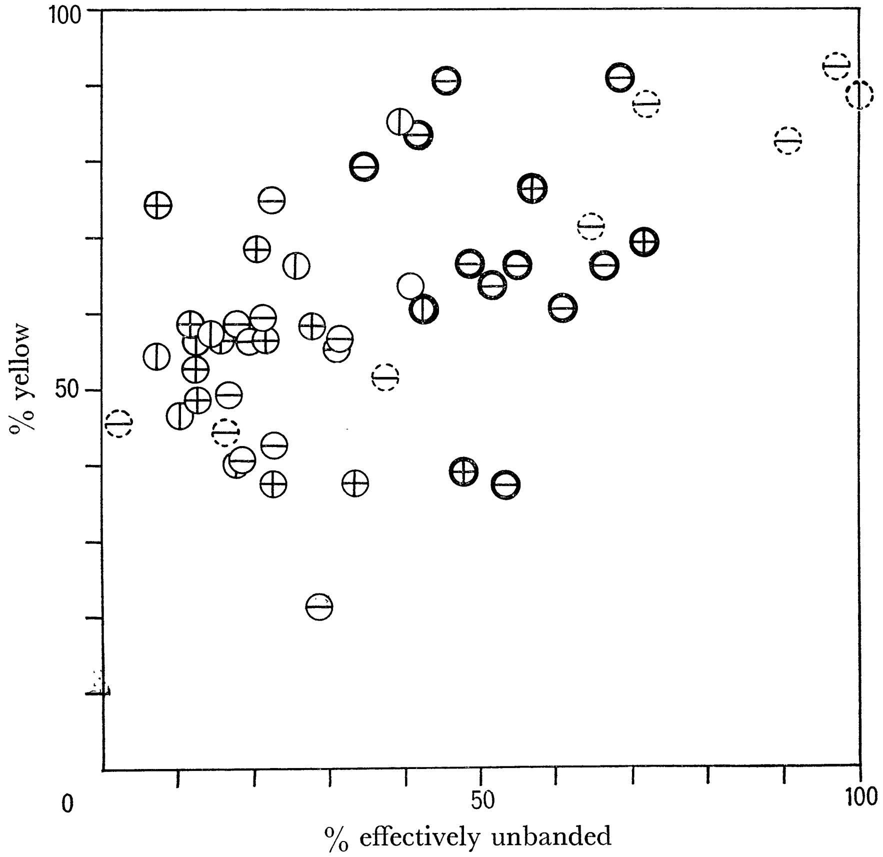

FIGURE 14. Scatter diagram for all samples taken in the Garonne main valley except paired wood samples. Thick circles: lower zone samples. Thin circles: intermediate zone samples. Broken circles: the highest eight samples, Garonne 43–50. *Habitat symbols*. Grass: vertical line; rough herbage: horizontal line; hedgerow: cross; scrub: open circle.

The areas of high frequency of unbanded in the Valle de Aran and at the heads of the Andorran valleys can be regarded as area effects; for morph frequencies either change without respect to change in background features, as grassy habitats predominate in the higher regions of some of the tributaries against which it is likely that unbanded shells are less cryptic than banded shells, or they change irrespective of background constancy; thus, a change in frequency of unbanded from 0 to 100% takes place in the highest Garonne samples, in which all the habitats are rough herbage, and frequencies range from 9·6 to 96·8% in the Iñola valley, where all the samples were taken from grass habitats. Furthermore, the areas of high or constant frequency may be very large in comparison with the panmictic unit of about 30 yards diameter (Lamotte 1951; Murray 1962); unbanded is at very high frequency in all samples taken in and near the Malo valley and the head of the Garonne valley (figure 5), an area of at least 10 km^2, and in many of the tributary valleys, high frequencies characterize more than 1 km of riverside. The same argument applies to the upper zones in Andorra, although the frequencies are less extreme, and the areas smaller in extent.

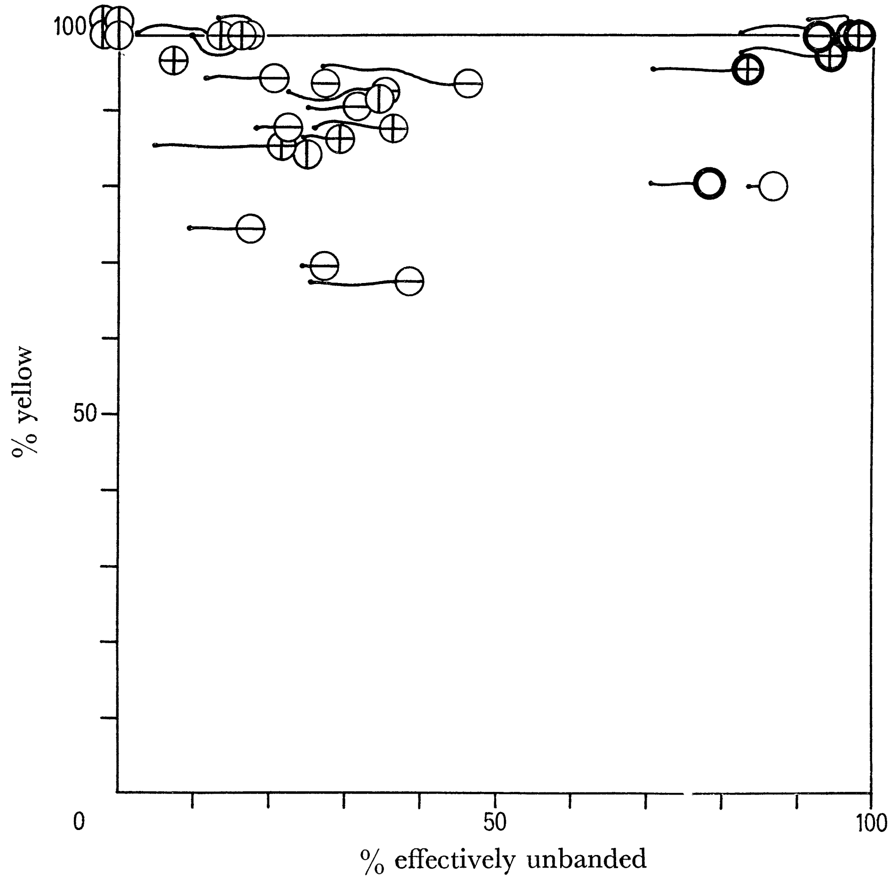

FIGURE 15. Scatter diagram for all samples taken in the Segre-Valira main valley. The percentage unbanded point of each sample is shown. Symbols as in figure 14.

Samples from the lower zones of the two regions are shown in figures 14 and 15 as thick circles. The very high frequency of effectively unbanded (and especially unbanded) morphs in the Segre-Valira lower zone indicates that a strong area effect for unbanded is operating over at least the 40 km between Segre-Valira 1 and 6. Lower Garonne samples 1 to 14 are significantly more effectively unbanded than those in the intermediate zone (median test, $\chi_1^2 = 17{\cdot}19$, $P < 0{\cdot}001$) due to an increase in the frequency of unbanded. On the whole, though, they are appropriate visually to the habitats in which the snails were living. The six woodland samples taken in the lower zone permit a direct test of the effectiveness of visual selection. These samples are shown in figure 16 paired with the nearest open habitat samples. All the woodland samples have high frequencies of yellow, and it is unlikely that the relatively high frequencies of effectively unbanded shells in these samples is due to visual selection, for yellow effectively unbanded is probably at a greater visual disadvantage than yellow five-banded (Cain & Sheppard 1954; Arnold 1966). Visual selection appears to exert little or no effect on morph frequencies in the lower Garonne.

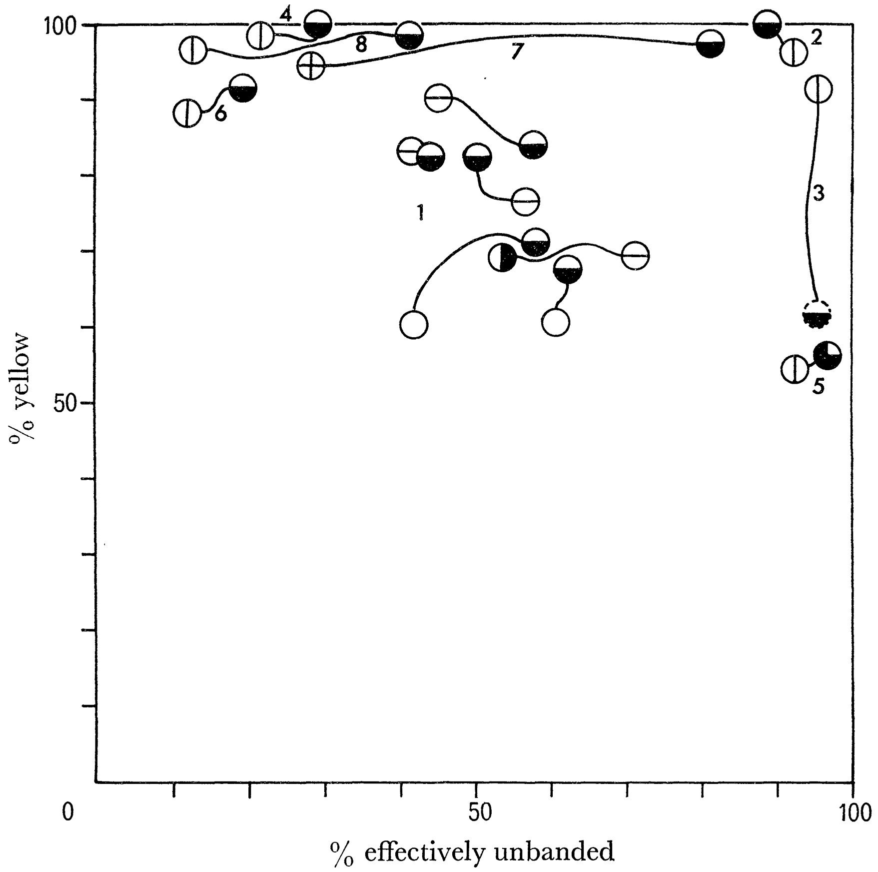

Figure 16. Scatter diagram for all wood samples paired with the nearest open habitat samples. *Habitat symbols.* Mixed deciduous wood: horizontal black hemisphere; oakwood: vertical black hemisphere; coniferous wood: three-quarter black circle. Open habitat symbols as in figure 14. *Pairing.* 1, Lower Garonne; 2, Barrados 3 and 4; 3, Barrados 5 and 6; 4, Arinsal 1 and 2; 5, Arinsal 5 and 6; 6, Valira del Norte 4 and 5; 7, Valira del Norte 2 and 3.

