The Spatial and Temporal Distribution of Phenotypes in a Colony of Cepaea nemoralis (L.)

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STUDIES ON *CEPAEA*

VI. THE SPATIAL AND TEMPORAL DISTRIBUTION OF PHENOTYPES IN A COLONY OF *CEPAEA NEMORALIS* (L.)

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(With an appendix by C. Diver)

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CONTENTS

In 1924 one of us (C.D.), with the late Professor A. E. Boycott, F.R.S., collected random samples from populations of the polymorphic land snail *Cepaea nemoralis* L. on sand-dunes at Bundoran, County Donegal, Eire. In 1961, the other two revisited the area and sampled, as nearly as possible, the same localities.

A total of 23857 live snails were collected and scored for various inherited shell characters. The data are considered from three points of view. First we have examined the distribution of morphs within individual samples, hoping to detect associations indicating linkage or selection. Secondly, we have studied the differences between contemporary samples and attempted to relate them to environmental factors. Thirdly, we have compared the two series (1924 and 1961) in order to detect any evolutionary changes that might have occurred.

(1) *Associations within samples*

In both series there are consistent linkage disequilibria involving the loci for shell-colour, for banded *v.* unbanded shell, for hyalozonate *v.* fully pigmented bands, and for white *v.* black lip. It is likely that these disequilibria are maintained by selection. There is also a suggestion of disequilibrium between the shell-colour locus and the loci determining the extent of band-fusions. We find no significant differences between adults and young in the proportions of any of the morphs.

(2) *Variation between samples*

Most of the characters show morph-ratio clines on an east/west axis. This pattern may be related to the fact that the western part of the area is predominantly mobile or semi-mobile dune, whereas the eastern part is generally more stable.

The overall proportions of yellow and 'effectively unbanded' shells very roughly correspond to those found by Cain & Sheppard (1954) in hedgerows and rough herbage. They occupy the range of frequencies expected according to the hypothesis of visual selection by predators. Nevertheless, their precise distributions within the area are not evidently related to local changes of background, nor are the distribution of unbandeds (*sensu stricto*), hyalozonates, whites, white lips or fusions. There may possibly be come correspondence in the case of browns, 00300 and 00345, and it is conceivable that the local distribution of pinks is the result of visual selection by rabbits. A final interpretation must await further detailed studies of other sand-dune populations.

(3) *Comparison of the two series*

A comparison of the series collected in 1924 with that collected in 1961 provides no evidence of consistent evolutionary change. There may have been small local changes, which in our data would be indistinguishable from differences due to errors in relocating the sampling areas; but in general the populations seem to have remained stable. There have certainly been no changes comparable to those observed at Berrow, Somerset (Clarke & Murray 1962*a*). This apparent constancy may be related to the fact that the habitat at Bundoran has not greatly altered since 1924. At Berrow, on the other hand, the dunes have gradually become more stable, and larger parts of them have become overgrown with *Hippophae*. In each case the evolutionary situation seems to reflect the history of the habitat. It will clearly be of great interest to follow future developments at both localities.

INTRODUCTION

During the past few decades, several long-term studies of individual animal populations have provided valuable information about the role of natural selection in microevolutionary change. Notable among them have been the classic investigations of Gershenson (1945) on *Cricetus cricetus* L., of Fisher & Ford (1947) and Sheppard (1951, 1956) on *Panaxia dominula* L., of Dobzhansky (1947, 1958) on *Drosophila pseudoobscura* Frolova and of Kettlewell (1958, 1961) on *Biston betularia* L.

In earlier publications we have reported studies on microevolutionary changes in populations of the polymorphic land snail *Cepaea nemoralis* (L.) (Clarke & Murray 1962*a*, *b*). The changes were detected by comparing samples taken from particular populations in 1926 with those taken in 1959. They allowed us to estimate the selective values of individual genotypes. The present paper describes a study using similar comparisons. Unlike the earlier work, however, it has revealed a state of apparent evolutionary stability.

In 1924 one of us (C.D.) with the late Professor A. E. Boycott, F.R.S., took forty-four random samples from a series of populations of *C. nemoralis* on the sand-dunes at Bundoran, County Donegal, Eire. Some details of these collections have already been published (Diver 1932, 1939). In 1961 the other two authors revisited the area and sampled, as nearly as possible, the same localities. The two sets of data constitute a detailed survey of the distribution of phenotypes, and they allow us to compare the state of the populations in 1924 with that at the present day. They also provide a basis for future studies on the population genetics of *Cepaea* at Bundoran.

DESCRIPTION OF THE SAMPLING AREA

The collections were taken from an area of sand-dunes which lies a mile to the north-east of Bundoran. The area, about $1\frac{1}{3}$ square miles, is bordered on the south by the Bundoran Ballyshannon road; on the west by Tullan Strand and the sea; on the north by the River Erne; and on the east by fields and the Murvagh Saltings. Finner Camp, an Irish Army Post, occupies the south-east corner (see figure 1).

Within this area there is a primary ridge of dunes facing the sea, and a higher secondary ridge rising to a height of about 200 ft. behind it. Both ridges are made up of mobile and semi-mobile calcareous sand. The dunes are interspersed with extensive areas heavily eroded by wind ('blow-outs'). On the eastern side of the secondary ridge the dunes pass into lower-lying stable rolling grasslands which are bordered on the north by a line of small semi-mobile dunes along the banks of the Erne.

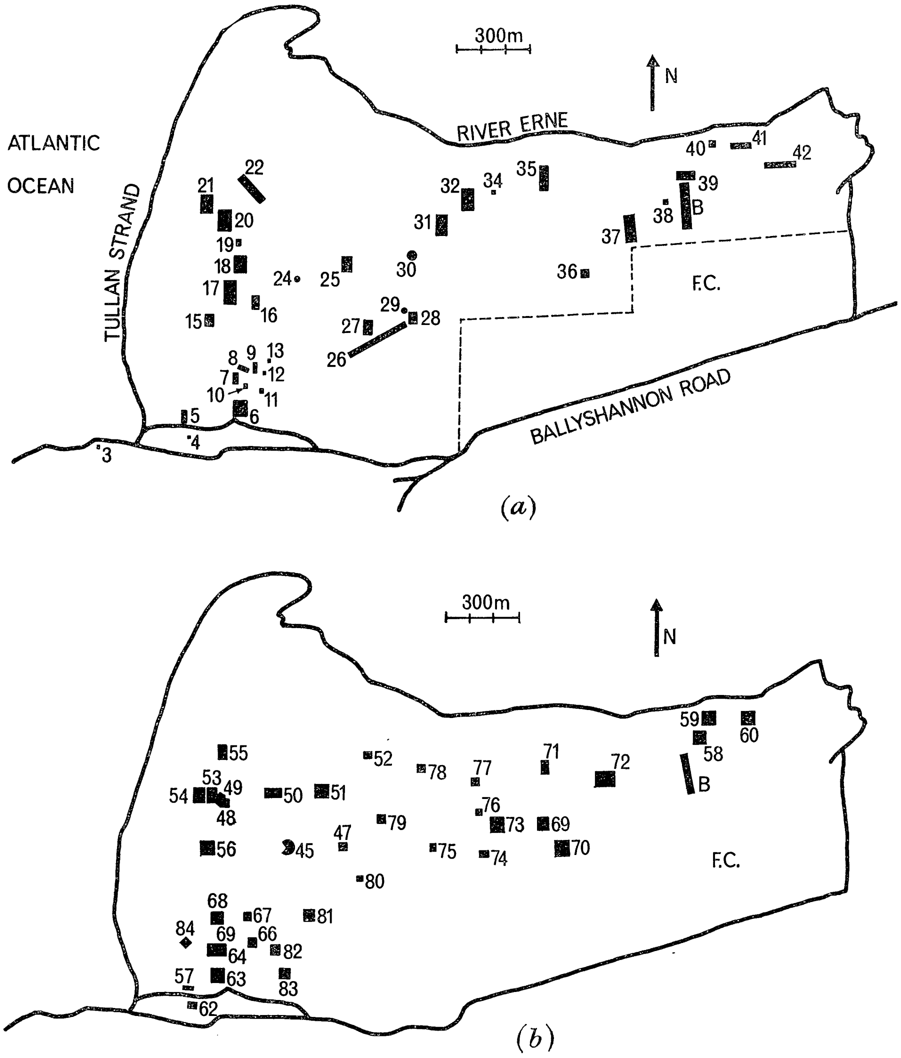


FIGURE 1. The area of study at Bundoran, County Donegal, Eire. The collecting places are marked in black and drawn to scale. (*a*) shows the 1924 localities (numbered 3 to 43), and (*b*) shows the 1961 localities (numbered 45 to 84). The rectangle marked 'B' represents the butts of the rifle range, F.C. marks the centre of Finner Camp.

The pattern of vegetation reflects the development of the dunes. Marram grass (*Ammophila arenaria*) occurs almost everywhere, and in the mobile dunes it provides the only available cover. Landward, as the dunes become more stable, a covering of short turf and moss develops between the marram tufts, and this in turn is often occupied by clumps of bedstraw (*Galium verum*) and ragwort (*Senecio jacobaea*). Various legumes (*Trifolium repens*, *Trifolium campestre*, and others) occur sporadically throughout the area. Three species of plants (*Tussilago farfara*, *Viola tricolor* and a *Euphorbia*) are associated with regions of mobile and semi-mobile dunes. Others (like *Galium verum*, *Rosa pimpinellifolia* and *Salix repens*) are associated with stable regions of short turf. In the centre of the area there are patches of bracken (*Pteridium aquilinum*) indicating places where the ground tends to acidity. Table 1 gives a list of plants and the localities from which they were recorded. Figure 2 shows the distribution (in 1961) of the major types of vegetation in the sampling areas.

TABLE 1. THE SPECIES OF PLANTS RECORDED AT BUNDORAN (IN ORDER OF FREQUENCY)

species	localities at which recorded
Ammophila arenaria (L.) Link	everywhere
Senecio jacobaea L.	24, 25, 37, 42, 52, 53, 54, 55, 56, 59, 60, 61, 63, 64, 70, 71, 72, 74, 75, 81, 82, 83, 84
Trifolium repens L. *T. campestre* Schreber	7, 9, 18, 25, 38, 49, 53, 54, 61, 62, 63, 64, 67, 75, 76, 79, 80, 81, 82, 83, 84
Galium verum L.	47, 54, 61, 62, 63, 64, 66, 67, 70, 71, 72, 74, 75, 76, 78, 79, 80, 81, 83, 84
Euphorbia sp. (?*E. portlandica* L.)	20, 48, 49, 50, 53, 54, 84
Pteridium aquilinum (L.) Kuhn	36, 38, 71, 72, 75, 76, 78
Tussilago farfara L.	5, 20, 24, 40, 41, 45, 51
Cirsium sp. (?*C. arvense* (L.) Scop)	25, 41, 55, 56, 59, 60
Rosa pimpinellifolia L.	31, 70, 71, 72, 79, 80
Viola tricolor L.	25, 47, 49, 53, 54, 55
Plantago lanceolata L.	61, 63, 75, 82, 84
Centaurium erythraea Rafn.	55, 70, 76
Salix repens L.	37, 69, 73
Polygala sp.	49, 69
Prunella vulgaris L.	78, 79
Thymus drucei Ronn.	47, 73
Achillea millefolium L.	75
Anagallis arvensis L.	77
Iris pseudacorus L.	59
Primula veris L.	74
Stellaria graminea L.	74

The names are those given by Clapham, Tutin & Warburg (1962). Grasses, apart from *Ammophila*, were not recorded.

Cepaea nemoralis is extremely common almost everywhere except on the western side of the primary ridge. Some of the blow-outs have accumulated large numbers of empty shells. One was estimated to contain more than a million shells in 1924.

In addition to *C. nemoralis*, the molluscan fauna includes *Agriolimax agrestis* (L.), *Cochlicella acuta* (Müll.), *Cochlicopa lubrica* (Müll.), *Helicella itala* (L.), *Helix aspersa* (Müll.), *Hygromia hispida* (L.), *Hygromia striolata* (Pfeiffer), and *Pupilla muscorum* (L.). None of them is very common.

The evidence of broken shells shows that *C. nemoralis* is attacked by small mammals and birds, predominantly by the former. Rabbits are common, particularly in the region of stable grassland, where the turf is kept short by their activities. Song-thrushes (*Turdus ericetorum* Turton) are also seen, but much more rarely. Thrush-stones were found only near the southern margin of the area.

