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STUDIES ON *CEPAEA*

IV. CLIMATE AND SELECTION OF BANDING MORPHS IN *CEPAEA* FROM THE CLIMATIC OPTIMUM TO THE PRESENT DAY

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CONTENTS

A number of samples of subfossil *Cepaea nemoralis* and *hortensis* from sites in southern Britain of archaeological interest, ranging in date from about 4500 B.C. to Romano-British and Anglo-Saxon, have been scored for frequency of the major banding morphs, and compared with present-day samples taken on each site or as near to it as these species could be found. In *C. nemoralis* there is a significant decrease of unbandeds from pre-Iron Age samples to the corresponding ones for the present day, but no indication of systematic change from Iron Age samples to the present day. Spread banded also shows changes from pre-Iron Age samples to present-day ones, but very little change from the early Iron Age to the present day. The smaller samples of *C. hortensis* available give no sign of a trend although there is much change from pre-Iron Age times to the present; Iron Age samples and the corresponding present-day ones do not show the relative constancy of composition seen in *C. nemoralis*—as usual these two very closely related species are behaving differently. At the present day there is evidence (experimental and distributional) that the frequencies of banding morphs of *C. nemoralis* are affected by climate, unbandeds and mid-bandeds being favoured by better summers than those normal in Britain at present. The available evidence, from pollen analysis and other sources, of changes in the climate of southern Britain in the last 6500 years suggests that the observed differences in morph frequencies can be related to known climatic changes, in agreement with present-day evidence. One area effect (south-west Marlborough Downs) has contracted and become less intense since pre-Iron Age times, as perhaps have others; in some cases a site has remained in an area effect, but the effect itself has changed. Two pairs of samples from lowland sites appear to have changed from frequencies indicating area effects in pre-Iron Age times to others consistent with visual selection at the present day. Area effects seem to have been rather constant from the Iron Age to the present day.

1. Introduction

When conditions of preservation are favourable, fossil and subfossil shells of polymorphic snails offer an opportunity of surveying morph frequencies over long periods of time, as Diver (1929) has pointed out. With the discovery of markedly different régimes of variation and selection in present-day populations of *Cepaea nemoralis* (Cain & Currey 1963 *a–c*) investigation of ancient populations of this and related species gains additional interest. The present paper gives an account of subfossil populations of *C. nemoralis* and *hortensis* ranging from Romano-British times to the 'climatic optimum' about 4500 B.C., and a comparison with modern samples.