A direct test for the efficacy of visual selection in influencing morph frequencies can be made in only a few localities in the upper valley complexes and intermediate morph frequency zones. Neither wood sample from the Barrados in the Valle de Aran has morph frequencies that are appropriate to the brown backgrounds encountered there (figure 16; compare Cain & Currey 1963*a*, p. 18) and the same is true of the five wood samples taken from Andorra. It is evident that there is no variation of populations with habitat, and that those populations in woods resemble fairly closely in morph frequency those living in nearby open habitats.

The absence of suitable woods in the main Garonne valley in the Valle de Aran, and in the main valley of the Valira in Andorra, where populations on the whole resemble their backgrounds (they tend to be moderately or very yellow, and very five-banded, figures 14 and 15) means that it is difficult to test conclusively whether visual selection controls morph frequencies there. In both regions, the range of colour and banding frequencies is not great, however, despite the considerable diversity of open habitat types in which the populations were living. Comparison of the families of open habitat points in the intermediate zones in figures 14 and 15 with that for the Oxford region (Cain & Currey 1963*a*, p. 18) shows that the spread of morph frequencies in the intermediate zone valley samples in the Pyrenees is considerably less. Yet, as far as direct comparison is possible, the range of open habitat types is similar in the two districts under consideration, and they are of comparable magnitude in geographical extent: colonies were sampled within a radius of 16 km of Oxford, and the zones in the Pyrenees are large. Cain & Sheppard (1954) pointed out that a range of frequencies was to be expected in open habitats if visual selection were effective, for open habitats taken as a class are heterogeneous—i.e. visual selection will favour different morph frequency optima so that populations will be visually adjusted closely to each habitat. (Recently, though, experimental evidence (Arnold, in preparation) allows another interpretation: that the strength of visual selection may be greatly reduced in some types of open habitats compared with woods and that this effect, therefore, could cause morph frequencies in such habitats to respond to physiological, area effect-type, selection more so than those in woods.) The relative closeness of the scatters (figures 14 and 15) for the Pyrenean intermediate morph frequency zones combined with the evidence from the few wood samples taken indicates that visual selection may well not be responsible for the resemblance to background features found in the zones, but that area effects favouring five-banded and sometimes moderate frequencies of pink are operating. There is good reason to believe that area effects operate generally on colour in districts not so far considered in this context for similar reasons. In the Valle de Aran, colonies in the upper reaches of five of the tributaries may be monomorphic for yellow; the highest six samples from the Saliente, the highest five from the Negro, the highest three from the Valarties, the highest two from the Iñola, and all the Malo samples contain no pinks. Although the yellow morph is probably visually more cryptic, both the change in frequency between the main Garonne intermediate zone and the tributaries, and the evidence that the allele for yellow is often at fixation in the upper zones, argue that area effects are operating for colour as well as banding, there as in the intermediate and lower zones.

It can be concluded, therefore, that the upper and lower banding zones in both regions are area effects, and that there is evidence that the intermediate banding zones are also area effects. Likewise, areas rather than habitats are characterized by colour morph frequencies. Visual selection appears thus to play little or no part in influencing morph frequencies in either of the two regions, and explanations for the morph frequencies found must be sought elsewhere.

(4) *Climatic selection in the upper valleys*

That there is in the upper valley complexes a broad correlation between morph frequencies and altitude immediately suggests that climatic factors associated with altitude may be the selective agents, perhaps acting indirectly. Two sets of data and observations strengthen the suggestion, and permit a hypothesis to be formulated as to which climatic aspect favours unbanded, yellow, and white-lip at higher altitudes.

(*a*) *Morph frequencies on the hillsides*

Each hillside sample was paired with a nearby (usually the nearest, but sometimes this would have meant double pairing) riverside sample below it. The pairing is shown in tables 3 and 4. Morph frequencies in the two situations were then compared, first taking three districts separately. These are the main valley in the Valle de Aran (thirteen pairs), the tributaries in the Valle de Aran (nine pairs), and the upper valley complex in Andorra (five pairs). The results are summarized in table 1. The numbers in each are small, and since there is no significant heterogeneity between districts for any of the three compared morph frequencies, the data have been combined in the table.

Table 1. Comparison of morph frequencies in riverside and hillside paired samples

Pairs which have the same frequency (at 0 or 100 %) of any one character have been omitted.

Banding	more unbanded	less unbanded	total
riverside samples are:	21	5	26
	$\chi_1^2 = 8{\cdot}65$	$0{\cdot}001 < P < 0{\cdot}01$	
Colour ...	more yellow	less yellow	total
riverside samples are:	10	15	25
	$\chi_1^2 = 0{\cdot}64$	$0{\cdot}30 < P < 0{\cdot}50$	
Lip colour ...	more white-lipped in yellow	less white-lipped in yellow	total
riverside samples are:	16	6	22
	$\chi_1^2 = 3{\cdot}68$	$0{\cdot}05 < P < 0{\cdot}10$	

The hillside samples have significantly lower frequencies of unbanded than the riverside samples; this is so both for samples taken along the Garonne (exact probability = 0·020), and for samples taken in the tributaries (exact probability = 0·039) in the Valle de Aran.

There is no evidence that colour morph frequencies differ in the two types of sample. All three districts are consistent in that the hillside samples have lower frequencies of white-lip in yellow than the riverside samples, and when the results are combined, the 5 % level of significance is almost reached (table 1; the exact probability is 0·052). These frequency differences are not related to habitat differences: 10 of the riverside samples and 12 of the hillside samples came from grass, and the rest from hedgerows, rough herbage, and scrub.

The same trend for unbanded and for white-lip in yellow is found when the hillside transects Peyra Blanca and Aran Hill are compared with those samples from the nearest tributary valleys to them (see figure 2). Banding morph frequencies are compared in samples matched as nearly as possible altitude-for-altitude between those taken on the open slopes of Peyra Blanca and those from the nearest river valley, the

Iñola less than 1 km to the west, in figure 17. Included in the Peyra Blanca profile is Garonne 44, and in that for the Iñola, Garonne 43. The top four samples on Peyra Blanca and all the Iñola samples were from grass, although *Juniperus*, *Helleborus* and *Vaccinium* were frequent in both districts at higher altitudes. The scatter diagrams in figure 17 compare the visual characters of the samples (effectively unbanded morphs other than unbanded were rare; a total of seven individuals only were found).

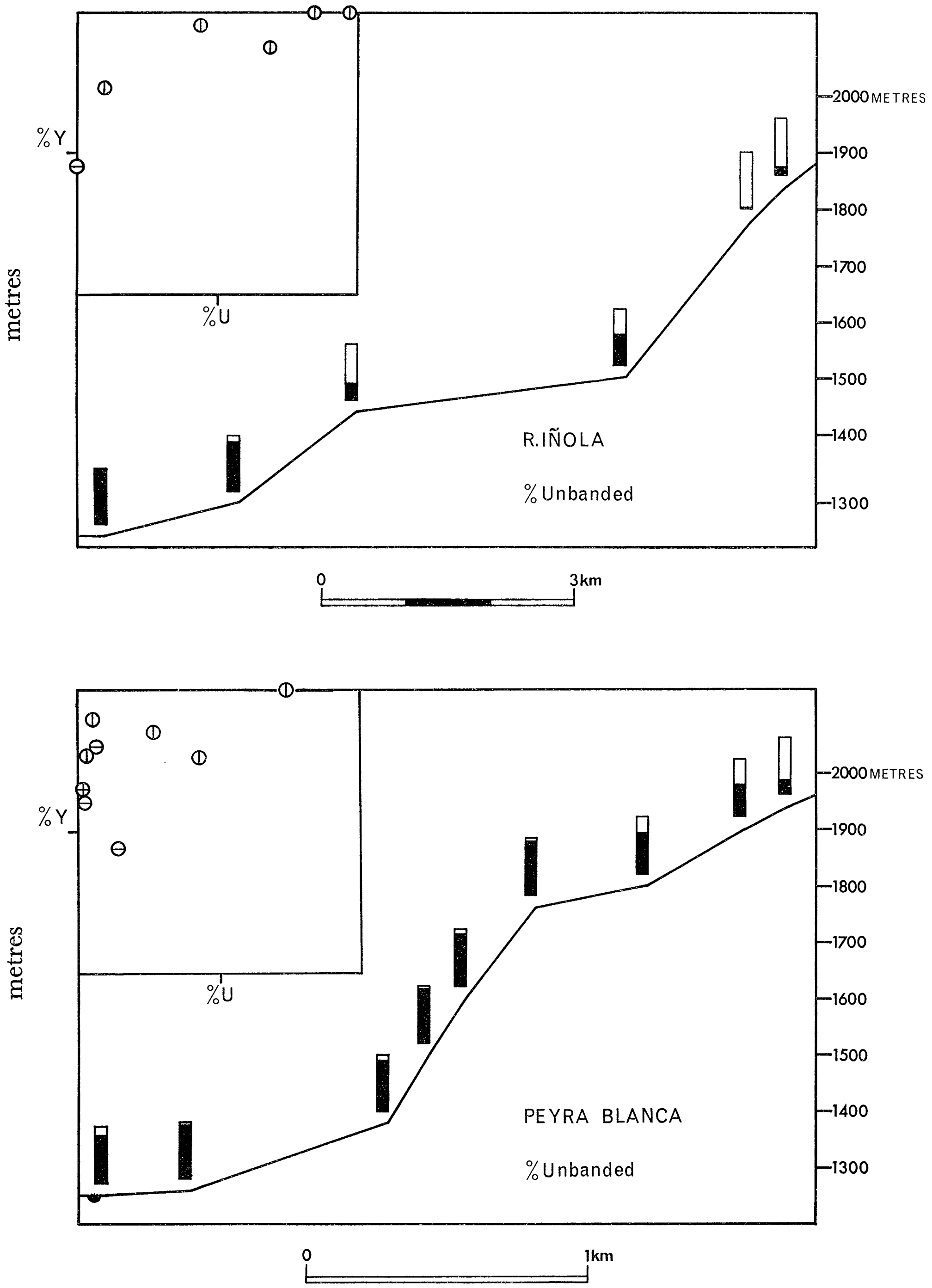

FIGURE 17. Profiles of the Iñola valley and Peyra Blanca hillside, with the frequencies of banded (black) and unbanded (white) shells shown for each sample. The scatter diagrams show percentage yellow and percentage unbanded for the samples. Habitat symbols as in figure 14.