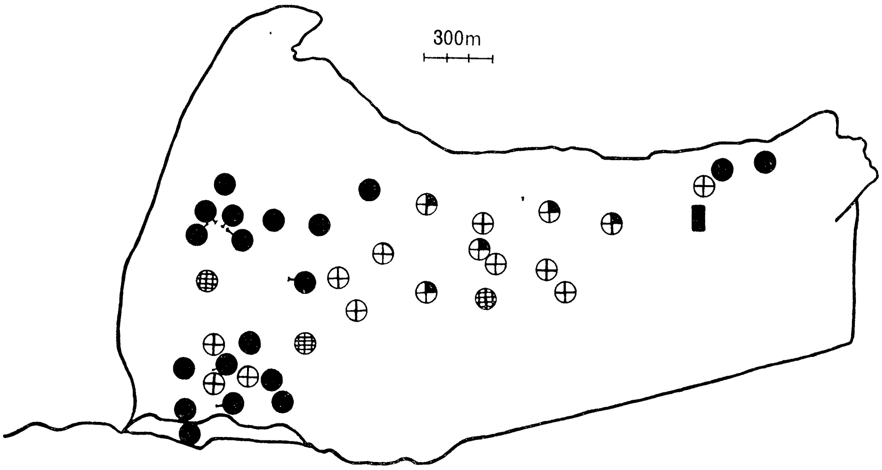


FIGURE 2. Bundoran: the predominant vegetation at the collecting places in 1961. Black circles represent places at which marram (*Ammophila arenaria*) predominates (in regions of mobile or semi-mobile dunes). Hatched circles represent places where other long grasses predominate. Crossed circles represent areas of short turf. Crossed circles with black quadrants represent areas of short turf with clumps of bracken (*Pteridium aquilinum*). The black rectangle shows the position of the butts.

METHODS

(i) *Mapping*

Figures 1 (*a*) and (*b*) are sketch maps of the area drawn to scale from the Irish Ordnance Survey map (25 in./mile). Collecting places are marked in black and are drawn to scale. Figure 1 (*a*) shows the 1924 localities (numbered 3 to 43), and figure 1 (*b*) shows the 1961 localities (numbered 45 to 84).

In 1924 the collecting sites were not pin-pointed on a map, but indicated in relation to recognizable features, since a return visit at an earlier date was expected. A gap of 37 years in a dune area on the Atlantic Coast makes the exact location of the earlier sites virtually impossible. The positions given on figure 1 (*a*) are therefore subject to various errors, whose magnitudes depend upon the topography and upon the precision of individual descriptions. Table 2 gives estimates of the maximum errors (on the east/west and north/south axes) for each locality.

In 1961 the collecting places were fixed by triangulation with a prismatic compass and plotted on the 25 in. map. All the locations given on figure 1 (*b*) have a maximum error of ±15 m on each axis.

The sizes of the collecting areas on the map are accurate to ±3 m in each direction, except for localities 10–13, 15, 82 and 84 which are accurate to ±15 m, and locality 26 which is accurate to ±50 m in length and ±10 m in width.

(ii) *Sampling*

In 1924 random samples of living *C. nemoralis* were taken from thirty-seven localities in the study area, and from four localities (1, 2, 43 and 44) outside it. In 1961, samples were taken from thirty-eight localities in the area. Four further samples (23, 33, 46 and 61) contained only dead shells. During sampling, each area was searched carefully to avoid taking too high a proportion of snails that were obvious to the eye.

(iii) *Scoring of samples*

The snails were scored for age (mature or immature), condition, colour and banding according to the criteria given by Taylor (1907–14), Cain & Sheppard (1950, 1954) and Clarke (1960). The collections from Bundoran are remarkable in showing high frequencies of forms that are rare or absent elsewhere. Notable among them are *whites* (W), in which the ostracum (the ground-material of the shell) totally lacks pigment. The whites are usually banded, but the bands are always unpigmented. Forms with unpigmented bands (known as *hyalozonates* (hy)) are also common at Bundoran among shells with a pink or brown ground-colour. *White-lipped shells*, in which the peristome is unpigmented, are found not only among whites (which are invariably white-lipped) but also among yellows, pinks and browns. In yellows and pinks they occur most frequently among banded forms. The lip-colours of the 1924 series were originally divided into four categories: *white-lips*, *self-lips* (in which the ground-colour of the shell extends into the peristome), *pale-lips*, (in which the pigment of the peristome is diluted, a condition associated with paleness of the bands on the shell), and *black-lips* (in which the peristome is fully pigmented). In the 1961 series, only white-lips were distinguished (see below).

Table 2. Estimates of maximum errors in locating the collections of 1924

localities	error (± metres)	
	east/west	north/south
4, 24, 25, 39	25	25
5, 20, 21	50	50
6–18, 19, 22, 37, 38, 40–42	100	50
27, 30, 31	200	100
26, 28, 29, 32–36	300	150

Pale browns (Clarke & Murray 1962*a*) are common, but the great majority (if not all) of them are banded. The *dark browns* are generally quite distinct, although variable in tone. They appear unbanded, but often show faint traces of bands ('ghost bands') which are not recorded here. Ghost bands are seen more rarely on yellow and pink unbanded shells.

A few samples contain unbanded shells that might be classified as pale browns. A few others contain banded shells that are doubtfully dark browns. Such forms are very uncommon, and nowhere are they clearly distinct. For this reason we have included all unbanded browns in the 'dark' category, and all banded ones in the 'pale' (grouped with pink banded, see below).

The 1924 series was first scored by C.D. and the late Professor A. E. Boycott, F.R.S., each checking the other's scores. The 1961 series was similarly treated by B.C. and J.M. Afterwards, B.C. rescored most of the 1924 series. Apart from the exceptions mentioned below, differences were slight. There was none in the scoring of 00000, 00300, and dark browns, In a few samples some of the hyalozonate shells showed very faint traces of colour, and it was difficult to decide if they were pink, brown, yellow or white. Such shells, however, were rare, and in no case could the uncertainty give rise to an error of more than 2 % of the number of snails scored. There were also a few pale unbanded shells whose colours were uncertainly yellow or white. Two samples (1, 43) contained 2 % of these shells. All the rest contained 0·5 % or less.

The scoring of banded shells presented some problems. In general, the yellows were quite distinct, but the pale brown and pink bandeds were often extremely difficult to separate, the colours tending to grade into one another. The separation was undertaken in 1924, but in 1961 we found it impossible to get consistent scores. For the present analysis we have grouped the two forms into one category.

There were also difficulties in the scoring of 00345 and 10345 (as distinct from 12345). These were due to the occurrence, in many shells, of very faint traces of the first and second bands on the upper whorls when these bands were absent on the lower ones. The frequencies of 00345 and 10345 have not been analysed in detail.

In 1924, band-fusions were not scored. Later, however, B.C. re-examined the 1924 collections and recorded the frequency of fusions in fifteen samples selected to give a general coverage of the area.

As we have mentioned, the lip-colours of the 1924 series were divided into four categories. This division was attempted for the 1961 series, but it was soon abandoned. We could not be sure that the categories were being demarcated at the same levels of pigmentation, and it was impossible to check the shells against the 1924 series because the lips of the latter had faded to some extent during the intervening period. For this reason each sample in the 1961 series has been divided into two groups (white-lips and others) at the point of maximum tonal discontinuity. Scores of lip-colour *within* series can be regarded as consistent, but comparisons *between* series cannot accurately be made.

RESULTS

Table 3 records the phenotypes of 23026 live adult snails collected at Bundoran (16307 collected in 1924, 6719 in 1961). Table 4 gives the phenotypes of 831 live young (468 collected in 1924, 363 in 1961). Empty shells are not recorded because of the difficulty of distinguishing recent dead from subfossil material. In table 3, the classification of phenotypes (vertical columns) is straightforward except that the column headed 00345* includes the rare forms 00005 and 00045 as well as 00345. The column headed 'F in 12345' gives the number of 12345 shells that have two or more bands fused together. The figures in brackets represent the numbers of white-lipped shells in each class. In table 4 the column headed 12345* includes 00005, 00045, 00345, 10345, 12045, 10305, and 10045 as well as 12345. It is frequently impossible to separate these forms among young shells. In neither table are pale or interrupted bands distinguished from the normal full bands.

Figures 3 to 12 show the distribution of various phenotypes in the two series of samples. On each figure the upper diagram refers to the 1924 series and the lower to the 1961 series. Each locality is represented by a circle in which the black segment gives the percentage of the phenotype. The scale is 8 degrees to 1% except in figure 6 where it is 6 degrees and figure 10 where it is 5 degrees.

Figure 3 shows the percentages of yellow unbanded (Y00000) shells. In both series of samples this phenotype appears to be concentrated in the north central and western parts of the area.

Figure 4 gives the percentage of yellow banded shells. This category includes all forms of banding (e.g. 12345, 10345, 00345, 00300, etc.). Yellow bandeds are most frequent

TABLE 3. THE COMPOSITION OF SAMPLES OF ADULT *CEPAEA NEMORALIS* COLLECTED AT BUNDORAN, EIRE

The 00345* column includes the number of 00045 and 00005 as well as 00345.
The figures in brackets represent the numbers of white-lipped shells in each class.

		white			yellow						pink and pale brown										
locality	collectors and dates	00000	hy 10345	hy 12345	00000	00300	00345*	10345	12345	00000 pink	00300	00345*	10345	12345	hy 10345	hy 12345	00000 dark brown	F in 12345	unusual banding types	total	comments
1	BD, 13. ix. 24	2 (1)	—	—	14	11	—	—	21 (1)	14	10	—	—	34	—	2	—	NS	—	107 (2)	heavy fusions. North-facing grass bank at top of cliffs to west of area
2	BD, 13. ix. 24	—	—	—	—	2	1	—	9 (2)	1	5	—	—	16	—	—	—	NS	—	34 (2)	as above, but more herbs
3	BD, 14. ix. 24	—	—	—	2	—	—	—	5	—	—	—	—	4	—	—	1	NS	—	12 (0)	cliff face—see figure 1*a*
4	BD, 13. ix. 24	—	—	—	3	—	—	—	12	10	—	1	—	15	—	4	6	13	—	51 (0)	apex of most southerly sand-dune
5	BD, 14. ix. 24	—	—	7 (7)	18	—	—	—	36 (1)	4	—	—	2	51 (4)	—	1	59	27	1-Y 02345 Wl	179 (13)	—
6	BD, 14. ix. 24	—	—	8 (8)	12	—	—	6	64 (5)	8	—	—	6 (1)	100 (5)	—	9	27	NS	1-Y 7-banded Wl	241 (20)	—
6*a*	BD, 14. ix. 24	—	—	1 (1)	4	—	—	1	5 (1)	—	—	—	—	14	—	2	1	NS	—	28 (2)	—
7	BD, 14. ix. 24	—	1 (1)	24 (24)	28	—	—	16	129 (11)	32	—	—	27	270 (19)	—	21	109	63	1-Y 12045	658 (55)	Some W.hy are ? B.hy
8	BD, 14. ix. 24	—	—	2 (2)	3	—	—	—	13	2	—	—	1	19 (2)	—	3	11	NS	1-P/B 12045	55 (4)	fusions present
9	BD, 14. ix. 24	1 (1)	—	3 (3)	8	—	—	5	56 (5)	5	—	—	9	152 (10)	—	20	70 (4)	NS	1-P/B 12045	330 (23)	fusions present
10	BD, 14. ix. 24	—	—	6 (6)	7	—	—	2	33 (3)	2	—	—	5	60 (5)	—	3	26 (1)	19	1-Y 12045	145 (15)	—
11	BD, 14. ix. 24	1 (1)	—	12 (12)	49	—	1	7 (1)	130 (23)	16	—	—	27 (1)	181 (16)	2	20 (1)	88 (1)	53	1-Y12045	535 (56)	—
12	BD, 14. ix. 24	—	—	—	3	—	—	2	24 (2)	8	—	—	5	57 (3)	1	4	35	NS	—	139 (5)	some fusions
13	BD, 14. ix. 24	—	—	—	3	—	—	1	10 (2)	4	—	—	1	24 (1)	—	2	16	NS	—	61 (3)	some fusions
15	BD, 14. ix. 24	—	2 (2)	3 (3)	31	—	1	53 (3)	165 (11)	9	—	1	42 (2)	181 (18)	—	1	65 (4)	20	1-Y 12045, 1-P/B 12045	556 (43)	—
16	BD, 18. ix. 24	4 (4)	—	3 (3)	31	—	—	31 (1)	271 (23)	8	—	—	30 (2)	238 (22)	—	1	116 (4)	NS	2-P/B12045	735 (59)	—
17	BD, 18. ix. 24	—	1 (1)	4 (4)	39	—	—	66 (3)	287 (28)	13	—	—	86 (2)	312 (23)	1	—	154 (3)	NS	1-P/B02045	964 (64)	fusions present
18	BD, 18. ix. 24	—	1 (1)	13 (13)	367	—	—	9 (1)	136 (5)	24	—	1	—	73 (2)	—	8	106	29	—	738 (22)	—
	BD, 18. ix. 24 (2nd Coll.)	—	1 (1)	8 (8)	349	—	—	4	89 (5)	21	—	—	1	91 (6)	—	8	88	25	2-P/B12045	662 (20)	—
19	BD, 18. ix. 24	—	—	3 (3)	—	—	—	—	4	—	—	—	—	31	—	36	34	NS	—	108 (3)	—