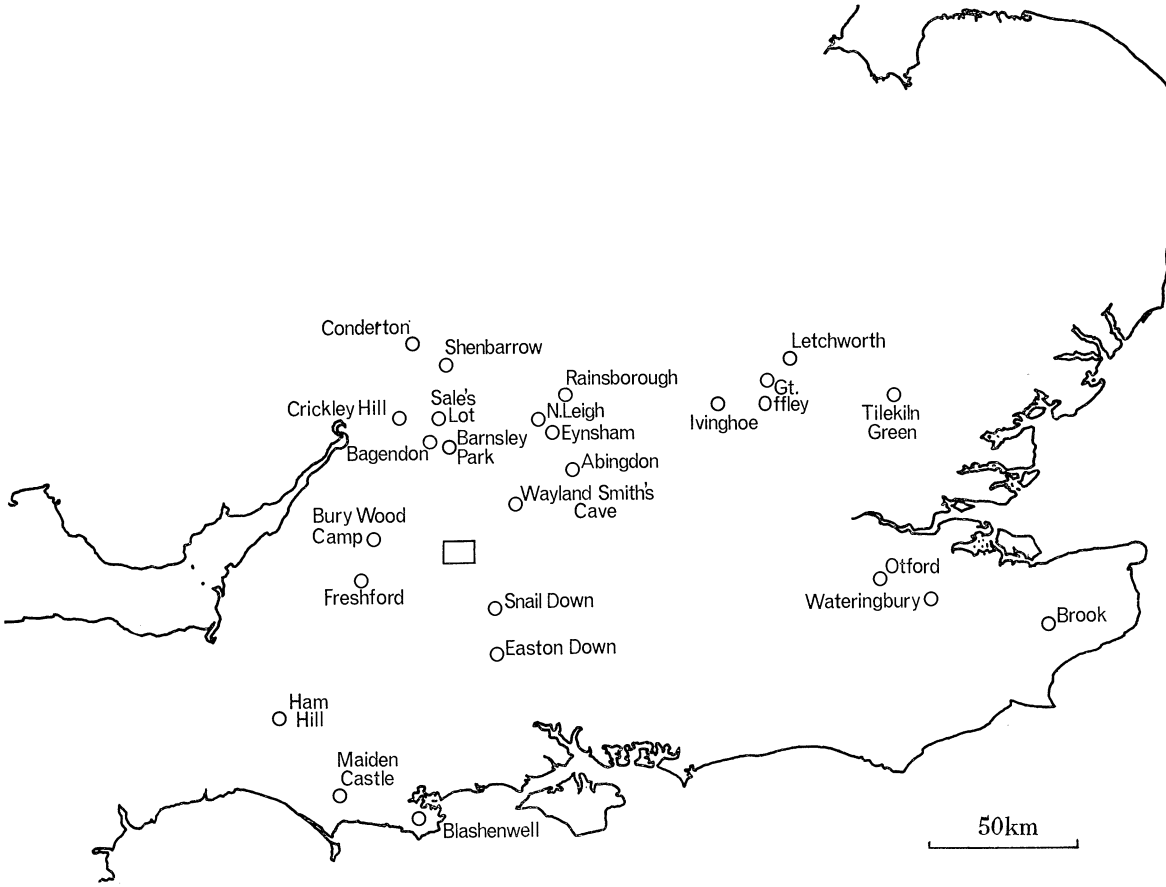

FIGURE 1. Distribution of sites from which subfossil material has been seen. The rectangle shows the Avebury district, given in detail in figure 6.

2. Collections

2·1. *Subfossil material*

We have used material only from inland sites in southern England south of a line running through Stratford-on-Avon and Cambridge (figure 1) since all detailed studies of variation in morph frequency in English *Cepaea* have so far been made from this region. Subfossil material has been admitted only from excavations by archaeologists or geologists of repute; the sites, therefore, were originally selected for their archaeological or geological interest and without *Cepaea* in mind. Since the lighter soils in England were the first colonized during the Neolithic agricultural revolution, it follows that many of the sites are on the Chalk and higher and purer limestones. Comparatively few are in lowland areas. At most of them the ancient structure was made within a relatively short time and only rarely can one hope for samples from more than one period from the same site.

Where possible we have contacted personally the archaeologists making the excavation, and sometimes have been able to visit the site during the excavation. All sites have been visited to collect present-day samples. A number of excavations were made many years ago and we have seen the molluscan material from them in the collections of the British Museum (Natural History), almost entirely in the A. S. Kennard collection, a very few in the A. G. Davies collection. The two main difficulties arising in this work have been to ensure that subfossil material is indeed of the age ascribed to it, and (as far as possible) is representative of the local population at that period. Archaeologists have less difficulty over age with artifacts, since these are usually more or less dateable, or at least recognizable, by the style, and their presence in inappropriate levels (e.g. Roman sherds in a supposedly undisturbed Neolithic barrow) gives warning of subsequent disturbance. Snail shells carry no such convenient stylistic characters, and since conditions of preservation can vary considerably locally, degree of wear or staining of the shell may be useless as a guide—though the occurrence of one fresh (or even live) shell in an otherwise irreproachable collection suggests that a modern snail has fallen into an excavation and can be ignored. Shells only a foot or so below ground level can be churned up by ploughing, or by burrowing animals such as moles, rabbits or rodents; modern snails may fall down open burrows or creep into crevices which, if produced by the rotting of tree roots, may go down several feet. Hibernating *Cepaea* do not seem to bury themselves more than an inch or so below the present surface.

It is essential, therefore, to accept only subfossil material from well-stratified and undisturbed deposits, preferably from layers sealed over by a firm and compact layer, so that the chances of disturbance having occurred are slight. Mixing by disturbance can only make two samples from different layers more alike, and differences in morph frequency observed may therefore be minimum ones. Where no differences can be seen between subfossil and modern material in morph frequencies, particular care must be taken.

When subfossil shells are found scattered over an old land surface covered many feet deep by a barrow or similar structure, there is no reason to doubt that they form a random sample of the population at the time of building the barrow. Where the material was collected together by man for food, and later thrown into a midden, again there is no reason to suspect a biased sample. The use of particular varieties for decoration as in the necklaces figured by Taylor (1914, p. 279) would no doubt produce bias. Mr J. Alling Prins tells us that in Friesland children play games with shells of *Cepaea*, in which the rarer varieties have high token values and are actively sought out. It is also perhaps possible that particular varieties might have had some religious significance in earlier times. We have found no evidence of special attention being paid to snails by early man, except for food (Freshford, Rainsborough) and in neither case are the morph frequencies abnormal.