Unbanded is at low frequency until about 1800 m on Peyra Blanca, whereas in the Iñola valley, a high frequency of unbanded is reached at 1440 m, an altitude considerably lower than that on the hillside. The contrast between Peyra Blanca and the Malo valley, to the east, for banding is much greater (figure 5). The area effect for unbanded intensifies there, and in the middle of it is the Aran Hill transect; above about 1800 m, samples are monomorphic for unbanded. The lowest two samples, however, at 1540 m and 1680 m (Aran Hill 1 and 2) are both more banded than Malo 1 and 2, which are roughly at the same altitude. Again, there is evidence that colonies on the hillsides remain banded to greater altitudes than those in the valleys.

TABLE 2. COMPARISON OF IÑOLA AND PEYRA BLANCA, AND MALO AND ARAN HILL, MATCHED ALTITUDE-FOR-ALTITUDE AS NEARLY AS POSSIBLY

No., number of samples; %Y, % yellow; %Wh-l; % white-lip in yellow;
Alt., altitude in metres; %U, % unbanded.

River Iñola					Peyra Blanca hillside				
No.	Alt.	% Y	% U	% Wh-l	No.	Alt.	% Y	% U	% Wh-l
1	1280	73	10	92	1	1260	60	2	90
2	1440	88	68	94	2	1380	80	6	85
3	1500	96	44	96	3	1500	66	2	88
—	—	—	—	—	4	1600	90	5	94
4	1780	100	97	100	5	1760	77	3	89
5	1840	100	84	97	6	1800	85	27	100
—	—	—	—	—	7	1900	76	43	100
—	—	—	—	—	8	1940	100	73	100

River Malo					Aran Hill				
No.	Alt.	% Y	% U	% Wh-l	No.	Alt.	% Y	% U	% Wh-l
1	1540	100	81	81	1	1540	98	72	98
2	1700	100	97	92	2	1680	97	79	88
—	—	—	—	—	3	1760	100	100	94
—	—	—	—	—	4	1820	100	100	89
3	1900	100	100	85	5	1900	97	100	75
4	2100	100	100	67	—	—	—	—	—

Morph frequencies are compared altitude-for-altitude between samples taken in the Iñola valley and those on the Peyra Blanca hillside, and between Malo valley samples and those from the Aran Hill transect, in table 2.

In one pair, the frequencies of unbanded are the same, and this case has been ignored; in the other seven pairs, the hillside sample has without exception a lower frequency of unbanded (exact test, $P = 0{\cdot}016$). Hillside samples have higher frequencies of pink in all eight cases (for which the exact probability is 0·008), and six of the eight hillside samples exhibit lower frequencies of white-lip in yellow (a trend which is not significant, $P = 0{\cdot}289$, but which is in the same direction as that for the other hillside-riverside pairs, table 1).

These comparisons indicate that the selective factors favouring unbanded, probably yellow, and white-lip in the upper valley complexes do not act at the same strength altitude-for-altitude: the topographical position of a colony is important in modifying the strength of the selection.

FIGURE 18. The Valle de Aran, looking west-north-west down river. The valley of the Garona de Ruda is in the foreground, and continues as the main valley of the Garonne towards the left of the picture. The main valley is partly obscured by the shoulder of the eastern side of the Valarties valley on the left. The entrance to the Aiguamoch valley is at left centre (closely resembling it is the entrance to the Valarties valley, out of sight in this picture). On the right, starting at the bottom, are Aran Hill, the Malo valley entrance (partly obscured), Peyra Blanca hillside at far right centre, and the entrance to the Iñola valley to the right of the first village.

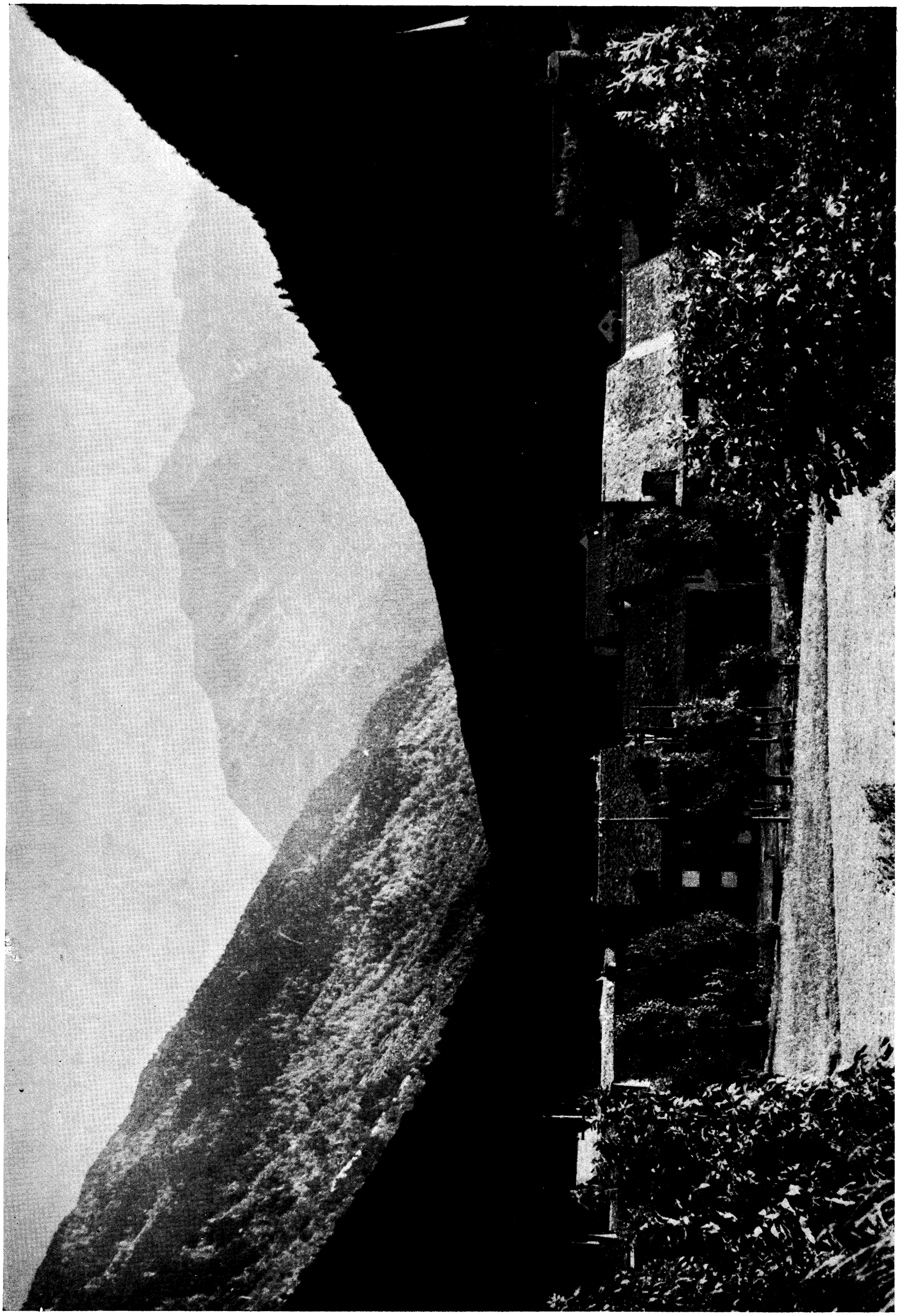

FIGURE 19. The entrance to the Valarties valley at 16.20 h, Central European Time, on 24 September 1966, looking southwards from the Garonne valley. Garonne populations are in sunshine, but the western side of the Valarties valley casts a shadow over populations by the Valarties river. In the distance is Pico de Montarto, around which the valley bifurcates.

(*b*) *Aspect*

The distribution of morph frequencies—particularly frequencies of unbanded—in the Valle de Aran relates quite well to aspect and to the orientation of valleys. Populations in the north–south running tributary valleys generally have higher frequencies of unbanded and yellow than those in the main east–west running valley. In the main valley, a frequency of unbanded exceeding 70% is not reached until above 1360 m, whereas this frequency is exceeded at lower altitudes in the Garonne de Joué, Barrados, Negro and Valarties (the confluences of the Malo and Aiguamoch valleys with the Garonne are higher than 1360 m). The two tributary valleys which do not accord with this, the Saliente and the Iñola, open to the south, and this may explain their exception. The main valley is broad and open; the tributaries, particularly the Barrados and the entrance to the Valarties, tend to be narrow and steep-sided (figure 18, plate 34). Thus, the river in the Barrados runs almost throughout its length in a steep gorge, and it is likely that because of the occluded position of the riverside, it is cooler than in the more open valleys like the Iñola, Saliente, and main valley. Of all the upper valleys, the Barrados is the one which has the highest frequencies of unbanded at the lowest altitudes—above 70% in all colonies above 960 m (figure 5). Figures 9 and 12 show that the same considerations apply broadly to ground colour and lip colour.

The change in frequency of unbanded in the Valarties is particularly abrupt (figure 5); frequencies change from about 10% at the Garonne confluence to 80% a kilometre away inside the Valarties valley. Observations made at the valley entrance in early September showed that the entrance to this valley was in shadow at about 17.00 h Central European Time, confirming that it received less sunlight than the main valley populations nearby, probably about 3 h per day less in September, a result of the shadowing effect of the steep and high sides of the entrance to the valley (figure 19, plate 35).

The Valarties valley is unusual in that it bifurcates approximately equally in its higher reaches around a mountain, one arm leading eastwards as the River Rencules; this is the only tributary of a tributary river of any substantial size in the Valle de Aran, and it was the only one designated as 'River' on the field-map used. At the point of dichotomy, the valley is open and relatively wide. One of the effects of this opening of the hitherto narrow valley is that the riverside will receive more sunlight and be warmer than that at lower levels. Banding (though not colour, and dubiously, lip-colour) frequencies appear to adjust at this point, for the valley is also unusual in that in the upper reaches, a reversion to a lower frequency of unbanded takes place in populations found there, frequencies lower than might be expected when compared with colonies at similar altitudes but in other tributaries. Valarties 8, at 1370 m, and Valarties 9, at 1420 m, have frequencies of unbanded of 40·7 (±9·5)% and 25·0 (±8·8)% respectively.