TABLE 3 (*cont.*)

locality	collectors and date	white			yellow					00000 pink	pink and pale brown						00000 dark brown	F in 12345	unusual banding types	total	comments
		00000	hy 10345	hy 12345	00000	00300	00345*	10345	12345		00300	00345*	10345	12345	hy 10345	hy 12345					
20	BD, 18. ix. 24	—	10 (10)	35 (35)	4	—	—	3	92	—	—	—	6	136 (3)	—	8	77	4	2-Y12045, 2-P/B12045	375 (48)	—
21	BD, 18. ix. 24	2 (2)	14 (14)	45 (45)	2	—	—	4 (1)	23 (3)	—	—	1 (1)	31 (7)	86 (33)	18	39 (1)	198 (1)	NS	1-W.hy 10305 Wl	464 (109)	fusions rare
22	BD, 18. ix. 24	—	—	18 (18)	48	—	—	1 (1)	133 (17)	8	—	3	6 (1)	112 (25)	—	—	127	NS	1-P/B12045, 1-P/B123X45 Wl	458 (63)	fusions present. Some W.hy are ? B.hy
24	BD, 17. ix. 24	—	—	2 (2)	4	—	—	—	46 (2)	19	—	—	3	520 (3)	—	5	107	328	2-Y12045, 1-P/B10045	709 (7)	by flag-pole on top of main secondary ridge
25	BD, 17. ix. 24	—	—	8 (8)	10	—	—	2	83 (8)	11	—	—	11	551 (8)	—	4 (1)	102	323	1-Y6-banded, 4-P/B12045 1-P/B02000	788 (25)	200 yards E. of 24. some W.hy are B.hy?
26	BD, 17. ix. 24	2 (2)	1 (1)	5 (5)	67	—	—	7	108 (8)	37	—	—	13	271 (12)	—	7 (1)	108 (3)	NS	1-Y12045, 1-P/B12045	628 (32)	some fusion. 3B00000 very pale and ? white.
27	BD, 17 ix. 24	—	—	8 (8)	40	—	—	21	129 (10)	32	—	—	34	354 (15)	—	3	54	NS	1-Y12045Wl, 2-P/B12045 1-P/B10045, 1-P/B10305 1-P/B 9-banded (sic)	681 (34)	some W.hy are ? pigmented
28	BD, 15. ix. 24 (E. side)	—	2 (2)	15 (15)	51	1	—	17	108	37	5	—	33	385 (2)	3	13	232	NS	1-Y12045, 1-Y6-banded	904 (20)	some W.hy are ? pigmented. Pale brown/pink/yellow banded are
	BD, 15. ix. 24 (W. side)	2 (2)	2 (2)	27 (27)	44	—	—	23	106	39	5	—	68 (2)	470 (5)	—	12 (2)	198	NS	4-P/B12045 (inc. 1. Wl)	1000 (41)	difficult to separate
29	BD, 15. ix. 24	1 (1)	—	3 (3)	1	—	—	1	5	1	—	—	6	22 (1)	—	—	7	9	—	47 (5)	—
30	BD, 15. ix. 24	—	—	2 (2)	13	—	—	—	21	18	4	—	2	81 (3)	—	—	24	NS	—	165 (5)	a good deal of fusion
31	BD, 19. ix. 24	—	—	2 (2)	45	—	—	2	46 (1)	37	3	—	—	123 (2)	—	1	46 (2)	NS	—	305 (7)	—
32	BD, 14. ix. 24	—	—	1 (1)	18	—	—	4	38	27	—	—	4	79 (1)	—	2	24	38	1-P/B12045	198 (2)	—
34	BD, 14. ix. 24	—	—	—	8	—	—	3	63	6	—	—	10	132	—	—	1	NS	1-Y02345	224 (0)	a lot of fusion
35	BD, 19. ix. 24	—	—	—	193	—	—	—	25	183	—	20	5	103	—	1	3	NS	—	533 (0)	a good deal of fusion
36	BD, 19. ix. 24	—	—	—	5	—	—	1	24	19	—	—	1	71	—	—	27	52	—	148 (0)	—
37	BD, 19. ix. 24	—	—	—	24	—	—	4	42	24	—	1	1	122	—	1	1	NS	—	220 (0)	considerable fusion
38	BD, 19. ix. 24	—	—	2 (2)	20	4	—	—	53	41	40	8	—	342 (1)	—	11 (5)	34	NS	2-P/B hy 00300	557 (8)	—
39	BD, 19. ix. 24	—	—	—	24	65	—	—	110	15	87	—	—	281	—	1	14	245	1-P/B hy 00300	598 (0)	—
40	BD, 19. ix. 24	—	—	—	3	3	—	2	8	2	—	—	—	20	—	—	3	NS	—	41 (0)	a little fusion
41	BD, 19. ix. 24	—	—	—	7	3	—	—	38	4	7	—	—	75	—	1	7	NS	—	142 (0)	some fusion
42	BD, 19. ix. 24	—	—	—	40	—	—	8	107	54	1	—	4	306	—	—	20	152	—	540 (0)	—

TABLE 3 (*cont.*)

		white			yellow						pink and pale brown									
locality	collectors and date	00000	hy 10245	hy 12345	00000	00300	00345*	01345	12345	00000 pink	00300	00345*	10345	12345	hy 10345	hy 12345	00000 dark brown	F in 12345	unusual banding types	total	comments
43	BD, 16. ix. 24	1 (1)	—	—	5	—	2	—	35 (10)	2	—	1	—	40 (1)	—	—	1	NS	1-P/B hy 00(345)	88 (12)	a good deal of fusion. A copse on the S. side of the Bundoran-Ballyshannon road $\frac{3}{4}$ m. to the E. of the area (opposite Portnason House). 10 yd. N.S. by 60 yd. E.W.
44	BD, 16. ix. 24	2 (2)	—	4 (4)	31	2	—	3	38	14	2	—	4	43 (1)	—	1	10	NS	1-P/B12045, 1-P/B02345	156 (7)	dunes on N. bank of River Erne. dunes much more stable than in study area. Sample taken over whole area of dune
45	CM, 17. ix. 61	—	—	1 (1)	1	—	—	—	19 (1)	1	—	—	1	118 (1)	—	1	19	83	—	161 (3)	by flagpole on top of main secondary ridge
47	CM, 17. ix. 61	—	1 (1)	9 (9)	7	—	—	28	79 (1)	9	—	—	87	272 (7)	—	5	30 (5)	99 (7)	2-Y12045, 1-Y12305 1-P/B10045	531 (23)	200 yards E. of 45
48	CM, 17. ix. 61	—	—	—	5	—	—	6	6	—	—	—	2	7	—	—	4	—	1-Y12045	31 (0)	—
49	CM, 17. ix. 61	—	—	2 (2)	28	—	—	49	26	4	—	—	30 (1)	25 (2)	2	1	64 (6)	—	1-Y12045	232 (11)	scoring of W1 not reliable in B00000
50	CM, 17. ix. 61	—	—	2 (2)	34	—	—	11	48 (1)	3	—	—	6	26	—	—	53 (4)	12	—	183 (7)	—
51	CM, 17. ix. 61	—	—	2 (2)	1	—	—	—	22	1	—	—	—	42 (1)	—	—	6	34 (1)	—	74 (3)	—
52	CM, 17. ix. 61	—	—	—	18	1	—	1	31	12	4	—	8	92 (3)	—	—	27 (3)	29	—	194 (6)	difficult to score B00000 lips
53	CM, 17. ix. 61	—	3 (3)	10 (10)	31	—	1	32 (1)	51 (1)	3	—	—	31 (5)	90 (9)	2	6	101 (34)	10	—	361 (63)	white lips distinct
54	CM, 17. ix. 61	1 (1)	6 (6)	7 (7)	18	—	—	22 (1)	59 (1)	7	—	—	18 (3)	63 (10)	8	5	82 (28)	6 (1)	2-P/B12045	298 (57)	—
55	CM, 17. ix. 61	1 (1)	7 (7)	7 (7)	10	—	—	34 (4)	27 (4)	2	—	1	37 (9)	65 (18)	11	7	73 (35)	2 (1)	1-Y10305, 1-P/B12045 1-P/B hy 12045	285 (85)	—
56	CM, 17. ix. 61	—	—	1 (1)	59	—	—	26 (1)	75 (3)	27	—	1	33	84 (2)	—	4	47 (8)	17	1-Y02345 W1	358 (16)	—
57	CM, 17. ix. 61	2 (2)	1 (1)	6 (6)	6	—	—	1	21	1	—	—	1	32 (2)	—	5	41 (10)	15 (4)	—	117 (21)	—
58	CM, 18. ix. 61	—	—	—	2	2	—	7	27	4	2	1	4	51	—	—	5	17	—	105 (0)	near 100 yd. mark on rifle range
59	CM, 18. ix. 61	—	—	—	1	1	—	2	14	2	—	—	—	4	—	1	2	4	—	27 (0)	—
60	CM, 18. ix. 61	—	—	—	2	—	—	4	11	9	2	9	5	52	—	1	—	19	—	95 (0)	—
62	CM, 18. ix. 61	—	—	—	2	—	—	—	1	1	—	—	—	6 (2)	—	—	1	2 (1)	—	11 (2)	—
63	CM, 18. ix. 61	—	—	4 (4)	7	—	—	1	30 (1)	7	—	—	7	28 (1)	—	5	27 (6)	10 (2)	—	116 (12)	—
64	CM, 18. ix. 61	—	—	3 (3)	5	—	—	6	36 (1)	3	—	—	5	41 (3)	2	—	26 (11)	13	1-Y12045, 1-P/B12045	129 (18)	—

TABLE 3 (*cont.*)

		white			Yellow						pink and pale brown										
locality	collector and dates	00000	hy 10345	hy 12345	00000	00300	00345*	10345	12345	00000 pink	0030	00345	10345	12345	hy 10345	hy 12345	00000 dark brown	F in 12345	unusual banding types	total	comments
65	CM, 18. ix. 61	1 (1)	—	1 (1)	4	—	—	15	23 (1)	2	—	—	13 (1)	32 (8)	—	—	17 (5)	10 (1)	—	108 (17)	—
66	CM, 18. ix. 61	—	1 (1)	2 (2)	3	—	4	25	63 (5)	6	—	1	62 (6)	107 (8)	2	4	29 (11)	45 (5)	1-Y10045, 1-P/B12045 Wl 1-P/B00305	312 (34)	1-Y12345 is *sinistral*
67	CM, 18. ix. 61	—	—	1 (1)	9	—	—	18	45 (4)	3	—	—	29	87 (4)	1	8	22 (5)	38 (3)	1-Y hy 12345	224 (14)	—
68	CM, 18. ix. 61	1 (1)	—	—	12	—	—	63 (3)	91 (8)	5	—	3	2	119 (4)	—	—	40 (8)	21 (1)	1-Y10045	337 (24)	—
69	CM, 19. ix. 61	—	—	—	12	—	—	17	39	23	1	—	17	101 (1)	—	1	2	38	—	213 (1)	—
70	CM, 19. ix. 61	—	—	—	21	1	1	3	28 (2)	10	2	1	1	82 (1)	—	1	8	31	—	159 (3)	—
71	CM, 19. ix. 61	—	—	—	41	—	1	—	9	74	—	1	3	89	—	2	2	46	—	222 (0)	—
72	CM, 19. ix. 61	—	—	—	4	—	—	—	8	12	—	7	1	47	—	—	9 (1)	24	—	88 (1)	—
73	CM, 19. ix. 61	—	—	1 (1)	5	2	—	8	44	21 (1)	4	—	9	77 (1)	—	1	5	39	1-P/B 10045	178 (3)	—
74	CM, 19. ix. 61	—	—	—	1	—	—	—	16	5	1	—	4	67	—	—	7	35	—	101 (0)	—
75	CM, 19. ix. 61	—	—	—	4	—	—	4	17	20	5	—	3	52	—	—	34 (3)	25	—	139 (3)	—
76	CM, 19. ix. 61	—	—	—	9	6	—	4	23	24	24	—	9	87	1	3	4	27	—	194 (0)	—
77	CM, 19. ix. 61	—	—	—	14	1	—	5	23	6	3	—	6	91	—	—	—	37	—	149 (0)	—
78	CM, 19. ix. 61	—	—	—	15	—	—	14	23	20	—	—	7	71	—	2	16 (4)	42	—	168 (4)	scoring of colour difficult
79	CM, 19. ix. 61	—	—	—	4	—	—	2	30	6	4	—	9	67 (1)	—	—	18 (3)	42	—	140 (4)	scoring of colour very difficult
80	CM, 19. ix. 61	—	—	1 (1)	6	—	—	4	23	9	1	—	6	73	—	2	40 (7)	31	—	165 (8)	—
81	CM, 19. ix. 61	—	—	—	5	—	—	6	23	7	—	—	9	74 (4)	1	1	26 (7)	19 (1)	1-P/B12045	153 (11)	—
82	CM, 19. ix. 61	—	—	3 (3)	7	—	—	1	18	2	—	—	1	39 (2)	—	6	25 (6)	16 (1)	—	102 (11)	—
83	CM, 19. ix. 61	—	—	—	2	—	—	6	26	3	—	—	6	23	1	2	18 (4)	7	1-Y10045	88 (4)	—
84	CM, 19. ix. 61	1 (1)	2 (2)	7 (7)	5	—	—	7	38 (1)	2	—	—	8	60 (9)	—	1	40 (12)	18	—	171 (32)	—
	grand totals	24 (24)	56 (56)	344 (344)	2098 —	105 —	12 —	741 (21)	4173 (222)	1167 (1)	222 —	62 (1)	964 (43)	9191 (357)	56 —	330 (11)	3407 (249)	963 (29)	74 (8)	23026 (1337)	

Abbreviations: B = brown, BD = Boycott & Diver, CM = Clarke & Murray, F = band-fusions. hy = hyalozonate, NS = not scored, P = pink, P/B = pink or pale brown W = white, Wl = white lip, X = additional band, Y = yellow.

along the western seaward margin of the dunes, but there is also a small concentration at the north-east corner. Very roughly, the regions of high frequency correspond to areas of more mobile dunes.