One unnecessary difficulty we have encountered is the biasing of samples after they were collected. A. S. Kennard was an exceptionally careful and accurate worker who identified Mollusca from many important excavations and kept detailed notebooks with records of his identifications from each site. We have very rarely dissented from his taxonomic findings. On checking the actual samples in the Kennard collection against his notebook, we have several times found far fewer than he recorded. Some material from the same sites is in the A. G. Davies collection, at least once recorded as from Kennard, and it is clear that the latter gave away material to his friends. Where Kennard makes a note of the varieties, we can check what was given away, and in more than one case the residue is not a random sample of the original material. Unfortunately, for some sites he makes no mention of the morphs, only of the totals for each species, and if there is a discrepancy, we do not know whether what is left is representative. We have had to reject, therefore, some samples of good material from important sites. A few we have been able to reconstitute from other collections, notably the *C. nemoralis* from Maiden Castle, which, in spite of Kennard's statement that they 'would be deposited for the use of students in the British Museum (Natural History)' are partly in the Geological Survey Museum; many of the *C. hortensis* from this site are missing.

2·2. *Present-day populations*

In collecting modern snails for comparison with ancient ones we have taken a sample as close as possible to the site, without regard for habitat. Most collections came from within 500 m of the site, and in no case farther away than 1·5 km. Sometimes, when the faunal composition at the site has changed, we have had to get *nemoralis* and *hortensis* from different places. Although morph frequencies can vary over short distances, choosing the nearest place in which a species occurs at the present can hardly introduce a systematic bias. At each locality all shells found during a careful search were taken; at Easton Down, where there was a considerable scatter of Neolithic potboilers, old shells, and spoil from the flint mines on the present surface, we took our collections some distance away (700 m) to avoid mistaking old shells from the mines for modern but very worn ones. Even where we have obtained modern and subfossil populations within 100 m of each other, there is, of course, no guarantee that they are samples from the same persistent population.

2·3. *Scoring*

Scoring of the present-day populations and their habitats was as in Cain & Currey (1963*a*, *c*). In ancient shells the general colour is usually not determinable and has not been used in this paper, since what is determinable is likely to be highly biased through differential fading. Lip and banding pigmentation are much more durable and often can be determined as easily as on fresh shells. Conditions of preservation vary greatly, not according to age of site; some of our best material is the oldest, embedded in contemporary tufa and still retaining a high polish although the bands have faded to orange-brown. Neolithic material protected by the bulk of a long barrow is as good as present-day material for banding. Where the soil is highly calcareous, preservation is usually good. In badly rotted shells the outer layers, carrying much of the banding pigment scale off, and the shell looks unbanded. When in *nemoralis* the lip still shows pigment, the surface of the shell is good, and no bands are seen, the shell is unbanded. At Brook it is apparent that lip colour fades before band-colour, but many lips are still pigmented, and the texture of the shells and the presence of numbers of well-banded *hortensis* confirm a massive occurrence of unbandeds at this locality. Where we have had any doubts about the scoring of unbandeds we have rejected the sample. This has been necessary with very few samples. It is highly unlikely that Kennard rejected any samples on the scorability of morphs since he was primarily concerned with the occurrence of species. We have seen no completely unbanded samples of *hortensis* (in which the check on lip pigmentation cannot be made) and have been able to compare undoubtedly banded shells with unbandeds in all the samples. White lip is so rare in *nemoralis* in southern England that its occurrence is most unlikely to affect our results, and the two species can normally be distinguished by size and lip-shape. One sample (Rainsborough) has given us trouble in separating the species.

3. Comparison of subfossil and present-day populations

3·1. *Cepaea nemoralis*

(*a*) *Pre-Iron Age*

Table 1 gives details of all our collections relating to pre-Iron Age sites, and the comparisons of morph frequencies with those of modern samples are shown in figure 2. The banding variation has been classified only into the three principal morphs: unbanded 00000, mid-banded 00300, and five-banded 12345, the last including variants of five-banded such as 00345. These three major morphs can be treated as mutually exclusive classes phenotypically and summarized in triangle diagrams.