There are two samples in Andorra which are exceptional in having frequencies of unbanded usually found at much higher altitudes. Valira del Norte 1 and 2, with 46·2 (±9·8)% and 68·9 (±4·9)% unbanded respectively (frequencies which are significantly different at the 5% level from the lower frequencies in their nearest samples, Valira del Norte 3 and Segre-Valira 23) at 1125 and 1150 m, were both taken from the bottom of a very steep gorge about 50 m across and with sides about 200 m high. The gorge is oriented north–south, and opens into a broad valley just above Valira del Norte 3. As with with Barrados and the entrance to the Valarties, unbanded again seems to be favoured in positions that are occluded due to local topographical features.

(*c*) *The selective agent*

Three climatic features change fairly regularly with increase in altitude: the degree of insolation increases, the amount of precipitation increases (although it may decrease again above a certain altitude), and air temperature decreases, the lapse rate being approximately 1 °C per 200 m, although this varies from place to place (Kendrew 1949).

It is highly unlikely that increased insolation is responsible for the area effects in the upper valley complexes, for the changes in morph frequency occur at widely different altitudes; as shown in section IV-4a, hillside populations have more conservative morph frequencies than those below them in the valleys, changes in morph frequency occurring at higher altitudes on the hillsides than in the valleys. Peyra Blanca at 1800 m is likely to experience greater insolation than the floor of the Negro valley at 1120 m, where populations are unbanded and yellow. Further, many populations in Andorra have lower unbanded frequencies at higher altitudes than those in the Valle de Aran.

The effects of decreasing temperature and increasing rainfall with increase in altitude are less easy to separate. At Pic du Midi, however, 60 km west-north-west of the Valle de Aran, there is a precipitation inversion varying with season from 1250 m to 1850 m (Kendrew 1949); *Cepaea* is found above 1850 m occasionally in the Valle de Aran, and there is no indication that populations become less unbanded either above that height, or, with the exception of the Valarties already discussed, at any of the heads of the valleys.

The distribution of morph frequencies in the upper valley complexes agrees very well, however, with what may be inferred about temperature from considerations of altitude, aspect, and general topography. It is a general rule that hillsides, with convex surfaces, experience less extreme conditions than concave valley bottoms. The air on hillsides is more liable to disturbance than air in valleys, such that warm air does not tend to accumulate as it does in valleys, and, during the night, cold air moves into the valleys from the hill slopes, causing the former to be liable to lower night temperatures (Geiger 1959); and a farmer in the Valle de Aran, when I asked him why a number of the villages were perched high up on the hill slopes, replied that they were warmer, especially in winter. Night inversions are a regular feature of hilly country in Britain. That riverside populations tend to be more unbanded, more white-lipped, and possibly more yellow, than hillside populations suggests that low night temperatures resulting from the accumulation of cold air by the riverside might be important as the selective agent favouring these morphs. Conditions on hillsides, milder altitude-for-altitude, would not restrict the polymorphism until greater altitudes are reached; the data are in agreement.

The aspect and shape of the valleys, and the conjectured effect on climate, add further support to this. The aspect of land masses has a profound effect on modifying local climate (Geiger 1959; Miller 1943); it is the valleys that face south that are likely to be warmer than the north-facing ones, and it is these which on the whole have more conservative morph frequencies (with the exception of the Barrados, which, as noted, is exceptionally steep-sided and gorge-like). Further, the broad east–west main valley in the Valle de Aran has populations that are more polymorphic than those in the tributaries, altitude-for-altitude, which run north–south and which are likely to receive less sunlight for this reason.

The effects of increased altitude, and the influence of local topography on air movements and on the amount of sunlight received, may be part of one over-all effect; that at certain times of year, low temperatures exert a selective effect on the polymorphism. It may be that the time of disappearance of winter snow in spring is critical (and if this were so, then precipitation effects would be closely associated with temperature effects), the snow perhaps lying longer at higher altitudes in valley bottoms, and in localities in which a reduced amount of sunlight is received.

A comparison between the climates of the Valle de Aran and Andorra supports the hypothesis. Andorra is both warmer in summer (the 23 °C July isotherm crosses it), and drier (800 to 1000 mm of total precipitation, with 100 to 150 rain days per year) than the Valle de Aran (21 to 22 °C, 1000 to 1200 mm, 150 to 200 rain days). The climatic data are from the *Atlas de France*. Populations in Andorra do not exhibit such high frequencies of unbanded at high altitudes, which, *ex hypothesi*, is expected. This argument does not apply conclusively to lip-colour, nor to colour morph frequencies, though.

(5) *Climatic selection in the lower valleys*

The lower morph frequency zones in the lower valleys of both regions resemble one another in that compared with the intermediate zones, they are more unbanded and tend to be more yellow (significantly so in the case of the Garonne), but they differ in the magnitude of the change in unbanded frequency. The Segre-Valira lower zone samples have significantly higher frequencies both of unbanded and of yellow than those in the Garonne lower zone ($P < 0{\cdot}05$ in both cases). That the same change takes place in both regions implies that similar selective forces are responsible; and the difference in the magnitude of the changes indicates that the intensity of selection is different in the two lower zones. Both clines in unbanded are stepped.

The lower valleys are likely to experience higher temperatures than the upper valleys as a result of their lower altitudes, and they are drier. The difference is far more pronounced, though, in the Segre valley which runs south towards the River Ebro. The flora is essentially mediterranean in type, and land-snail species like *Eobania vermiculata* (Müll.), *Pseudotachea splendida* (Drap.), and *Rumina decollata* (L.) occur, species not found in Andorra, nor in any part of the Garonne region surveyed. It is the drier of the two lower valleys, receiving 600 to 700 mm of precipitation per year, compared with 800 to 1000 mm in the lower Garonne (data from the *Atlas de France*).

Comparison of environmental conditions and the direction and magnitude of the changes in morph frequency are consistent with the hypothesis that unbanded and yellow are favoured by warm and dry conditions, again probably acting selectively at certain limiting times of year, in this case in the summer.

The argument can only partly be applied to lip colour; for although there is a progressive decrease in the frequency of white-lip in yellow with decreasing altitude in both regions, suggesting that it is at a disadvantage in associated conditions, it remains at a higher frequency in the lower valley of the Segre-Valira (figures 12 and 13). Comparison of the frequencies of white-lip in yellow between populations living between 400 and 600 m in both regions (Segre-Valira 2–11, Garonne 1–18) shows that frequencies are significantly higher in the Segre-Valira (median test, $\chi^2_1 = 7{\cdot}62$, $P < 0{\cdot}01$).

There are indications that two other banding morphs may be favoured in warm and dry conditions. The mid-banded gene, M^3, reaches higher frequencies in the main Garonne valley in the lower colour and banding zones than in the intermediate zones—five of the lower zone samples have frequencies of M^3 higher than any of the intermediate zone samples; the range of frequencies in both zones is great, however, and there is no evidence for an overall difference (median test, $\chi^2_1 = 0{\cdot}11$, $P > 0{\cdot}05$). It is present in the Segre-Valira in only five samples, all below 800 m. In three, Segre-Valira 15–17, it is at very low frequency, but it reaches moderate frequencies in the two lowest samples, Segre-Valira 1 and 2. Secondly, the punctate banding morph, in which the dark banding pigment is not at equal intensity along the bands, is found only in the lowest Garonne sample, Garonne 1, and in eight samples between Segre-Valira 1 and 11, five of them in the lower zone (tables 3 and 4); it is absent in the other samples.

(6) *Results on climatic selection*

The evidence indicates that unbanded and yellow morphs are favoured whenever some aspects of the climatic environment, particularly temperature, are relatively severe for at least some time during the year, and, conversely, that banded (especially five-banded) and pink are favoured or less disadvantageous respectively in milder climates; the results further demonstrate that area effects can be caused by climatic selection.

The clearest correlation between the distribution of a morph frequency and inferred climatic conditions is that with banding, and it seems likely that climatic selection at least near the altitudinal edge of range exerts a direct effect on the polymorphism, for the clines are smooth, and the adjustment of morph frequencies to the local climatic environment is close. The surveys in the lower valleys, where the clines are stepped without obvious relation to features which might cause sharp discontinuities in climate, indicate that other factors such as co-adaptive selection may also influence the banding morph frequencies there.

The correlation between climate and colour morph frequencies is less close; no explanations on climatic grounds can be advanced for colonies exhibiting anomalous frequencies in the zones, and results obtained from the hillside samples are ambiguous. It is possible that climatic selection on colour is indirect—climate acting through an environmental concomitant, for example—or that colour is more subject than banding to other forms of more local selection; these would account for the less clear pattern of colour morph frequencies.

White-lip is clearly favoured by some aspect of the Pyrenean mountain environment, probably low temperatures and high rainfall. The hillside results support a climatic interpretation for its frequency distribution, although comparisons between its frequencies in the two lower valleys show that the explanation advanced may be too simple.

V. Discussion

Lamotte (1951) gives the frequencies of unbanded for colonies sampled in four major Pyrenean valleys on the north side of the watershed, and notes (pp. 146 to 148) that unbanded tends to be at higher frequencies both at altitudes below 450 m and above 1000 m. He points out, however, that this tendency is feeble in these valleys, and subject to considerable variation both within and between valleys. He concludes that climatic selection is affecting the phenotypic composition of the populations there, but that this selection is comparatively unimportant compared with other evolutionary effects.

The wide range of frequencies of unbanded in Lamotte's valleys contrasts somewhat with the relatively narrow range in the Garonne and Segre-Valira; zones of banding morph frequencies are certainly not as clear-cut. The difference could be explained if samples were not taken from uniform positions, but from various topographical positions in the valleys, for it has been shown above that the strength of climatic selection varies with position. Alternatively, morph frequencies may not be at equilibrium; the valley which he studied most intensively, the Ariège, is probably one of the most disturbed by human activity, and evolutionary factors like gene-flow, founder effect, and forms of selection associated with intensive human activity may well be more important there than in valleys where disturbance has been less severe.