The data shown on figures 3 and 4 can be combined to give the total frequency of yellow shells at each locality. The highest values are found along the northern and western edges of the area. 'Inland' colonies tend to have lower percentages of yellows.

TABLE 4. THE COMPOSITION OF SAMPLES OF YOUNG *CEPAEA NEMORALIS* COLLECTED AT BUNDORAN, EIRE

The 12345* column includes all forms of banding except 00300.
Samples of less than 10 shells are excluded

	whites		yellows				pinks and pale browns				
locality	00000	12345*	00000	00300	12345*	00000 pink	00300	12345*	hy 12345*	00000 dark brown	total
5	—	4	7	—	20	3	—	16	3	23	76
6	—	1	—	—	4	—	—	2	2	1	10
15	—	—	1	—	8	1	—	7	—	1	18
18	—	1	9	—	2	—	—	1	2	4	19
25	—	—	1	—	2	1	—	4	—	2	10
27	—	—	1	—	2	1	—	7	2	1	14
29	—	—	—	—	4	1	—	4	—	2	11
30	—	1	8	—	14	9	2	31	—	12	77
36	—	—	11	1	16	21	—	61	1	25	136
37	—	—	1	—	5	—	—	8	—	—	14
43	6	—	6	—	40	2	—	28	1	—	83
45	—	—	—	—	4	—	—	29	—	5	38
47	—	1	—	—	5	—	—	5	—	2	13
50	—	2	1	—	9	—	—	5	—	4	21
51	—	5	—	—	9	1	—	14	—	1	30
57	—	1	1	—	7	1	—	8	2	4	24
60	—	—	—	—	3	1	—	7	—	—	11
62	—	—	2	—	6	1	—	3	—	1	13
65	—	1	—	—	9	—	—	12	—	4	26
69	—	—	3	—	14	6	—	51	1	—	75
70	—	—	3	1	7	4	—	17	—	2	34
71	—	—	6	—	—	7	—	11	—	—	24
73	—	—	3	—	5	2	2	13	—	—	25
76	—	—	—	1	1	—	2	7	—	—	11
84	—	2	2	—	1	1	—	9	1	2	18
	6	19	66	3	197	63	6	360	15	96	831

Figure 5 shows the percentages of pink unbanded (P 00000) shells. Both series agree in showing a concentration of this phenotype in the central region of stable grassland. The pinks of the central and eastern regions tend to be deeper in colour than those of the west.

Figure 6 gives the combined percentages of pink banded and pale brown banded shells. They have a fairly uniform distribution, but are generally higher in the central and eastern parts, and lower in the west. The scoring carried out in 1924, when an attempt was made to distinguish pink and pale brown forms, gives us some idea of how the two individual varieties are themselves distributed. Although many samples are likely to be subject to errors in scoring, the pink banded forms seem to be concentrated in the east, whereas the pale browns seem to reach their highest frequencies in the west. This is also true of unbanded forms (see figures 5 and 7).

Figure 7 shows the percentages of dark brown unbanded (DB 00000) shells. In both series there is evidence of a cline from west to east, the highest frequencies being found on the mobile and semi-mobile dunes of the north-west and south-west corners.

Figure 8 gives the percentages of white (W) shells. Almost all of them are banded, hyalozonate, and white-lipped. Their distribution roughly corresponds to that of the browns, but the frequencies are much lower.

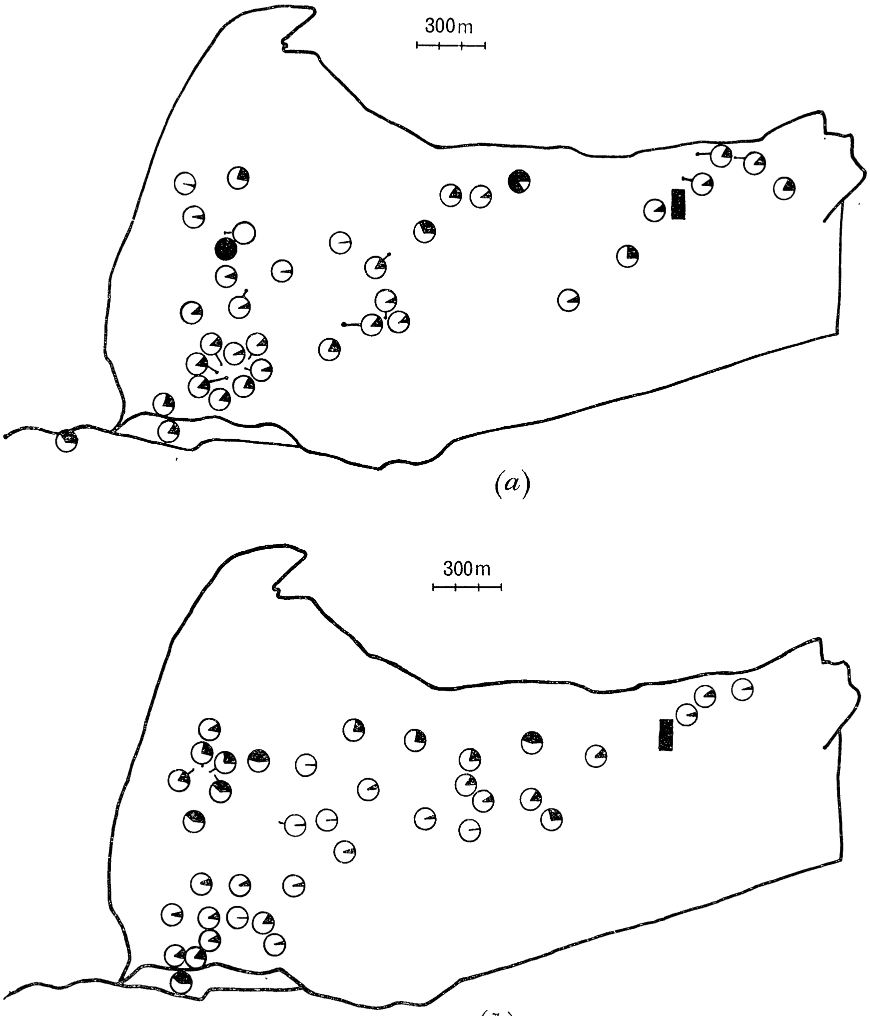
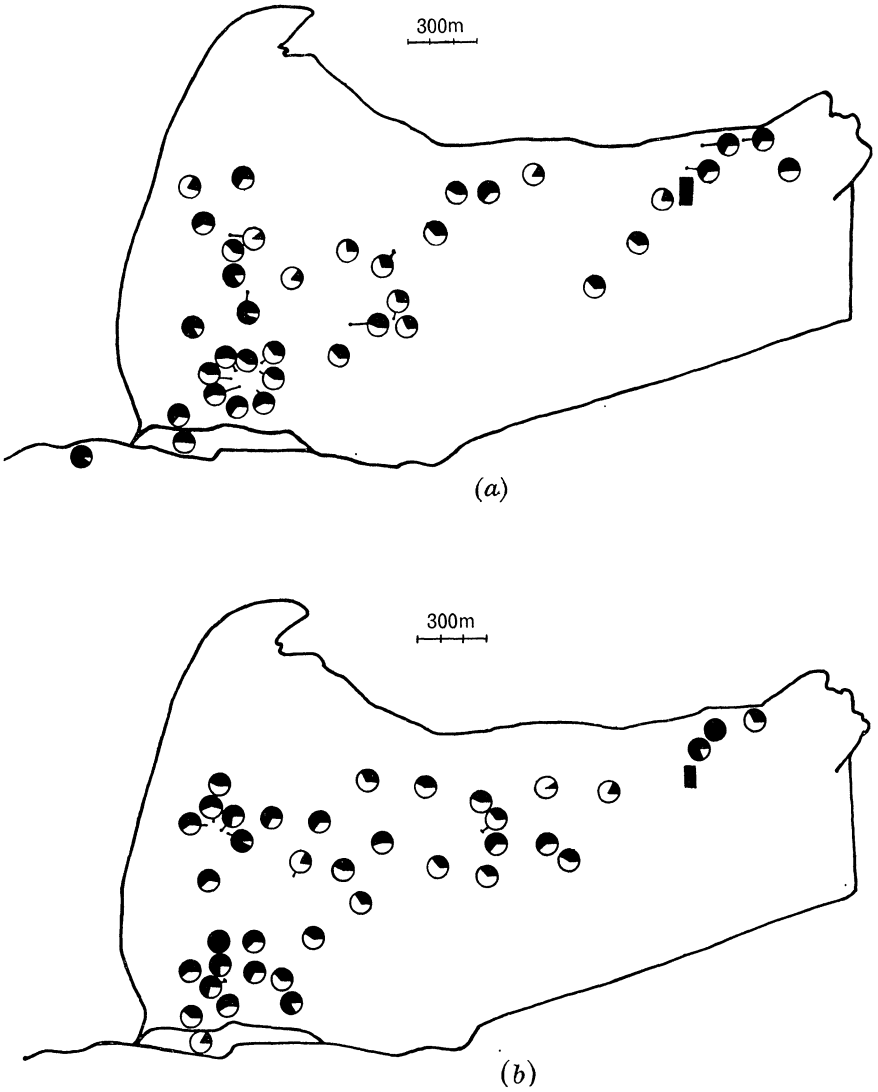


FIGURE 3. (*a*) The percentages of yellow unbanded shells at Bundoran in 1924. (*b*) the percentages in 1961. Eight degrees of arc represent 1%.

On figure 9 are recorded the percentages of hyalozonate (hy) shells other than whites. They are all either pink or pale brown. Their distribution also roughly corresponds to that of the browns.

Figure 10 shows the proportions of five-banded (12345) shells with two or more bands fused together. The frequency at each locality is expressed as a percentage of the total number of five-banded shells. The upper figure shows the percentages in those samples of the 1924 series which were scored for fusions. The data are sufficient to indicate that the distribution is approximately the same in the two series. Band-fusions are concentrated in a belt stretching north-east and south-west from the north central region, corresponding roughly to the area of the stable grassland (and of high P 00000).

Figure 11 gives the distribution of single-banded (00300) shells. Because the gene for the unbanded condition is known to be epistatic to the gene for 00300 (Lamotte 1954; Cain & Sheppard 1957; Cain, King & Sheppard 1960) the frequency of this form is expressed



(*a*)

(*b*)

FIGURE 4. (*a*) The percentages of yellow banded shells at Bundoran in 1914. (*b*) the percentages in 1961. Eight degrees of arc represent 1%.

as a percentage of the total number of banded shells at each locality. The figure shows that 00300 is most frequent in the central and eastern regions, and totally absent from the seaward margin of the dunes. 00345 is similarly distributed, except that there are a very few examples of this phenotype in the western part of the area. The western records may be due to mistakes in scoring (see above).