It is clear from figure 2 that there is no great tendency for frequencies to stay constant at each site, and indeed for many there is considerable alteration. Since several of the samples are small, non-parametric tests will be used. If we tabulate the changes in morph frequency for all the sites shown in figure 2 we find:

	00000	00300	12345
increase	2	7	12
same	0	1	1
decrease	15	9	4

Overall, therefore, unbandeds have declined in frequency (exact probability $P = 0{\cdot}0023$). There is also a strong indication that five-bandeds have increased ($P = 0{\cdot}077$).

(*b*) *Iron Age and later*

Data for these are given in table 1 and comparisons in figure 3. There is a strongly marked tendency in these samples (in contrast to those just discussed) not to alter as much as would be expected if they were changing at random over the diagram. This can be tested by a method suggested to us by Dr M. G. Bulmer. If we suppose that the ancient and modern samples are distributed at random with respect to one another, then taking any ancient sample and its distance on the triangular diagram to its modern one, on the average half of the other modern samples should be closer to it and half further away, than its own modern sample. Therefore we take each ancient sample in succession, count up the modern samples nearer to and further from it than its own (including its own in the 'nearer' category). Then for each site the frequency of the 'nearer' samples over all samples (in this case 13) is the probability that the ancient and modern samples for that site would be as close if they were arranged at random. These probabilities can

TABLE 1. SUBFOSSIL AND MODERN SAMPLES OF *CEPAEA NEMORALIS*

grid reference	locality	period	0	3	3S	5	5S	total
—	Blashenwell	VII *a*	121	—	—	—	—	121
SY 953809	—	modern	12	5	—	3	—	20
TQ 076450	Devil's Kneading Trough, Brook	VII *a*	25	1	—	1	—	27
		modern	7	1	—	66	1	75
—	Wateringbury	VII *a*	8	1	—	6	—	15
TQ 671529	—	modern	1	1	—	27	—	29
—	Tilekiln Green	VII *a*	36	7	2	127	3	175
TL 550211	—	modern	3	—	—	31	—	34
TL 154267	Great Offley	?VII *b*	2	—	—	13	—	15
		modern	—	—	—	13	—	13
SU 066677	Bishop's Canning	Neolithic	47	—	—	—	—	47
SU 067676	Long Barrow	modern	4	1	1	2	5	13
SU 104700	Avebury	Neolithic	25	—	1	—	—	26
SU 119701	—	modern	59	11	—	—	—	70
SU 087714	Windmill Hill	Neolithic	34	—	—	—	—	34
SU 085715	—	modern	19	6	—	14	2	41
SU 281854	Wayland Smith's Cave	Neolithic	7	2	1	11	7	28
		2500 B.C.	1	2	—	—	—	3
SU 281859	—	modern	26	2	—	63	—	91
SU 514984	Abingdon	Neolithic	58	28	—	—	—	86
		modern	24	—	—	36	—	60
TL 239344	Letchworth	Neolithic	2	1	—	11	1	15
TL 240345	—	modern	3	—	—	20	—	23
SP 048159	Sale's Lot	Neolithic	6	4	—	31	—	41
SP 049160	Long Barrow	modern	21	—	—	55	—	76
SO 971384	Conderton, Bredon Hill	Late Neolithic, 1700–1800 B.C.	4	4	5	—	—	13
		modern	—	—	—	36	—	36
SU 118679	The Sanctuary, West Kennet	Neolithic	5	—	—	—	—	5
SU 119683	West Overton Barrow 6*b*	*c.* 1650 B.C.	12	—	—	—	—	12
SU 119691	—	modern	28	16	—	—	—	44
SU 218522	Snail Down	Bronze Age	14	—	—	1	—	15
		modern	25	29	1	1	—	56
—	Easton Down	Bronze	9	1	—	—	10	20
SU 244369	—	modern	13	8	—	12	—	33
SP 429116	City Farm, Eynsham	Middle Bronze, *c.* 1450 B.C.	1	3	4	—	—	8
		pre 500 B.C.	1	1	2	—	3	7
SP 443117	—	modern	8	7	—	35	—	50
SU 131699	Down Barn, West Overton	300–600 A.D.	37	—	—	—	—	37
		modern	21	2	—	—	—	23
ST 773608	Hayes Wood, Freshford	Romano–British	6	3	1	3	1	14
ST 773611	—	modern	16	4	1	9	2	32
—	Ham Hill	Romano-British	6	4	—	2	10	22
ST 479171	—	modern	7	—	7	—	99	113
SY 668885	Maiden Castle	Iron Age?	2	3	1	7	1	14
		Early Iron Age	44	23	—	57	10	134
SY 664885	—	modern (east)	3	6	—	48	4	61
SY 673883	—	modern (west)	4	8	1	29	2	44
ST 820741	Bury Wood Camp	Iron Age (?Belgic)	50	10	17	—	—	77
		modern	18	8	5	1	3	35