Nevertheless, his data are broadly consistent with mine, both in that there is evidence that unbanded is more frequent at either ends of the surveyed parts of the valleys, and also in that comparison of its morph frequencies between valleys conforms with the Garonne and Segre-Valira situation, populations in the east being more banded at higher altitudes. July isotherms cross the Pyrenees from north to south, temperatures increasing towards the Mediterranean. Similarly, annual rainfall decreases eastwards (*Atlas de France*). Thus, valleys in the east are warmer for much of the year, and drier. At the lower altitudinal limit of his collecting in the Pyrenees, it is populations in the Ariège valley, the one nearest the Mediterranean, which exhibit the highest frequencies of unbanded (39 %) between 300 and 450 m (Lamotte 1951, p. 147); and in his samples taken above 1000 m, unbanded is at its highest mean frequency (55 %) in the Adour valley, the most western of his four valleys. The Ariège has the second lowest mean frequency in samples above that height. His highest sample was taken from the Ariège at about 1400 m, an altitude below which comparatively few populations sampled by me in the Pyrenees exhibit high frequencies of unbanded; this may explain the paucity of samples with really high frequencies in his surveys. There is, hence, some agreement with the hypothesis that higher frequencies will be found in the lower parts of the valleys in the warmer and drier regions, and that they will be found at higher altitudes in the cooler, and perhaps wetter, valleys.

Lamotte (1951) considers that insolation favours unbanded at higher altitudes as well as at low ones, the incidence of cloud cover, he points out, being greater in the more banded parts of the valleys. Both his data and mine for any one region and for riverside samples only would agree with this; however, as argued here in section IV-4, the evidence from topographical considerations favours a different interpretation, for hillside populations are more banded at higher altitudes than riverside ones, and not less so, as would be expected if insolation favoured unbanded. Further, Lamotte's data themselves indicate that populations in the easternmost valleys are more banded than those in the most western at high altitudes, and not less so, as again would be expected if insolation were the factor favouring unbanded at higher altitudes.

The idea that unbanded snails are favoured in insolated places is an old one—for example, Taylor (1914) and Haviland & Pitt (1919) thought that this was so. Schnetter (1950) working, though, with *C. hortensis*, reported a change to a higher frequency of unbanded after the destruction of cover in the habitat by bombing. Lamotte (1951) indicates that unbanded *C. nemoralis* were more frequent in sunny localities in three regions in France, but commented that his evidence was not strong: in two regions, Aquitaine and the Parisian region, the mean frequencies are not significantly different from one another, while in the third (the Somme valley) all the sunny biotopes were in one part of the valley, with the shaded ones elsewhere. As a result of extensive collecting throughout France, he concluded (1951) that climatic factors play very little role in influencing the polymorphism, for the correlation between various climatic aspects and banding morph frequencies is low, and within any one climatic region, significant differences could be observed between populations in districts in it. Nevertheless, as Cain & Sheppard (1954) commented: 'His published results (p. 141) do suggest a correlation between the frequency of unbanded shells and temperatures in both July and January, but these two factors may not be independent'.

In his 1959 paper Lamotte is more emphatic about the role of climate as a selective agent. He considers that the clear and consistent differences between colour morph frequencies in woods and open habitats in France is due to yellow being favoured by the drier and more insolated conditions in the latter habitat-type, and he affirms that unbanded snails are more frequent in districts in France with higher July temperatures; further, he shows that although there is no correlation between colour morph frequencies and summer temperatures, there is an obvious negative one between the frequency of yellow and mean January temperature. Guerrucci-Henrion (1966) has recently demonstrated in Brittany a convincing correlation between the amount of precipitation and colour morph frequencies, yellow being significantly more frequent near the coast than inland, where the amount of precipitation is much higher. She found no evidence for a correlation between banding-morph frequencies and rainfall.

Taken together, the foregoing results and observations amount to a body of evidence indicating that unbanded is favoured over banded in both sunny and warm environments, and also possibly in cold climates, and that yellow may be favoured over pink in such circumstances too. They agree well with results from the Pyrenees, and there appear to be no areas of serious disagreement.

A number of workers have investigated the capacity of different morphs to survive periods of unusually high or low temperatures, in an attempt to correlate differences with the observed field distribution of morph frequencies. Boettger (1954) performed a number of experiments in which snails of both species of *Cepaea* were subjected to temperatures of up to 60 °C for short periods, and showed that yellow unbanded *C. hortensis* had a higher survival rate than yellow banded ones; he used far fewer *C. nemoralis* in the experiments, and differences in survival were not apparent. Sedlmair (1956) confirmed Boettger's result for *C. hortensis*, using conditions that approximate to those that might obtain in the field—snails were exposed in cloth bags out of doors in summer for a month; with *C. nemoralis*, she found a higher survival rate in pink, though. She showed that yellow unbanded *C. hortensis* and yellow *C. nemoralis* preferred warmer and drier resting places than yellow five-banded *C. hortensis* and pink *C. nemoralis* when live snails were permitted to choose their resting places in humidity and temperature gradients.

Lamotte (1959) performed similar experiments to Boettger's, but using *C. nemoralis* only; exposure to an electric light bulb for 40 h at 35 °C resulted in more yellow and unbanded snails surviving than pink and five-banded snails. He also subjected *C. nemoralis* to a cold régime, (3 h at −8 °C), and again found that yellow and unbanded snails survived better. Carter (1965) raised young *C. nemoralis* for about 6 months at temperatures of 32, 20 and 2 °C, and concluded that yellow five-banded and yellow mid-banded snails were more resistant to extreme temperatures than pink five-banded ones.

As Lamotte (1959) commented, the experimental results are fragmentary, but they agree quite well with what would be expected from the field distribution of the morphs, with yellow and unbanded frequent in insolated and warm places and pink and banded snails frequent in sheltered environments. Yellow and unbanded morphs survive low temperatures better also: that is, they appear to be the more *resistant* morphs. They appear to be found at higher frequencies in districts that tend towards having extreme temperatures. In the Pyrenees, climate may well control morph frequencies in populations, but elsewhere, a complex of selective factors may override climatic selection (for example, in lowland England, where visual selection controls morph frequencies generally).

The Pyrenees results suggest that when certain climatic factors become sufficiently extreme, area effects in unbanded and yellow will be found; and they further suggest that if the strength of visual selection is relaxed in regions where area effects occur, as recent observations and experiments indicate (Arnold 1966, and in preparation), area effects in five-banded and in pink may be expected in climatic conditions that are comparatively mild.

High frequencies of unbanded rarely occur in England (except in woods, a result of visual selection), and no strong area effects in unbanded have been described in southern England, where mid-banded and five-banded are responsible for area effects in banding in the regions so far surveyed. Where area effects in unbanded might be expected is in the north on high country; for conditions there at certain times of the year may approximate to those obtaining in the Pyrenees at higher altitudes, and thus may exert a similar restricting effect on the polymorphism. Trees do not grow in Britain above about 620 m (Manley 1952), the altitudinal limit being set by the length of growing period, limited by low temperatures over part of the year. Hence, populations of *C. nemoralis* are likely to experience cool conditions at very much lower altitudes than in the Pyrenees.

In 1964, I made one sample of thirty-one adult snails from the limestone uplands of Staffordshire at 275 m. Twenty-eight of them were unbanded and twenty-nine were yellow (table 5). One unbanded yellow had a white-lip. The only other sample at the time known to come from the same district was made by Dr D. A. West at Hall Dale. The sample is large, and consists only of unbanded shells; it does, however, have a relatively high frequency of brown, a colour morph which is usually unbanded. White-lip also is present (table 5). I am grateful to Professor A. J. Cain for drawing my attention to this sample. Recent extensive collecting on the high limestone of the regions shows that populations with high frequencies of unbanded are fairly common, and that white-lipped individuals occur (J. J. D. Greenwood, personal communication). A survey that Professor Cain and I have commenced to test the idea on the high limestone near Cross Fell in Cumberland, over 150 km north of the localities from which the above two samples were taken, indicates that at least unbanded may be more frequent at higher altitudes. Of the five samples so far made, the highest (at 535 m) has the highest frequency of unbanded (69 %), consists only of yellow shells, and white-lip is present (table 5). These surveys show that climatic area effects in banding may well occur outside the Pyrenees.

Table 5. Other samples referred to in the text

locality and map references	yellow						pink		total	remarks	habitat and altitude (m)
	0		3		5		0				
	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.			
near Ilam, Staffordshire. SK. 127496	1	25	—	3	—	—	—	2	31	EU 5, brown, absent	G 275
Meickle Awfell, Cumberland. NY. 629381	4	14	—	1	—	7	—	—	26	EU 5, brown, absent	G 535
							brown				
							0				
							wh.l.	d.l.			
Hall Dale, Staffordshire. SK. 132539	23	95	—	—	—	—	17	216	351	EU 5, pink, absent	G 275

Note: None of the samples contains pink or brown banded shells.

Area effects in banding on chalk along the south coast of England tend to be for five-banded. Thus, Carter's (1965) work on the Purbeck Hills, and Arnold's (1966) on the eastern South Downs suggest that area effects in mid-banded are rare, in contrast to the situation in south-central England (Cain & Currey 1963*a*, *b*; Carter 1965). It may be that the milder and more humid conditions near the coast favour predominantly five-banded area effects on chalk (Arnold 1966). Lamotte's (1954) data for the frequencies of the banding morphs in various regions in France indicate that five-banded is comparatively frequent in the departments of Nord and Pas-de-Calais, both predominantly calcareous and near the sea, as I pointed out (1966).

With respect to colour, both Carter (1965) and Arnold (1966) found very high frequencies of yellow in the highest parts of regions where area effects are operating, on the Berkshire Downs and South Downs respectively, and Professor Cain has told me that the same is true for the Marlborough Downs, suggesting that yellow is favoured in the most exposed conditions on chalk in England. Also, the only strong area effect for pink so far described is on the South Downs (Arnold 1966), one of the most temperate chalk regions surveyed, as pointed out above. The demonstration that yellow is favoured over pink in more extreme climates in the Pyrenees suggests that climatic selection may affect colour morph frequencies in England, although very much more evidence will be needed before this can be substantiated.

The extent of the area effects in the Pyrenees is often very large—much larger than ones so far described on chalk. Thus, the intermediate zones, for example, are 28 and 40 km long in the Garonne and Segre-Valira regions respectively, and the lower zone in the Segre-Valira is at least 40 km long. Yet stability in morph frequencies (especially in banding) is maintained despite altitudinal ranges of 700 and 1200 m in the intermediate zones, ranges in which climate is likely to alter considerably. In both regions, the clines between the intermediate and lower zone morph frequencies are stepped, suggesting that selective factors other than straightforward selection by climate are operating. Clarke (1966) has recently advanced a theory that may explain how stepped clines for one or more genes could be produced by a gradually changing environment through selection on modifiers of the gene being studied—i.e. co-adaptation of this kind may produce a stepped cline. Although the scale of distance is vastly greater in the Pyrenees than in English regions so studied, a parallel may be drawn with the change from mid-banded to five-banded area effects at the Barbury Gap on the Marlborough Downs (Cain & Currey 1963*a*), where it is also exceedingly difficult to recognize any obvious difference in the environment between the two areas; the selective factors responsible for the area effects are not, however, known here. Further work has been undertaken in the vicinity of both stepped clines in the Pyrenees, the data from which are as yet unanalysed (Arnold, in progress).