Finally, figure 12 shows the percentage of white-lipped (Wl) shells. As with dark browns whites and hyalozonates, there is a morph-ratio cline of decreasing frequency from west to east. This is not merely due to the fact that both whites and hyalozonates tend to have white lips, since the same distribution is found among shells which are neither white nor hyalozonate.

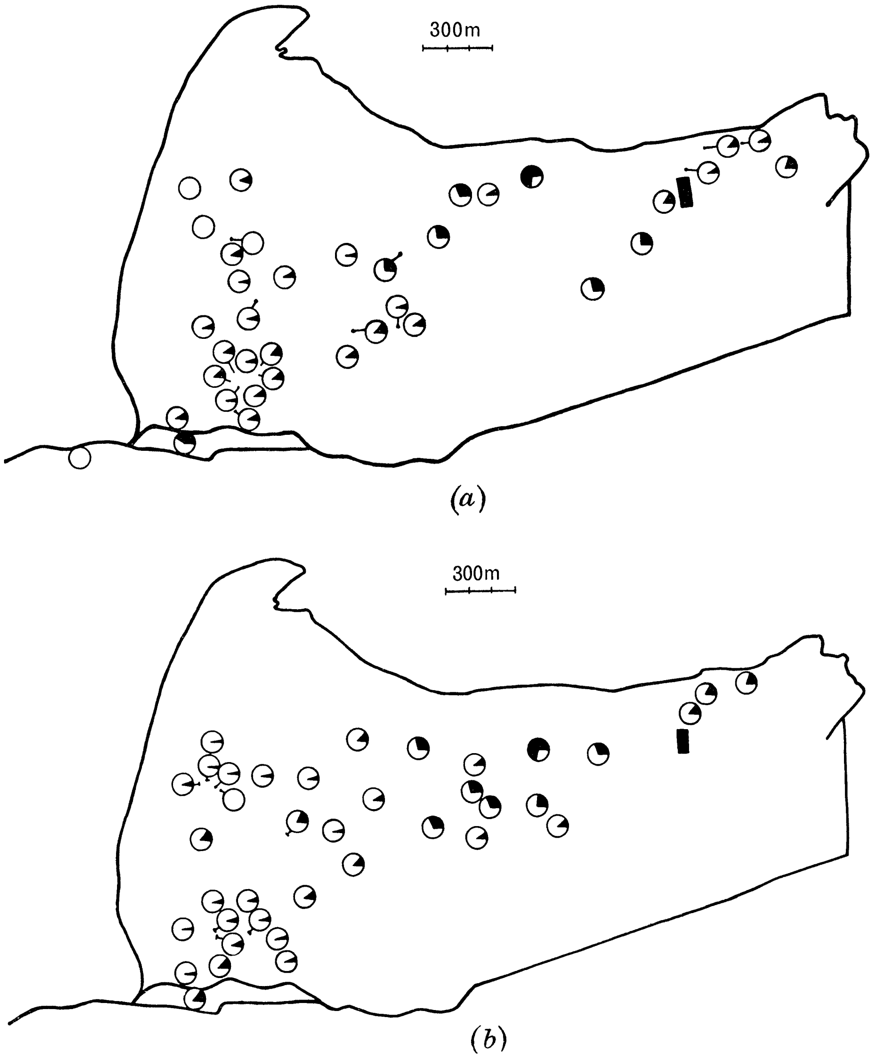


FIGURE 5. (*a*) The percentages of pink unbanded shells at Bundoran in 1924. (*b*) the percentages in 1961. Eight degrees of arc represent 1%.

DISCUSSION

We can consider the data from three points of view. First, we can examine the distribution of shell characters *within* samples and search for associations indicating linkage or selection. Secondly, we can study the distribution *between* samples and attempt to relate it to particular factors in the environment. Thirdly, we can compare the two series of samples, in order to detect any evolutionary changes that may have occurred between 1924 and the present day.

(i) *Associations within samples*

Most of the obvious colour and banding varieties of *Cepaea nemoralis* are known to be inherited (Lang 1904, 1912; Stelfox 1918, and unpublished; Lamotte 1951, 1954; Cain &

Sheppard 1957; Cain *et al.* 1960; Murray 1963) and we know that the environment has little or no direct effect on their phenotypic expression. With respect to these varieties, there is good evidence that mating is random (Schnetter 1950; Schilder 1950; Lamotte 1951; Wolda 1963).

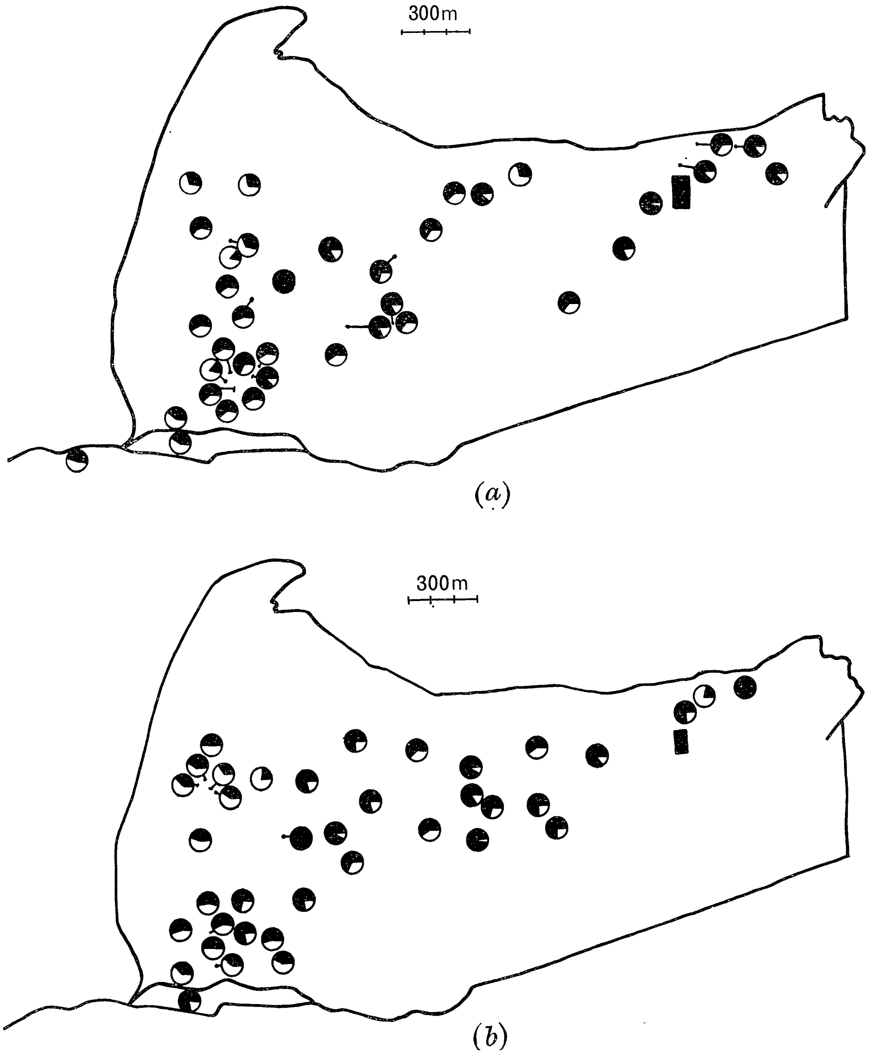


FIGURE 6. (*a*) The percentage of pink banded + pale brown banded shells at Bundoran in 1924. (*b*) the percentages in 1961. Six degrees of arc represent 1%.

Within a random-mating population, inherited characters will tend to be associated at random unless their assortment is disturbed by linkage, by selection, or by both. In the absence of linkage, detectable excesses or deficiencies of particular combinations can only be produced by extremely strong selection. In the absence of selection, disequilibria due to linkage will tend to disappear in the course of time (Li 1955; Falconer 1960). Long-term disequilibria are therefore likely to be due to the joint action of both factors (Cain & Sheppard 1954; Lewontin 1964). It should be noted, however, that *apparent* disequilibria can be produced by epistatic interactions between the genes controlling different morphs (see below).

Excesses and deficiencies of unbanded shells among different colour-classes have often been reported in *Cepaea* (Boycott & Bowell 1900; Diver 1939; Cain & Sheppard 1954; Clarke 1960). Almost all colonies of *C. nemoralis* show a deficiency of banded dark browns. This seems to be due, at least in part, to a tendency for the gene for dark brown directly to reduce the expression of banding (Cain *et al.* 1960). Differences in the proportions of unbanded shells between pinks and yellows also occur, but here there is no evidence of such direct epistatic interaction. Breeding experiments have shown that the loci for colour and banding are linked, and it is clear that the disequilibria are due to this linkage. As Cain & Sheppard (1954) suggest, they may be maintained by selection.

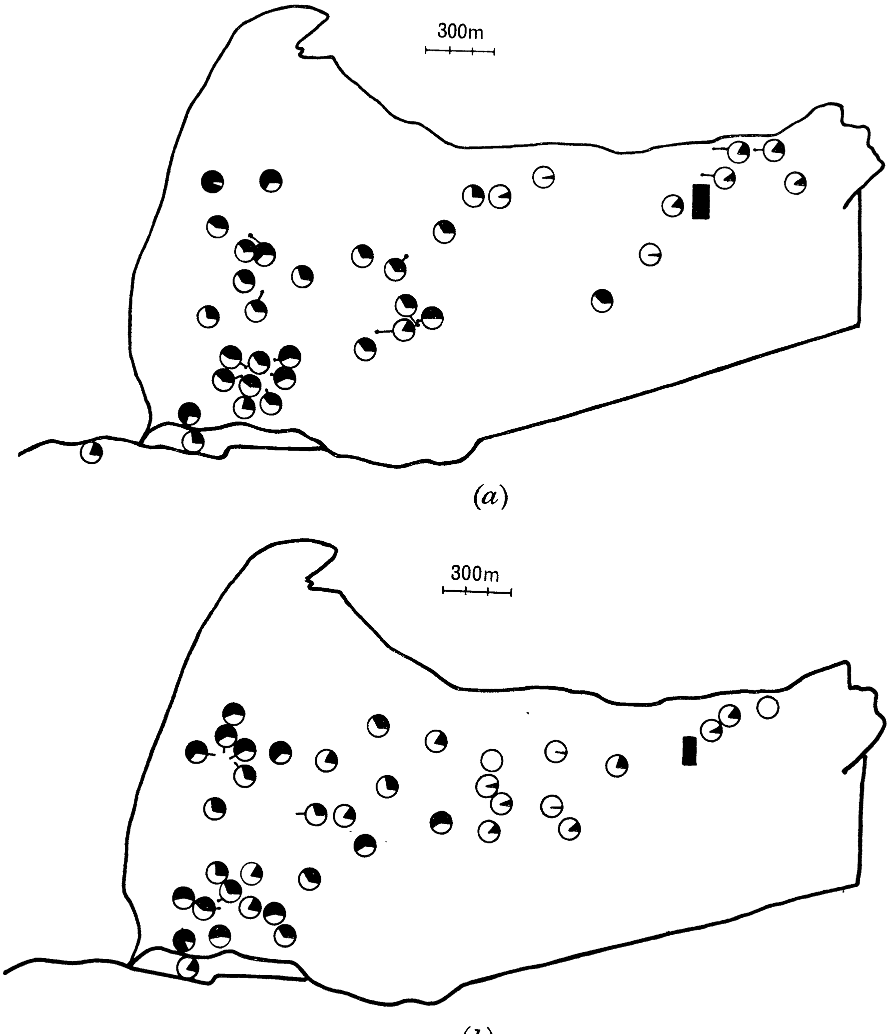


FIGURE 7. (*a*) The percentages of dark brown unbanded shells at Bundoran in 1924. (*b*) the percentages in 1961. Eight degrees of arc represent 1%.

At Bundoran, banded dark browns and unbanded pale browns are extremely rare. It is not clear to what extent the banded pale browns are genetically dark, since the presence of banding is known to reduce the intensity of shell-colour (at least among pinks and yellows: Boycott & Bowell (1900); Cain & Sheppard (1954). Unfortunately the genetics of pale brown has not yet been investigated.