Table 1 (*cont.*)

grid reference	locality	period	0	3	3S	5	5S	total
SP 525347	Rainsborough Camp	Iron Age	15	—	—	218	—	233
		modern	34	29	—	56	—	119
SP 374136	Shakenoak Villa, North Leigh	Romano-British	25	10	—	79	—	114
		modern	1	2	—	21	—	24
SP 019066	Bagendon	Iron Age	26	22	16	—	3	67
		modern	17	13	7	1	1	39
SP 080334	Shenbarrow Stanton	Iron Age	1	—	—	8	3	12
		modern	4	1	—	20	2	27
SP 081062	Barnsley Park	Roman	6	6	5	1	—	18
SP 083065	—	modern	—	11	3	15	5	34
SP 960169	Ivinghoe Beacon	Iron Age	2	2	—	63	—	67
		modern	—	—	—	104	—	104
—	Otford	A.D. 1–500	6	—	—	19	—	25
TQ 541593	—	modern	13	4	—	29	—	46
SO 928161	Crickley Hill	medieval	17	12	18	2	—	49
		modern	5	14	23	2	9	53

Note. In a few cases the exact locality of the ancient sample is uncertain and no grid reference is given for it. 0 = unbanded, 3 = mid-banded, 3S = mid-banded with spread bands, 5 = all other banding forms (mainly five-banded), 5S = other bandeds with spread bands. The single shell given as 3S in the Neolithic sample from Avebury was not seen and may be five-banded with complete fusion or 5S. Shells with a complete spread of very dark pigment are scored as 5S, but some might be 3S. Only shells with undoubted spread bands are scored as S (except that from Avebury just mentioned).

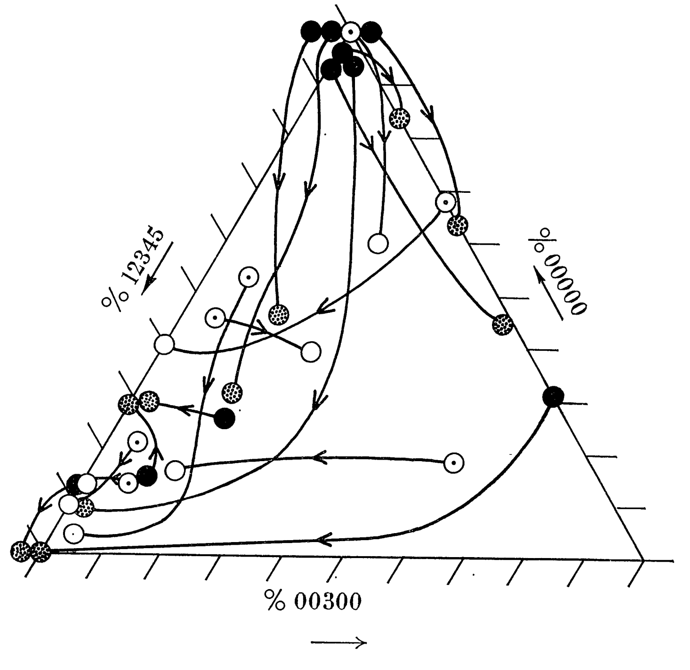

Figure 2. *Cepaea nemoralis*. Pre-Iron Age and corresponding modern samples. Triangle diagram for % unbanded, mid-banded and five-banded (including 00345, etc.). Ancient samples from upland sites: black circles; lowland sites: circle with dot; modern samples from upland sites: dotted circle; lowland sites: plain circle. Corresponding ancient and modern samples linked, arrowhead pointing towards modern sample.

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then be summed by converting to χ^2 (Fisher 1946). The result is $\chi^2_{26} = 39.4$, $P < 0.05$. Consequently the modern samples are closer to the ancient ones from the same site than would be expected if they were distributed at random.