The distribution of white-lip appears to follow regions where rainfall is relatively high, or where temperatures are seldom elevated. Thus, besides being found at high frequency in the high Pyrenees, it is found in some populations on the west coast of Ireland (Cook & Peake 1960), in Derbyshire and Staffordshire, on the Yorkshire limestone Cook (1966), in North Cornwall (Arnold 1966), and I have found it in North Wales. It appears to be exceedingly rare in southern England, and in northern France (Lamotte 1951).

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Explanation of tables 3, 4 and 5

(1) 0, 3, 5, E.U. 5: phenotypes of banding formulae 00000, 00300, 12345, and 00345, and minor variants of them, respectively.

(2) wh.l.: white-lip; d.l.: dark-lip; hyal.: hyalozonate.

(3) The presence of *C. hortensis* is recorded.

(4) Habitats: G: grass; RH: rough herbage; H: hedgerow; S: scrub; OW: oakwood; MDW: mixed deciduous wood; CW: coniferous wood. Altitudes are given in metres.

(5) In table 4, first column—R: riverside sample; HS: hillside sample.

(6) Pairing of samples: wood-riverside pairs are indicated in table 3 by the same sample numbers, the wood sample being shown by a prime. Hillside samples from the Valle de Aran are listed separately at the end of table 3, and where they are paired, the corresponding riverside sample is shown. Hillside samples from Andorra are listed with the riverside samples in table 4, and the riverside samples with which they are paired shown.

TABLE 3. THE COMPOSITION OF SAMPLES OF *C. NEMORALIS* FROM THE GARONNE REGION

Riverside and lower valley paired woodland samples

	yellow								pink											
	0		3		5		E.U.5		0		3		5		E.U.5					
locality	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	total	remarks	habitat and altitude (m)	
Garonne																				
(1)–Pointis	1	6	—	—	—	4	—	1	—	6	—	1	—	11	—	2	32	1 *punctata*	RH	400
(2)–Ausson	1	10	—	—	—	11	1	5	—	4	—	—	—	8	—	2	42	—	RH	410
(3)–Seilhan	—	3	—	1	—	5	—	—	—	4	—	—	—	7	—	3	23	—	H	420
(4)–Labroquère	4	8	—	—	1	5	—	2	—	1	—	—	—	1	—	—	22	—	RH	440
(5)–Loures-Barousse	1	8	1	1	1	10	—	—	—	3	—	1	—	6	—	1	33	—	RH	445
(6)–Luscan	4	14	—	6	1	7	1	1	—	8	—	1	—	6	—	—	49	—	H	450
(6′) —	2	8	—	—	—	7	—	1	—	3	—	—	—	5	—	—	26	—	OW	480
(7)–Galié	1	7	1	3	—	11	—	—	—	3	—	2	—	2	—	—	30	—	H	455
(7′)–Bertren	—	9	1	3	2	11	—	2	—	—	—	2	—	4	—	—	34	—	MDW	500
(8)–Bagiry	—	8	—	2	1	3	—	—	—	2	—	2	—	5	—	—	23	—	RH	455
(8′)–Bagiry	4	10	1	2	2	5	1	—	—	5	—	—	—	7	—	—	37	+ *C. hort.*	MDW	500
(9)–Frontignan	1	6	—	—	4	9	—	—	—	2	—	1	—	1	—	—	24	—	RH	459
(9′)–Frontignan	2	19	—	1	2	23	—	—	—	3	—	—	—	7	—	—	57	+ *C. hort.*	MDW	459
(10)–Frontignan	1	11	—	6	1	19	—	—	—	—	—	1	—	3	—	—	42	—	RH	459
(10′)–Frontignan	2	22	—	7	—	17	—	—	—	—	—	2	—	7	—	—	57	+ *C. hort.*	MDW	459
(11)–Esténos	—	6	—	6	—	9	—	—	—	3	—	1	—	7	—	1	33	—	RH	460
(12)–Rouziet	—	21	—	7	1	8	—	—	—	5	—	4	—	10	—	—	56	—	RH	470
(13)–Rap	3	4	—	2	2	12	—	—	—	7	—	—	1	7	—	—	38	—	G	490
(13′)–Sastrade	10	19	—	1	3	10	—	—	—	4	—	1	—	12	—	—	60	+ *C. hort.*	MDW	480
(14)–Méliande	1	7	—	—	1	14	—	—	—	1	—	1	—	4	—	—	29	+ *C. hort.*	RH	515
(15)–Argut-dessous	1	3	—	4	2	18	—	—	—	2	—	—	1	16	—	—	47	+ *C. hort.*	RH	525
(16)–Fos	1	6	—	1	—	8	1	—	1	2	—	3	—	22	—	—	45	+ *C. hort.*	H	537
(17)–Melles	1	2	—	2	1	9	—	—	—	3	—	1	—	21	—	—	40	+ *C. hort.*	H	560
(18)–Canéjan	—	—	—	1	—	5	—	—	—	1	—	6	—	15	—	—	28	—	RH	600
(19)–Lès	1	1	—	2	2	9	—	1	—	—	—	4	—	9	—	—	29	—	RH	620
(20)–Lès	1	—	—	—	2	17	—	—	—	1	—	—	—	6	—	—	27	+ *C. hort.*	H	640
(21)–Bosost	2	1	2	4	5	23	—	—	—	1	—	1	1	14	—	—	54	—	H	700
(22)–Bosost	3	2	1	1	10	10	—	—	—	—	1	—	—	8	—	—	36	—	RH	750
(23)–La Bordette	3	1	2	1	10	4	—	—	—	1	—	2	1	11	—	—	36	—	H	760
(24)–La Bordette	1	1	—	1	3	9	—	—	1	—	—	4	—	15	—	—	35	—	RH	770
(25)–Las Bordes	4	7	1	1	4	12	—	—	—	3	—	—	—	19	—	—	51	—	RH	790
(26)–Bénos	9	2	—	1	21	6	—	—	—	1	—	2	3	14	—	—	59	—	G	820
(27)–Bégos	5	—	—	1	18	5	—	—	—	3	—	2	2	15	—	—	51	—	H	850
(28)–Arros	3	—	—	—	15	6	—	—	—	2	—	1	—	15	—	—	42	—	G	860
(29)–Vila	1	—	1	—	9	—	—	—	—	3	—	—	—	13	—	—	27	—	RH	880
(30)–Aubert	2	1	—	1	10	5	—	—	—	—	—	1	2	17	—	—	39	—	H	900
(31)–Bellan	2	—	4	—	11	6	—	—	—	1	—	1	1	15	—	—	41	—	RH	920
(32)–Mig-Aran	14	2	2	1	11	9	—	—	—	5	—	1	1	15	—	—	61	—	S	940
(33)–Viella	1	—	2	—	13	4	—	—	—	—	1	—	1	12	—	—	34	—	H	960
(34)–Viella	4	—	—	—	11	3	—	—	—	—	—	—	1	13	—	—	32	—	G	980
(35)–Betren	2	—	2	—	11	3	—	—	—	—	—	4	1	22	—	—	45	—	G	1000
(36)–Escuñau	4	2	—	—	9	8	—	—	—	1	—	—	1	13	—	1	39	—	RH	1040
(37)–Caxard	18	2	4	1	32	5	1	—	—	3	—	—	—	8	—	—	74	—	G	1100
(38)–Caxard	2	—	—	—	27	2	—	—	1	—	1	—	1	23	—	—	57	—	G	1100
(39)–Arties	4	—	—	—	17	6	—	—	—	—	—	2	2	27	—	—	58	—	G	1110
(40)–Arties	5	1	2	—	18	6	—	—	1	1	—	1	3	27	—	—	65	—	RH	1130

TABLE 3 (*cont.*)

	yellow								pink										
	0		3		5		E.U.5		0		3		5		E.U.5				
locality	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	total	remarks	habitat and altitude (m)
Garonne																			
(41)–Arties	3	—	—	—	28	6	—	—	—	2	—	—	3	28	—	—	70	—	H 1180
(42)–Gesa	2	2	2	—	28	8	—	1	—	5	—	—	2	26	—	—	76	—	H 1190
(43)–Salardú	—	—	—	—	17	3	—	—	—	—	—	—	1	22	—	1	44	—	RH 1220
(44)–Salardú	3	1	—	—	11	3	1	—	—	2	—	—	1	21	—	—	43	—	RH 1250
(45)–Trédos	18	3	1	—	18	3	—	—	1	5	—	3	6	25	—	—	83	—	RH 1270
(46) —	20	3	—	—	8	—	1	—	—	3	—	1	1	7	—	1	45	—	RH 1320
(47)–Between Aiguamoch and Malo	21	1	—	—	5	1	—	—	1	—	—	—	—	3	—	—	32	—	RH 1360
(48)–Mouth of Malo	40	6	1	—	3	1	1	—	—	8	—	1	—	2	—	—	63	+*C. hort.*	RH 1410
(49) —	56	5	—	—	—	—	—	—	—	3	—	—	2	—	—	—	66	—	RH 1460
(50) —	21	2	—	—	—	—	—	—	—	3	—	—	—	—	—	—	26	—	G 1490
Garonne de Joué																			
(1) —	3	13	—	4	2	21	—	—	1	2	—	—	—	2	—	—	48	—	H 880
(2) —	—	5	—	8	—	12	—	—	—	2	—	—	—	2	—	—	29	—	RH 980
(3) —	2	12	—	2	—	26	—	—	1	3	—	—	—	1	—	—	47	+*C. hort.*	G 1100
(4) —	5	12	—	6	—	2	—	—	7	17	—	—	—	—	—	—	49	+*C. hort.*	G 1280
(5) —	43	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	44	—	G 1540
Barrados																			
(1) —	5	1	1	1	18	9	—	—	—	—	—	1	1	—	—	—	37	—	G 880
(2) —	12	1	—	—	13	3	—	—	—	—	—	—	—	—	—	—	29	—	G 950
(3) —	23	—	—	—	2	—	—	—	—	1	—	—	—	—	—	—	26	+*C. hort.*	RH 960
(4) —	8	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	9	+*C. hort.*	MDW 1040
(5) —	13	—	—	—	—	—	—	—	7	—	—	—	1	—	—	—	21	+*C. hort.*	MDW 1340
(6) —	20	—	—	—	1	—	—	—	2	—	—	—	—	—	—	—	23	—	G 1500
Saliente																			
(1) —	5	1	1	—	18	2	—	—	—	2	1	4	1	16	—	—	51	—	G 980
(2) —	2	—	—	—	16	—	—	—	—	—	—	—	1	6	—	—	25	—	H 1020
(3) —	18	1	—	—	40	4	—	—	—	—	—	—	—	5	—	—	68	—	S 1060
(4) —	16	—	1	—	12	—	—	—	—	—	—	—	—	—	—	—	29	+*C. hort.*	S 1140
(5) —	16	—	1	—	11	—	—	—	—	1	—	—	—	1	—	—	30	+*C. hort.*	G 1240
(6) (east arm)	35	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	37	—	RH 1400
(7) (between arms)	33	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	36	—	G 1300
(8) —	25	—	—	—	7	—	—	—	—	—	—	—	—	—	—	—	32	—	RH 1380
(9) —	49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	—	S 1520
(10) —	24	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	—	RH 1700
(11) —	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	—	G 1860