In the 1924 series, where an attempt was made to separate pinks and pale browns among the banded forms, it was possible to examine the ratio of unbanded to banded in pinks and yellows. Following Cain & Currey (1963), we calculated the cross-product ratio

$$\text{c.p.r. } 1 = \frac{\%\text{ yellow unbanded} \times \%\text{ pink banded}}{\%\text{ pink unbanded} \times \%\text{ yellow banded}}$$

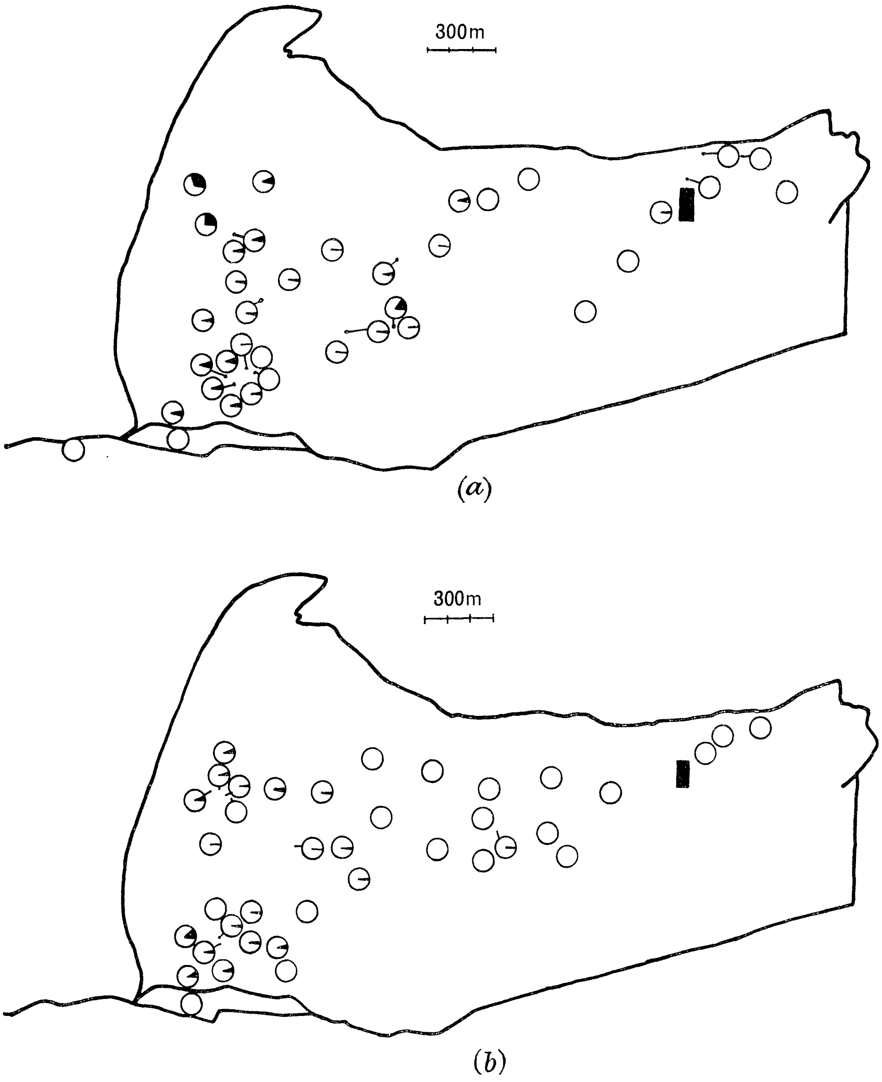


FIGURE 8. (*a*) The percentages of white shells at Bundoran in 1924. (*b*) The percentages in 1961. All the whites have white lips. Almost all are banded hyalozonates. Eight degrees of arc represent 1%.

for individual samples. Hyaline forms were excluded from the banded categories because of the uncertainty about the genetic constitution of whites (see below).

If the characters were distributed at random we would expect the cross-product ratio to have a value approximately equal to one. In fact, out of 33 samples for which the calculation could be made, 30 showed a value greater than one. The average cross-product ratio was 2·3, indicating a highly significant ($P < 0{\cdot}001$) excess of unbanded yellows and banded pinks throughout the area.

These observations are subject to errors in the scoring of banded pinks. If large numbers of pale browns were miscored as pinks, we would obtain spuriously high values of the cross-product ratio. In practice, however, it is unlikely that the result is seriously biased. Some of the highest values are found in the eastern part of the area, where browns (both pale and dark) are known to be rare. We can safely conclude that there is a genuine linkage disequilibrium.

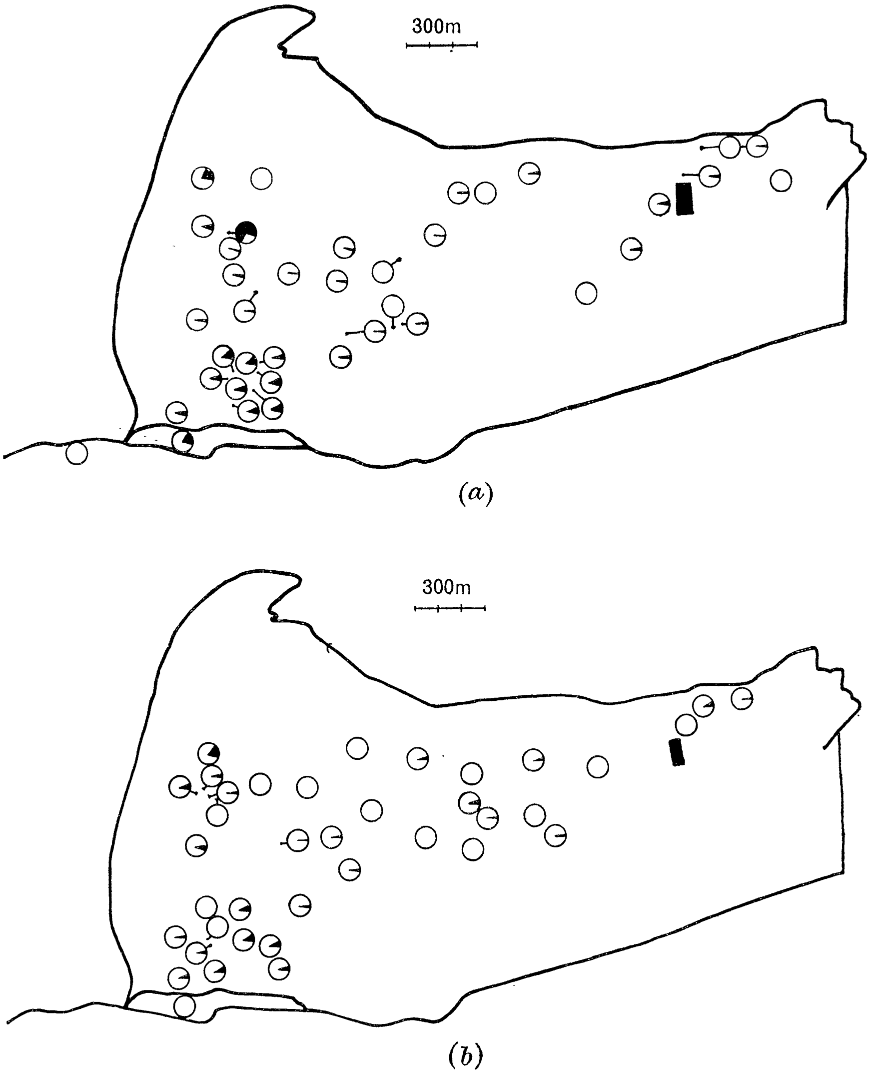


Figure 9. (*a*) The percentages of hyalozonates (other than whites) at Bundoran in 1924. (*b*) the percentages in 1961. All these hyalozonates are either pink or pale brown banded. Eight degrees of arc represent 1%.

Apart from the association between unbandedness and colour, there are other detectable disequilibria at Bundoran. There is, for instance, a clear association between hyalozonate and colour. Yellow hyalozonates do not occur, although it is possible that some (or all) of the white hyalozonates carry the yellow gene. However, Murray (1963) has shown that some white hyalozonates may be genetically pink. The scorings of 1924 suggest that the proportion of hyalozonate shells is higher among pale browns than it is among pinks. Table 5 shows the data from four samples in which both colours are common and can be distinguished. The phenomenon seems to be quite general and statistically highly significant ($P < 0{\cdot}001$).

Cain & Sheppard (1954) have also demonstrated an association between hyalozonates ('albinos') and colour. They suggest a similar association with banding, unbanded hyalozonates being detectable (in some populations) because of their white lips. At Bundoran, where white-lipped forms with fully pigmented bands are frequently found, the unbanded hyalozonates cannot be distinguished.

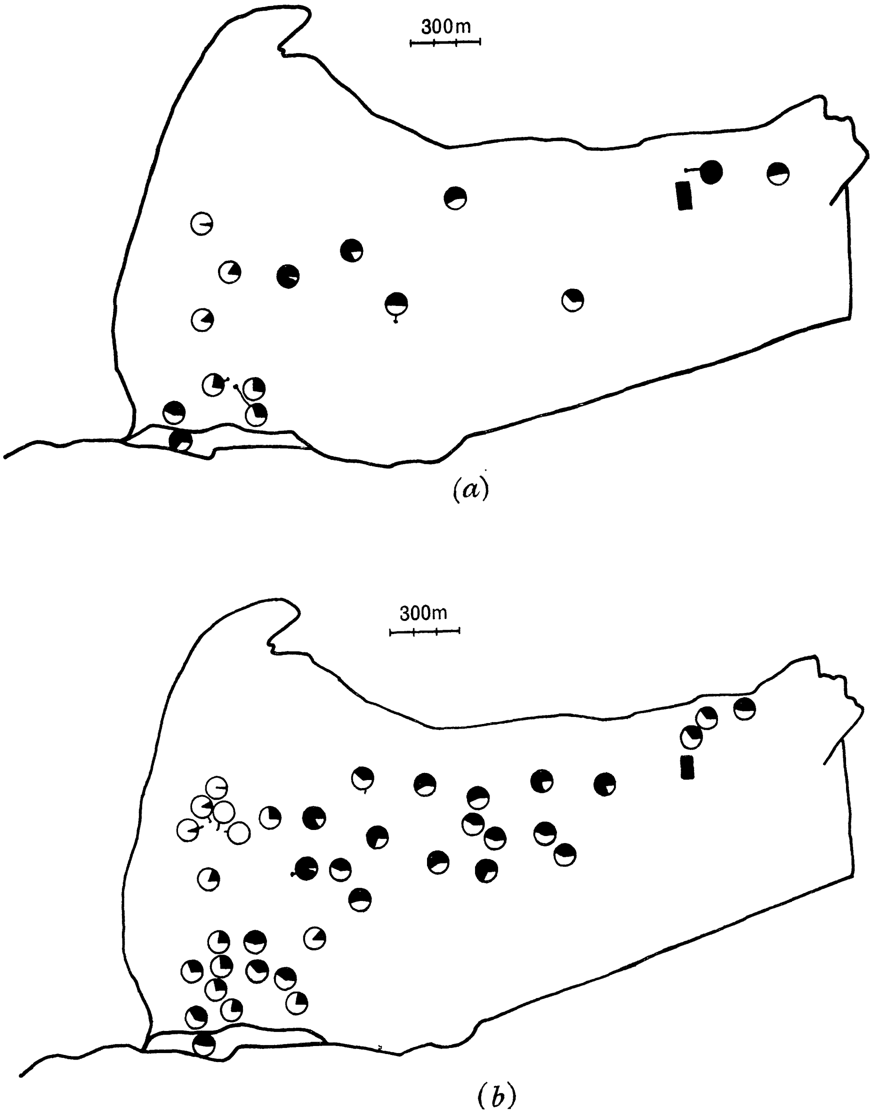


FIGURE 10. (*a*) The percentages of five-banded shells with two or more bands fused together at Bundoran in 1924. Fifteen samples were scored for fusions. (*b*) The percentages in 1961. All samples were scored for fusions. For each locality the frequency is expressed as a percentage of the total number of five-banded shells. Five degrees of arc represent 1%.

In our collections there are clear and significant associations between lip-colour and other shell characters. White-lips are absent among yellow unbanded shells and extremely rare among pink unbanded. Self-lips are also rare among these forms. There is an apparent difference between the 1924 and 1961 series in the occurrence of white lips among dark brown unbanded shells, but this is probably due to differences in the scoring conventions (see above). Among dark browns there are a large number of shells with lips grading from 'self' to 'white'. It is likely that in 1924 most of these were scored as 'self', whereas in 1961 most of them were scored as 'white'.