TABLE 3 (*cont.*)

	locality	yellow								pink								total	remarks	habitat and altitude (m)	
		0		3		5		E.U.5		0		3		5		E.U.5					
		wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.				
Negro																					
(1)	—	17	3	3	3	12	2	—	—	—	1	—	—	—	7	—	—	48	+ *C. hort.*	G	1020
(2)	—	14	3	4	2	11	3	—	—	—	2	—	—	—	5	—	—	44	+ *C. hort.*	RH	1060
(3)	—	51	2	7	—	19	1	—	—	—	3	—	2	—	2	—	—	87	—	H	1080
(4)	—	17	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	20	—	RH	1120
(5)	—	43	4	7	—	10	—	—	—	—	1	—	—	—	—	—	—	65	+ *C. hort.*	RH	1150
(6)	—	33	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	37	—	G	1220
(7)	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	+ *C. hort.*	RH	1250
(8)	—	42	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	42	—	G	1320
(9)	—	29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	+ *C. hort.*	G	1500
(10)	—	43	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43	—	G	1440
Valarties																					
(1)	—	14	8	—	—	3	2	—	—	—	3	—	—	—	2	—	—	32	—	RH	1180
(2)	—	29	10	—	—	2	3	—	—	—	—	—	1	—	—	—	—	45	+ *C. hort.*	RH	1210
(3)	—	35	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36	+ *C. hort.*	S	1220
(4)	—	14	6	—	—	3	1	—	1	—	—	—	—	—	—	—	—	25	+ *C. hort.*	G	1230
(5)	—	16	2	—	—	3	2	—	—	—	—	—	—	—	—	—	—	23	+ *C. hort.*	G	1280
(6)	—	11	5	—	—	1	1	—	—	—	7	—	—	—	3	—	—	28	+ *C. hort.*	H	1310
(7)	—	20	7	—	—	5	—	—	—	—	—	—	—	—	—	—	—	32	—	S	1340
(8)	—	4	7	—	3	8	5	—	—	—	—	—	—	—	—	—	—	27	+ *C. hort.*	G	1370
(9)	—	4	2	5	1	8	4	—	—	—	—	—	—	—	—	—	—	24	+ *C. hort.*	G	1420
Iñola																					
(1)	—	3	—	—	—	31	3	1	—	—	2	—	—	—	11	—	1	52	—	G	1280
(2)	—	24	2	1	—	9	—	—	—	—	2	—	—	—	3	—	—	41	—	G	1440
(3)	—	19	1	2	—	21	1	—	—	—	—	—	—	—	2	—	—	46	—	G	1500
(4)	—	30	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	31	—	G	1780
(5)	—	32	—	—	—	5	1	—	—	—	—	—	—	—	—	—	—	38	—	G	1840
Aiguamoch																					
(1)	—	28	—	3	—	21	—	—	—	—	1	—	—	—	1	—	—	54	—	RH	1370
(2)	—	24	1	—	—	2	—	—	—	—	1	—	—	—	—	—	—	28	—	H	1420
(3)	—	12	13	1	—	1	1	—	—	—	—	—	—	—	—	—	—	28	—	G	1460
(4)	—	21	9	—	—	1	—	—	—	—	1	—	1	—	—	—	—	33	+ *C. hort.*	G	1520
Malo																					
(1)	—	13	4	1	—	3	—	—	—	—	—	—	—	—	—	—	—	21	—	S	1540
(2)	—	35	3	—	—	1	—	—	—	—	—	—	—	—	—	—	—	39	—	G	1700
(3)	—	29	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34	—	G	1900
(4)	—	20	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	—	G	2100

TABLE 3 (*cont.*)

Hillside samples

locality, and paired riverside sample	yellow								pink								total	remarks	habitat and altitude (m)	
	0		3		5		E.U.5		0		3		5		E.U.5					
	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.				
R. Margarida–Garonne (21)	1	—	—	4	—	9	—	—	—	1	—	3	—	3	—	—	21	+*C. hort.*	H	1100
Arros – ,, (24)	—	—	—	1	2	13	—	—	—	—	—	1	—	7	—	—	24	—	G	1300
Vilamos – ,, (25)	—	—	—	—	4	25	—	—	—	—	—	—	—	2	—	—	31	—	G	1300
Vilamos – ,, (26)	—	—	—	—	12	11	—	—	—	—	—	—	—	14	—	—	37	—	H	1260
Vilamos – ,, (27)	2	—	—	(1) —	4	5	—	—	—	1	—	—	2	(1) 4	—	—	20	1 Y3 1 P5 unscorable for lip colour. +*C. hort.*	H	1220
Vila – ,, (29)	2	—	2	—	21	8	—	—	—	—	—	—	1	2	—	—	36	—	H	1050
Moncorbau – ,, (30)	2	—	1	—	29	3	—	—	—	—	—	1	—	18	—	—	54	—	H	1180
Mont – ,, (31)	4	—	—	—	40	5	—	—	1	—	—	—	6	15	—	—	71	—	G	1160
Gausach – ,, (32)	5	5	—	—	26	18	—	—	—	—	—	—	—	5	—	—	59	—	G	1250
Viella – ,, (33)	4	—	1	—	31	4	—	—	—	—	—	1	1	28	—	—	70	—	H	1150
Betren – ,, (34)	4	—	3	2	16	4	—	2	—	—	—	—	—	9	—	1	41	—	H	1150
Peyra Blanca																				
(1) –Garonne (44)	—	—	—	—	26	3	—	—	—	1	—	—	2	16	—	—	48	—	RH	1260
(2) —	4	—	—	—	41	8	—	—	—	—	—	—	1	12	—	—	66	—	RH	1380
(3) —	1	—	1	—	33	5	—	—	—	—	—	—	3	18	—	—	61	—	H	1500
(4) —	1	—	—	—	33	2	—	—	—	1	—	—	—	3	—	—	40	—	G	1600
(5) —	1	—	—	—	23	3	—	—	—	—	—	—	1	7	—	—	35	—	G	1760
(6) —	6	—	—	—	23	—	—	—	1	2	—	—	1	1	—	—	34	—	G	1800
(7) —	14	—	—	—	18	—	—	—	1	3	—	—	3	3	—	—	42	—	G	1900
(8) —	22	—	1	—	7	—	—	—	—	—	—	—	—	—	—	—	30	—	G	1940
Aran Hill																				
(1) –Garonne (49)	40	1	—	—	14	—	1	—	—	—	—	—	—	1	—	—	57	—	G	1540
(2) —	23	4	—	—	5	—	1	—	—	—	—	—	—	1	—	—	34	—	RH	1680
(3) —	31	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	—	S	1760
(4) —	25	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	—	S	1820
(5) —	38	13	—	—	—	—	—	—	3	—	—	—	—	—	—	—	54	—	G	1900
G. de Joué–G. de Joué (4)	1	15	—	—	—	11	—	—	2	3	—	—	—	1	—	—	33	—	G	1320
Barrados –Barrados (3)	7	—	—	—	3	—	—	—	—	1	—	—	—	—	—	—	11	—	RH	1150
Barrados –Barrados (5)	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	—	RH	1400
Saliente –Saliente (3)	8	—	1	—	47	5	—	—	—	—	—	1	2	3	—	—	67	—	RH	1250
Negro –Negro (1)	5	2	2	—	10	4	—	—	—	—	—	—	—	6	—	—	29	—	G	1060
Negro –Negro (6)	7	1	—	1	15	4	—	—	—	—	—	1	—	3	—	—	32	—	S	1200
Valarties –Valarties (1)	—	—	—	—	12	9	—	—	—	—	—	—	—	12	—	—	33	—	H	1200
Valarties (no pair)	10	6	—	1	9	9	—	—	—	—	—	—	1	2	—	—	38	—	S	1240
Valarties (no pair)	6	9	3	—	29	34	—	—	—	—	—	1	—	8	—	—	90	—	S	1250
Iñola –Iñola (2)	7	—	—	—	34	1	—	—	—	—	—	—	2	15	—	—	59	—	G	1460
Saliente –Saliente (10)	25	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	26	—	G	1600

TABLE 4. THE COMPOSITION OF SAMPLES OF *C. NEMORALIS* FROM THE SEGRE-VALIRA REGION

	yellow								pink										habitat and altitude (m)	
	0		3		5		E.U.5		0		3		5		E.U.5					
locality	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	total	remarks		
Segre-Valira																				
R (1)–Pons	9	18	—	4	—	2	—	—	—	1	—	—	—	—	—	—	34	2 *punctata*	H	365
R (2)–Tiurana	5	28	—	1	—	1	—	1	—	—	—	—	—	—	—	—	36	1 *punctata*	RH	400
R (3)–Oliana	3	18	—	—	—	9	—	3	1	7	—	—	—	—	—	—	41	10 *punctata*	S	440
R (4)–Embalse de Oliana	5	11	—	—	—	4	1	2	1	—	—	—	—	—	—	—	24	4 *punctata*	H	460
R (5)–Coll de Nargo	5	18	—	—	—	2	2	1	—	—	—	—	—	—	—	—	28	1 *punctata*, 1 hyal.	RH	500
R (6) —	28	20	—	—	—	1	—	—	—	—	—	—	—	—	—	—	49	—	H	520
R (7)–Orgañá	2	1	—	—	10	9	—	1	—	—	—	—	—	—	—	—	23	—	RH	535
R (8)–Orgañá	—	6	—	—	5	8	1	1	—	2	—	—	—	6	1	1	31	1 *punctata* + *C. hort.*	RH	550
R (9)–Orgañá	15	6	—	—	2	1	—	—	—	4	—	—	—	1	—	1	30	1 *punctata*	S	560
R (10)–Hostalets	3	6	—	—	18	4	—	—	—	—	—	—	—	2	—	—	33	—	RH	575
R (11)–Pla de Sant Tirs	2	4	—	—	3	13	1	—	1	1	—	—	2	6	—	—	33	1 *punctata* + *C. hort.*	RH	600
R (12)–Adrall	1	1	—	—	15	17	1	3	—	3	—	—	—	10	—	—	51	+ *C. hort.*	RH	640
R (13)–Arfa	10	—	—	—	27	16	2	1	2	4	—	—	—	3	—	—	65	+ *C. hort.*	H	670
R (14)–Séo de Urgel	1	—	—	—	19	12	2	1	1	—	—	—	—	1	—	4	41	+ *C. hort.*	H	700
R (15)–Séo de Urgel	4	5	—	1	21	15	3	2	1	5	—	—	—	1	—	—	58	+ *C. hort.*	H	720
R (16)–Arcabell	6	3	2	—	19	15	4	1	—	3	—	—	—	1	—	—	54	—	RH	760
R (17)–Arcabell	6	6	1	—	26	16	1	2	2	2	—	—	—	2	—	—	64	+ *C. hort.*	RH	800
R (18)–Arcabell	12	2	—	—	21	13	8	3	3	—	—	—	—	—	1	—	63	+ *C. hort.*	RH	875
R (19)–Arcabell	2	—	—	—	17	10	3	—	—	2	—	—	—	—	—	—	34	+ *C. hort.*	RH	900
R (20)–Sant Julia	2	4	—	—	41	11	3	1	—	—	—	—	—	—	—	—	62	+ *C. hort.*	H	900
R (21) —	1	—	—	—	21	5	—	—	—	1	—	—	—	—	—	—	28	+ *C. hort.*	H	975
R (22)–Andorra la Vella	1	2	—	—	29	9	2	—	5	1	—	—	—	—	—	—	49	+ *C. hort.*	RH	1000
R (23) —	1	—	—	—	39	—	5	—	—	—	—	—	—	—	—	—	45	+ *C. hort.*	H	1200
HS (Segre-Valira(23))–Sant Miguel d'Engolasters	18	1	—	—	6	2	16	—	—	—	—	—	—	—	—	—	43	2 hyal. + *C. hort.*	G	1500
R (24)–Radio des Vallées	—	—	—	—	32	1	—	—	—	—	—	—	—	—	—	—	33	+ *C. hort.*	H	1225
R (25)–Encamp	3	—	—	—	15	—	3	—	2	—	—	—	—	—	—	—	23	+ *C. hort.*	G	1275
R (26)–Mollerès	4	—	—	—	33	—	—	—	7	—	—	—	—	—	—	—	44	+ *C. hort.*	G	1400
R (27)–Canillo	—	—	—	—	21	—	—	—	—	—	—	—	—	—	—	—	21	+ *C. hort.*	G	1500
R (28)–Sant Joan de Casellas	—	—	—	—	22	—	—	—	—	—	—	—	—	—	—	—	22	+ *C. hort.*	G	1550
R (29)–L'Aldosa	—	—	—	—	25	—	—	—	—	—	—	—	—	—	—	—	25	+ *C. hort.*	G	1650
Os																				
R (1)–Xuvall	3	1	—	—	20	1	2	—	—	—	—	—	—	—	—	—	27	+ *C. hort.*	S	975
R (2) —	6	1	—	—	33	1	—	2	2	—	—	—	—	2	—	—	47	+ *C. hort.*	G	1025
R (3)–Vixesarre	2	1	—	—	33	7	1	—	2	3	—	—	—	2	—	—	51	—	G	1100
R (4) —	1	—	—	—	23	1	—	—	—	—	—	—	—	7	—	—	32	—	G	1125
R (5) —	—	—	—	—	34	2	—	—	—	2	—	—	—	2	—	—	40	—	G	1300
R (6)–Os	—	—	—	—	19	4	—	—	—	—	—	—	—	3	—	—	26	+ *C. hort.*	G	1500
R (7) —	18	—	—	—	23	—	—	—	—	1	—	—	—	—	—	—	42	—	G	1550
R (8) —	2	—	—	—	25	13	1	—	—	4	—	—	—	—	—	—	45	—	G	1650
R (9) —	—	1	—	—	39	12	—	—	—	3	—	—	—	—	—	—	55	—	RH	1825
R (10)–Coma de Seturía	4	—	—	—	5	—	—	—	1	—	—	—	—	—	—	—	10	1 hyal.	G	1890

Table 4 (*cont.*)

locality	yellow								pink								total	remarks	habitat and altitude (m)
	0		3		5		E.U.5		0		3		5		E.U.5				
	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.	wh.l.	d.l.			
Saleria																			
R (1) —	1	1	—	—	5	5	—	—	—	—	—	—	—	—	—	—	12	+*C. hort.*	G 1620
R (2) —	18	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	20	+*C. hort.*	G 1680
R (3) —	27	—	—	—	13	—	—	—	—	3	—	—	—	—	—	—	43	+*C. hort.*	G 1800
Valira del Norte																			
R (1)–Pont Pla	8	1	—	—	7	4	2	1	1	2	—	—	—	—	—	—	26	+*C. hort.*	RH 1125
R (2)–Tunnel	35	25	—	—	12	5	6	5	1	1	—	—	—	—	—	—	90	+*C. hort.*	MDW 1150
R (3)–Tunnel	3	2	—	—	26	11	3	5	—	2	—	—	—	1	—	—	53	+*C. hort.*	H 1150
R (4)–La Massana	3	—	—	—	21	17	—	2	1	3	—	—	—	—	—	—	47	+*C. hort.*	MDW 1200
R (5)–Ordino	1	1	—	—	29	11	2	—	1	1	—	—	2	2	—	—	50	+*C. hort.*	G 1225
R (6)–Ansalonga	3	—	—	—	33	23	—	—	4	—	—	—	—	—	—	—	63	+*C. hort.*	H 1300
R (7)–Llorts	3	—	—	—	32	4	1	—	—	2	—	—	—	—	—	—	42	+*C. hort.*	G 1400
R (8)–Llorts	4	—	—	—	47	—	—	—	—	—	—	—	—	—	—	—	51	+*C. hort.*	G 1525
R (9)–Lo Serrat	3	1	—	—	29	14	1	—	3	2	—	—	1	—	—	—	54	+*C. hort.*	G 1550
R (10)–Lo Serrat	13	2	—	—	11	2	—	—	1	2	—	—	—	—	—	—	31	+*C. hort.*	G 1575
R (11)–Rialp	3	1	—	—	1	2	1	1	—	—	—	—	—	1	—	—	10	+*C. hort.*	G 1625
R (12)–Tristany	42	—	—	—	13	—	—	—	1	—	—	—	—	—	—	—	56	—	G 1625
HS (Valira del Norte (12)) —	11	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	16	—	H 1675
Arinsal																			
R (1)–La Massana	6	1	—	—	20	14	3	4	—	—	—	—	—	—	—	—	48	+*C. hort.*	MDW 1300
R (2)–Ercz	5	2	—	—	29	14	4	—	—	1	—	—	—	—	—	—	55	+*C. hort.*	G 1350
R (3)–Arinsal	10	—	—	—	37	8	—	—	1	4	—	—	—	1	—	—	61	—	G 1425
R (4)–Arinsal	29	2	—	—	19	1	—	—	3	18	—	—	—	—	—	—	72	1 hyal. +*C. hort.*	G 1500
HS (Arinsal (4)) —	9	1	—	—	11	8	—	—	1	2	—	—	—	—	—	—	32	1 hyal. +*C. hort.*	G 1700
R (5) —	22	1	—	—	6	1	—	—	5	20	—	—	—	—	—	—	55	3 hyal. +*C. hort.*	G 1550
R (6) —	17	—	—	—	1	—	—	—	8	6	—	—	—	—	—	—	32	+*C. hort.*	CW 1725
Pal																			
R (1) —	5	3	—	—	29	8	11	6	—	1	—	—	—	—	—	—	63	+*C. hort.*	MDW 1500
R (2) —	1	2	—	—	22	5	—	—	—	1	—	—	—	—	—	—	31	+*C. hort.*	G 1550
R (3)–Pal	—	—	—	—	24	19	—	—	—	—	—	—	—	1	—	—	44	+*C. hort.*	G 1575
HS (Pal (3)) —	—	—	—	—	10	8	—	—	—	—	—	—	—	—	—	—	18	—	RH 1750
R (4) —	—	—	—	—	15	6	—	—	—	—	—	—	—	—	—	—	21	—	G 1600
R (5) —	10	1	—	—	38	6	—	—	—	—	—	—	—	—	—	—	55	—	G 1750
Ensagents																			
R (1)–Tremat	3	—	—	—	26	—	11	—	—	—	—	—	—	—	—	—	40	+*C. hort.*	G 1300
R (2) —	5	—	—	—	22	—	10	—	3	—	—	—	—	—	—	—	40	+*C. hort.*	G 1375
R (3) —	19	—	—	—	5	—	5	—	1	—	—	—	—	—	—	—	30	—	G 1650
R (4) —	10	—	—	—	11	—	16	—	—	—	—	—	—	—	—	—	37	—	G 1725
HS (Ensagents (4))–Sant Jaume	13	—	—	—	—	—	3	—	9	—	—	—	—	—	—	—	25	—	G 1800

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FIGURE 18. The Valle de Aran, looking west-north-west down river. The valley of the Garona de Ruda is in the foreground, and continues as the main valley of the Garonne towards the left of the picture. The main valley is partly obscured by the shoulder of the eastern side of the Valarties valley on the left. The entrance to the Aiguamoch valley is at left centre (closely resembling it is the entrance to the Valarties valley, out of sight in this picture). On the right, starting at the bottom, are Aran Hill, the Malo valley entrance (partly obscured), Peyra Blanca hillside at far right centre, and the entrance to the Iñola valley to the right of the first village.

FIGURE 19. The entrance to the Valarties valley at 16.20 h, Central European Time, on 24 September 1966, looking southwards from the Garonne valley. Garonne populations are in sunshine, but the western side of the Valarties valley casts a shadow over populations by the Valarties river. In the distance is Pico de Montarto, around which the valley bifurcates.