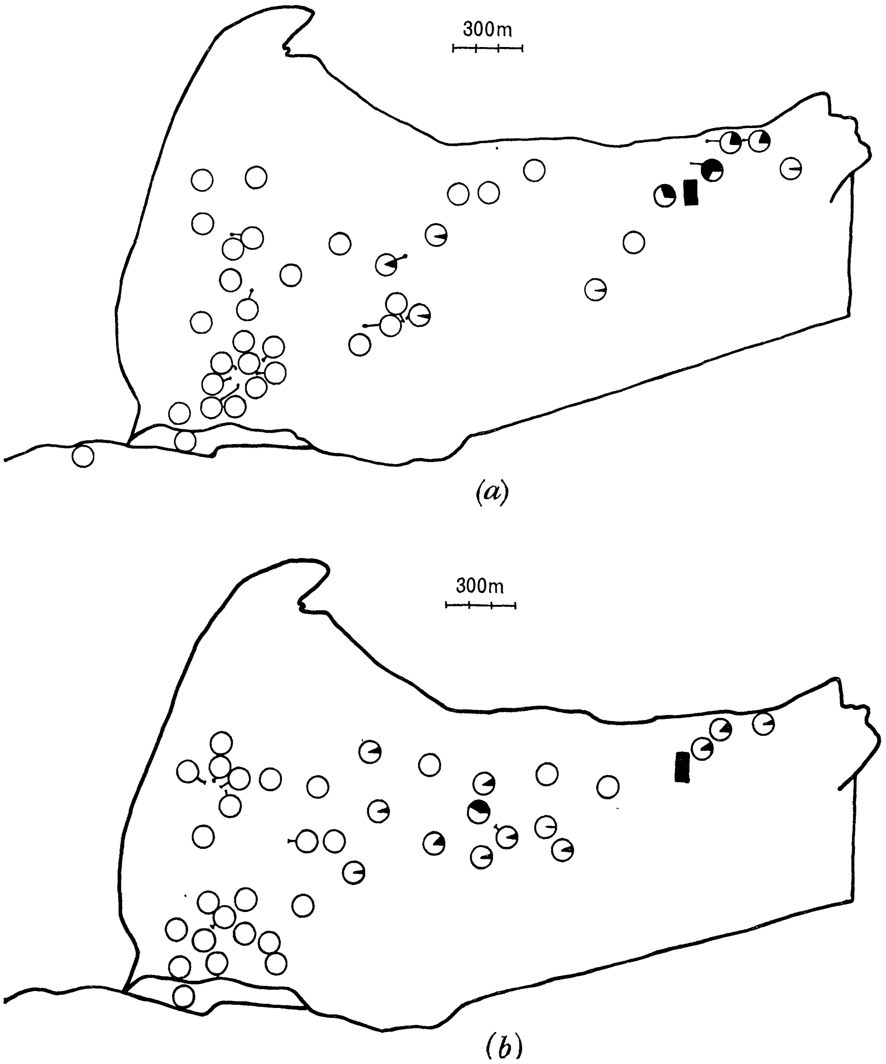


FIGURE 11. (*a*) The percentages of single-banded (00300) shells at Bundoran in 1924. (*b*) The percentages in 1961. For each locality the frequency is expressed as a percentage of the total number of banded shells. Eight degrees of arc represent 1%.

In the 1924 series it seems clear that there are more white-lipped shells among the pale brown banded than there are among the pink banded. Quite often there are more self-lips among the pinks, but this never equals the excess of white-lips among the pale browns. Some examples are given on table 6.

Pink and brown hyalozonate shells are predominantly self-lipped, the remainder being white-lipped. White shells are white lipped.

Among the samples of the 1924 series that were scored for fusions there is a suggestion, not statistically significant, of an excess of fusions among pink-banded shells. This type of association has been observed in *C. nemoralis* elsewhere (Clarke, unpublished), and it is probably genuine at Bundoran. The suggestion is strengthened by the fact that, in the 1961 series, the cross-product ratio

$$\text{c.p.r. } 2 = \frac{\%\ \text{Y12345 unfused} \times \%\ (\text{P12345 fused} + \text{PB12345 fused})}{\%\ (\text{P12345 unfused} + \text{PB12345 unfused}) \times \%\ \text{Y12345 fused}}$$

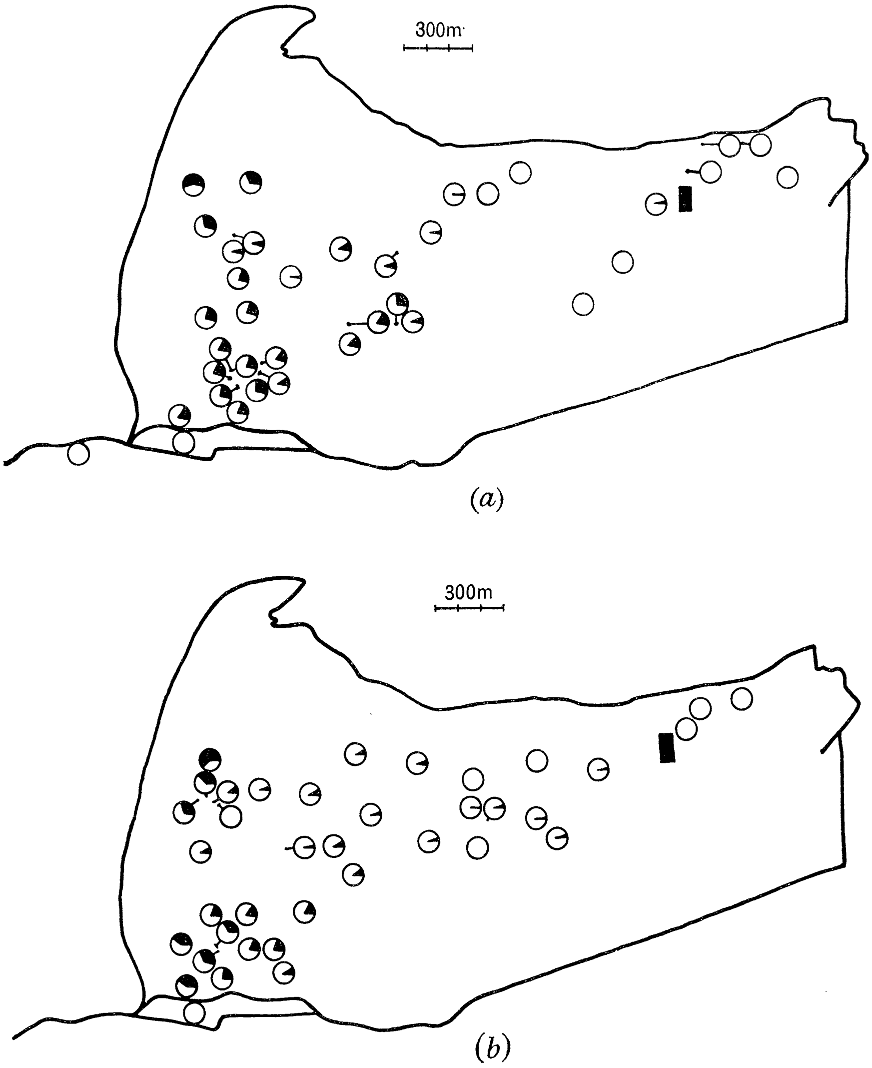


Figure 12. (*a*) The percentages of white-lipped shells at Bundoran in 1924. (*b*) The percentages in 1961. Eight degrees of arc represent 1%.

Table 5. The distribution of hyaline shells among pale brown banded and pink banded shells (1924 series)

locality	colour	hyalines	others	total
6	pale brown	8	51	59
	pink	1	55	56
7	pale brown	21	115	136
	pink	0	191	191
9	pale brown	12	60	72
	pink	8	102	110
11	pale brown	18	79	97
	pink	4	129	133

tends to be positively correlated with the frequency of pink unbanded (see also § (ii) below). The excess of fusions among pinks may possibly be due to pleiotropic effects of the pink gene, but it does not occur in all populations of *Cepaea*. For instance, it seems to be absent at Berrow (Clarke & Murray, unpublished). The presence of fusions seems to be associated with a general intensification of shell-colour, particularly among browns.

TABLE 6. THE DISTRIBUTION OF LIP-COLOUR AMONG PALE BROWN BANDED AND PINK BANDED SHELLS (1924 SERIES)

locality	phenotype	white-lips	self-lips	others	total
17	pale brown	25	0	123	148
	pink	0	1	252	253
21	pale brown	40	2	37	79
	pale brown hyaline	1	45	0	46
	pink	0	19	19	38
	pink hyaline	0	11	0	11
2	pale brown	27	0	64	91
	pink	0	0	29	29

No associations were observed between 00300 or 00345 and colour. The genes for these characters are known not to be on the same chromosome as the colour locus (Lamotte 1954; Cain *et al.* 1960).

It is sometimes possible to detect the action of natural selection within a population by comparing the proportions of particular phenotypes in different age groups. If the phenotypes remain constant during individual development any differences must be due to unequal mortality or fecundity. Goodhart (1962) has reported phenotypic differences between age groups in populations of *C. nemoralis* near Cambridge, and our work at Berrow in Somerset, showed a widespread and significant excess of yellow shells among young snails (Clarke & Murray, unpublished). No such differences are evident in the present data.

(ii) *Variation between samples*

Figures 3 to 12 show that there is a good deal of spatial variation in morph-frequencies at Bundoran. Significant changes may take place over distances of 100 m or less. We must inquire whether this variation can be related to environmental factors.

The most obvious environmental differences in the area are between the western mobile and semi-mobile dunes and the eastern region of more stable grassland. These differences, as we have already noted, are reflected in the vegetation. The frequencies of a number of morphs are distributed clinally from west to east, and it may be that the clines are due to differences in selective values at different places.

On the western dunes we find the highest frequencies of dark brown unbanded, pale brown banded, white, hyalozonate, and white-lipped forms. In the eastern region of stable grassland we find the highest frequencies of pink, 00300, 00345, unbanded among pinks and yellows, and fusions. It is worth noting that at Berrow in Somerset (Clarke & Murray 1962*a*) the stabilization of the dunes is associated with a decrease in the frequency of brown and an increase in the frequency of 00300. The distributions of brown and 00300 at Bundoran are compatible with these results.

It is possible that the distributions of some of the morphs may be influenced by selective visual predation. The stable grassland has a greener and more uniform background than does the marram on the mobile dunes. One would expect yellows, unbandeds, 00300 and 00345 to be favoured on the former, browns and 12345 to be favoured (relatively) on the latter. In fact, however, although the distributions of browns, 00300 and 00345 are roughly consistent with this interpretation, the proportions of yellows do not evidently correspond to the type of background.

The high frequency of pinks on the grassland does not agree with a hypothesis of visual selection by predators with colour vision (thrushes, for example), but might be interpreted in terms of selection by colour-blind animals such as rabbits. Cain (1953) has pointed out that there is often an unusually high proportion of pinks on grasslands where rabbit predation is intense. He has shown that in terms of *tone*, rather than colour, pink shells match the grassy background better than yellows. Our own observations at Bundoran suggest that thrushes are relatively uncommon predators. Thrush-stones are rare, but rabbits are frequently seen, particularly in the eastern region where pinks are common.

It is clear that interpretation in terms of visual selection alone are not satisfactory. They do not explain the distribution of yellows, unbandeds (apart from browns) hyalozonates, whites, white lips, or fusions (although it is possible that the distribution of unbandeds may be partly a secondary result of selection for browns). The high frequency of fusions in the east may be an effect of the high frequency of pinks, since the two are associated within samples. However, it is difficult to see how this association could be *visually* advantageous, and in the absence of some non-visual advantage we would expect it to break down. The occurrence of high frequencies of fusions on short turf has been noticed elsewhere, both in *C. nemoralis* and *C. hortensis* (Clarke unpublished data), but no explanation for it has yet been found.

Figures 13 to 15 are scatter diagrams showing, for the 1961 series, the proportions of various morphs in relation to the different types of vegetation. The symbols used are the same as those on figure 2.

Figure 13 plots the proportion of dark brown unbanded shells against the proportion of fusions. They are negatively correlated, as might be expected from their geographical distribution. There is also evidence of a separation, on both axes, into habitat classes (between marram and short turf). Unfortunately this cannot be tested by standard statistical procedures because the samples are not independent of each other. We must wait for further studies on sand-dune areas to determine whether these relations are genuinely the result of differential selection, or merely due to 'geographical accidents'.

The same applies to the clearer separation shown on figure 14, where the percentage of pink unbanded is plotted against the percentage of fusions. Here the localities with patches of bracken seem to form a third, more distinct, group.

Figure 15 gives the relation between the percentage of yellow, the percentage of 'effectively unbanded' (a category which includes all shells with the top two bands absent, i.e. 00345, 00300, 00000, etc.), and the habitat. It corresponds to the figure given by Cain & Sheppard (1954). There is no clear separation into habitat-classes on either axis, but the spots spots fall into the position of hedgerows and rough herbage on Cain & Sheppard's diagram. In other words, the samples very roughly correspond to the overall proportions expected according to a hypothesis of visual selection. They are, however, generally somewhat lower in the proportions of both yellows and 'effectively unbandeds' than most of Cain and Sheppard's hedgerow and rough herbage samples.

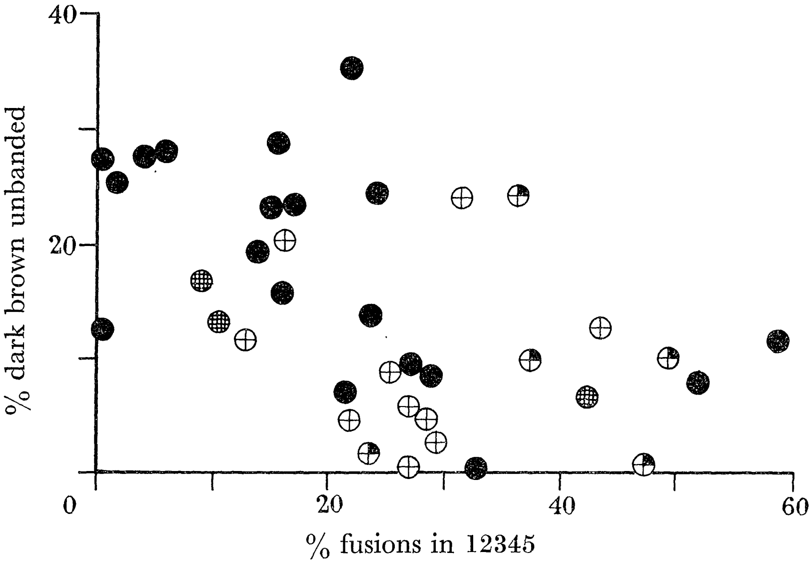


FIGURE 13. Bundoran 1961: a scatter-diagram showing the relation between the proportion of dark brown unbanded shells and the proportion of five-banded shells with two or more bands fused. For each locality the proportion of shells with fused bands is expressed as a percentage of the total number of five-banded shells. Symbols as in figure 2.

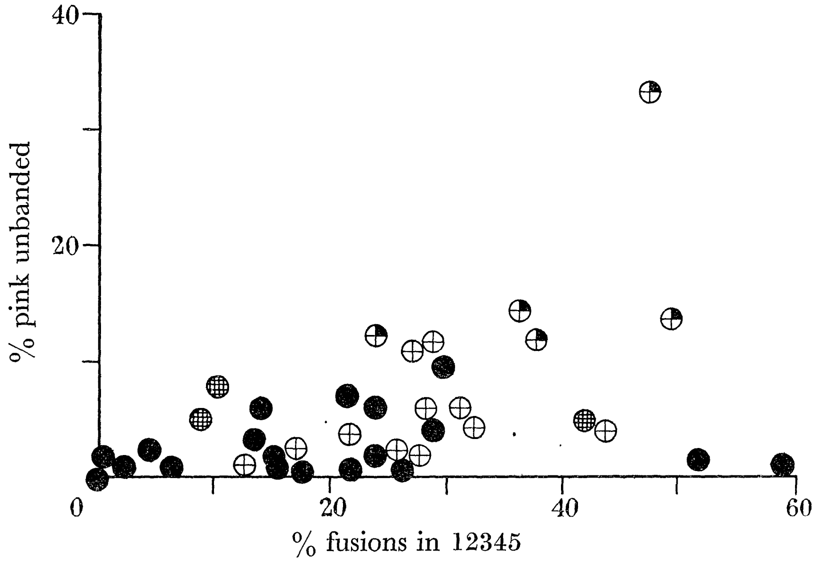


FIGURE 14. Bundoran 1961: a scatter-diagram showing the relation between the proportion of pink unbanded shells and the proportion of five-banded shells with two or more bands fused. For each locality the proportion of shells with fused bands is expressed as a percentage of the total number of five-banded shells. Symbols as in figure 2.

(iii) *Comparison of the two series*

The upper and lower diagrams on figures 3 to 12 show the composition of samples taken in 1924 and 1961 respectively. A glance of these figures will show that there is no very obvious evidence of widespread evolutionary change in the intervening period.

If we are to detect small changes that are not immediately obvious, it is necessary to study the history of individual populations. There are twenty-three localities where we can be reasonably certain that the sample staken in 1924 and 1961 are within 100 m of each other. This figure has been chosen because although it is possible that, within one series, populations separated by shorter distances may differ significantly from each other, errors of location in the 1924 samples are such that we cannot limit the distance further. This gives us twenty-three pairs of samples for comparison (4–62*, 5–57*, 6–63, 7–64, 8–66*, 9–66*, 10–66, 11–83, 12–82*, 13–66, 17–56, 19–48, 20–49*, 12–54, 24–45*, 25–47, 27–80, 32–77, 35–71, 36–70, 39–58, 40–59*, 41–60*). The asterisks denote those pairs that are believed to correspond most closely (within 50 m).

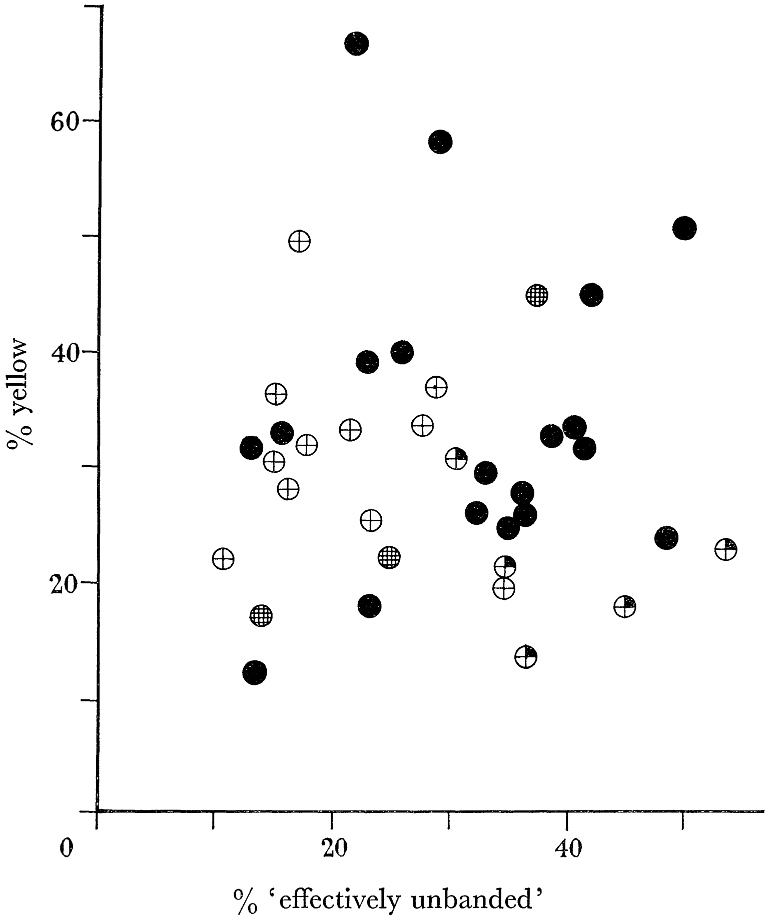


Figure 15. Bundoran 1961: a scatter-diagram showing the relation between the proportion of yellow and the proportion of 'effectively unbanded' shells. The latter category includes all shells with the top two bands absent. Symbols as in figure 2.

We have compared, in each pair, the proportions of all the morphs shown on figures 3 to 12 and also several compound percentages (% Y, % 00000 and cross-product ratios). In many cases we have found significant differences between them, but these differences are not consistent in direction from pair to pair (apart from an apparent overall increase in 00345* which is probably due to differences in scoring a small number of shells which are uncertainly 00345).

We conclude that there may have been small local evolutionary changes which we could not distinguish from differences due to errors of location, but that in general the populations have remained stable. In this respect they resemble the populations studied by Goodhart (1956, 1958). There have certainly been no changes comparable to those observed at Berrow (Clarke & Murray 1962*a*). This apparent constancy may be related to the fact that there has been little change in the habitat at Bundoran since 1924. At Berrow, on the other hand, the dunes have gradually become more stable, and large parts of them have become overgrown with *Hippophae* (Clarke & Murray 1962*a*). In each case, the evolutionary situation parallels the constancy or inconstancy of the environment. It will clearly be of great interest to follow future developments at both localities.

We owe a great debt to the late Professor A. E. Boycott, F.R.S., who collaborated in the first studies at Bundoran. We are grateful to the Royal Society, the University of Edinburgh, and the National Science Foundation for financial help. Professor A. J. Cain and Professor P. M. Sheppard, F.R.S., have given generously of their advice and criticism. Miss June Libberton and Miss Lorna Stewart have very kindly helped in preparing the tables and figures. Mrs Ann Clarke and Mrs Elizabeth Murray have taken an active and indispensable part in the collecting, and have generously helped in many other ways.

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Appendix

By C. Diver

In the present flood of scientific publications and the pressure on available time there is a tendency to lose historical perspective and to hail again as new knowledge what has been known for a long time.

I was first attracted by the polychromatic display of *Cepaea*'s variability when in Switzerland about the year 1900 (though owing to youth and disturbances in Europe I could not begin serious random sampling till 1920); but I was merely a recent recruit to the many before me. In the middle of the last century Moquin-Tandon (1855) analysed this variation, but without the benefit of any genetical knowledge. Boycott (Boycott & Bowell 1900), also before Mendel's work had been rediscovered, had already made in 1897 (and published that year in the *Hereford Times*) a detailed study, based on random sampling, of populations of *Cepaea* (or *Tachea*) in Herefordshire. As would be expected, his analysis was detailed and penetrating. Mr de Boinville had previously, about 1843, made collections of both species near Hereford and placed these at Boycott's disposal; as Boycott, later, placed a number of his early samples at my disposal. I am particularly glad to be able to continue this time-honoured custom by placing my earlier samples and experience at the disposal of Clarke and Murray.

It is worth remembering that Boycott drew attention to two facts pertinent to present-day inquiries: (*a*) that the presence of pigmented banding modifies the ground-colour of the unbanded parts of the shell, more particularly in the areas close to the bands, so that what we recognize as pink-unbanded shells were referred to as var. *rubella*, while their banded counterparts (*P-bd*) were referred to var. *mista*; and (*b*) that the proportions of yellows and pinks could be completely reversed in two lengths of the same hedgebank, the second being 'not markedly different from the first in any respect'. Among the first populations I sampled in 1920–21, I found a roadside hedgebank of reasonably uniform appearance on which, at one end, the pinks were all unbanded, while at the other they were mostly banded. I was unaware at that time of Boycott's findings, but this patchy distribution made it obvious that one was seeing the product of accidentally successful broods. As my experience of different populations increased, this early impression was steadily confirmed. Having joined Boycott in his experiments with sinistral *Limnaea*, and with out joint interest in *Cepaea*, the Bundoran dunes were an obvious place for us to visit because (*a*) large numbers of sinistral *nemoralis* had been recorded from these dunes, and (*b*) a prolific and relatively continuous population of *nemoralis* was available for sampling.

Our first object was defeated as only one living sinistral was found, not on the dunes but in locus 43 on the Ballyshannon road, and it died *sine prole*. In the large main blow-out of the dune system, where he estimated that there must have been about a million dead shells, Boycott counted 8000 of these and the 6021st was a sinistral.

My report on this grant, in 1925, drew attention to the associations found between shell colour, banding and band and lip pigmentation which are 'such as would be expected on the hypothesis of linkage, where the linkage was of an unusually high order. From the assumption that the factors concerned are behaving as a closely linked group and from the facts already established by breeding this species, it is possible to deduce from these natural populations the dominance relationships of pairs of characters which have not yet been analysed by means of experimental populations.'

This assumption was widely confirmed in both *nemoralis* and *hortensis*, and population diagrams illustrating this were shown at the Sixth International Congress of Genetics at Ithaca in 1932 (Diver 1932).

Another interesting feature shown by the Bundoran samples was the distribution of the band formula 00300 (also exhibited at Ithaca). This variant (epistatic to other band formulae), though common and widely distributed, was found at Bundoran in only a few interconnected samples (see figure 11). There was one centre of high frequency, 28 % of the single-banded snails, tailing off to 1 % in a long tongue that followed a well-populated valley on the landward edge of the dunes and virtually disconnected from the main high ridge to the north-west—a pattern that could only reasonably be interpreted as the random spread of a gene through sporadic out-breeding between a series of mainly inbreeding subpopulations, from the place of its occurrence in or near locus 39. The relatively unpopulated rising ground had also prevented the 'dotted' gene (epistatic to continuous band pigment) present in loci 30 and 31 from reaching the valley populations. The centre of the 00300 gene was about as far as it could be from the nearest other populations containing it, two loci on the cliffs to the south-west and separated from the dunes by a stream. This means either that an individual carrying this gene had accidentally been transported across the stream and over a well populated dune area, or that a mutant had occurred *in situ* and spread in the way that would be expected in a mating structure of the kind known to exist in *Cepaea*. The gene was absent from the nearest landward population (locus 43) by the Ballyshannon road.

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