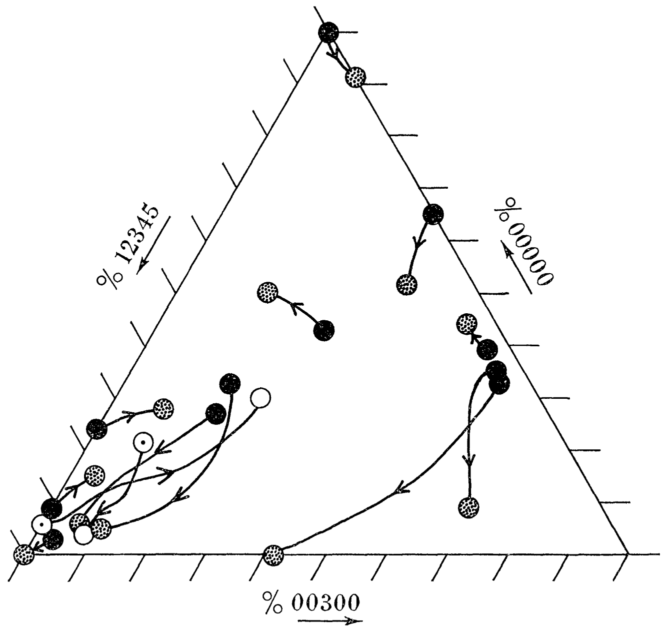

FIGURE 3. *Cepaea nemoralis*. Iron Age and later samples and corresponding modern ones. Symbols as in figure 2.

Not only is the amount of difference small but what movement there is shows no significant trends in any direction.

	00000	00300	12345
increase	5	6	9
same	0	0	1
decrease	8	7	3

(*c*) *Spread banded*

The percentages of the spread-banded morph (Cain & Currey 1963 *a, c*) in all banded shells for each pair of samples are shown in figure 4 for pre-Iron Age sites and in figure 5 for Iron Age and later. All the pre-Iron Age samples that show any spreads lose them completely in the modern samples. On the contrary, the proportions in samples from the Iron Age and later are very close to those in the modern ones, perhaps with a slight decrease to the present time. It should be noted that most of the samples with a high frequency of spread are from the Cotswolds. Too little is as yet known of the present distribution of spread banded for comment to be useful.

(*d*) *Area effects*

At the present day there are two main types of geographical distribution of morph frequencies in *C. nemoralis*.

(i) In lowlands and well-wooded and sheltered districts, visual selection produces considerable variation from place to place, in relation to local habitat (beech woods, mixed deciduous woods, hedgerows, rough herbage). These districts very seldom show a

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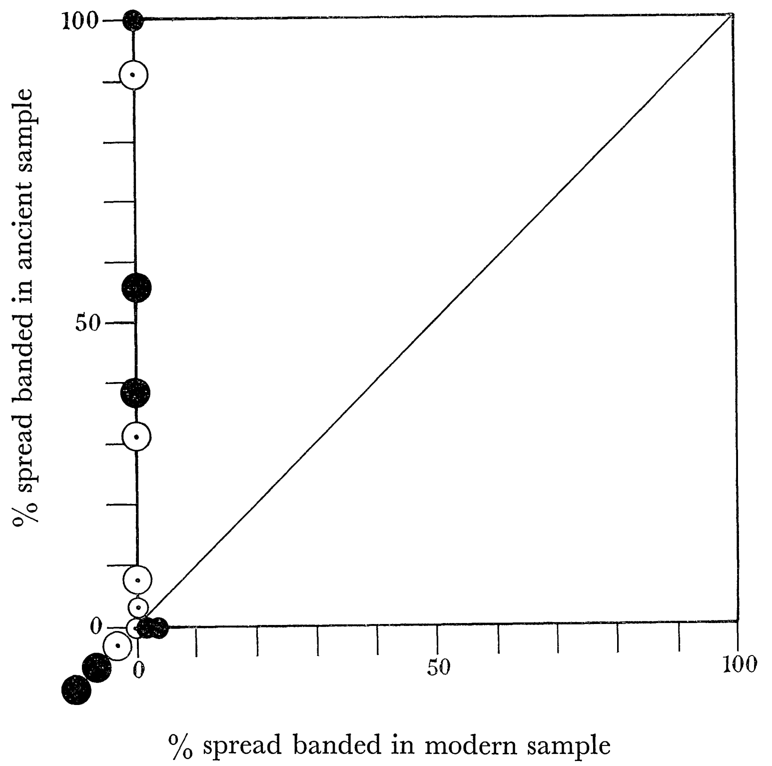

FIGURE 4. *Cepaea nemoralis*. Percentage spread banded in pre-Iron Age and corresponding modern samples. Smaller circles, one or other sample of a pair less than twenty shells. Black circles, upland sites.

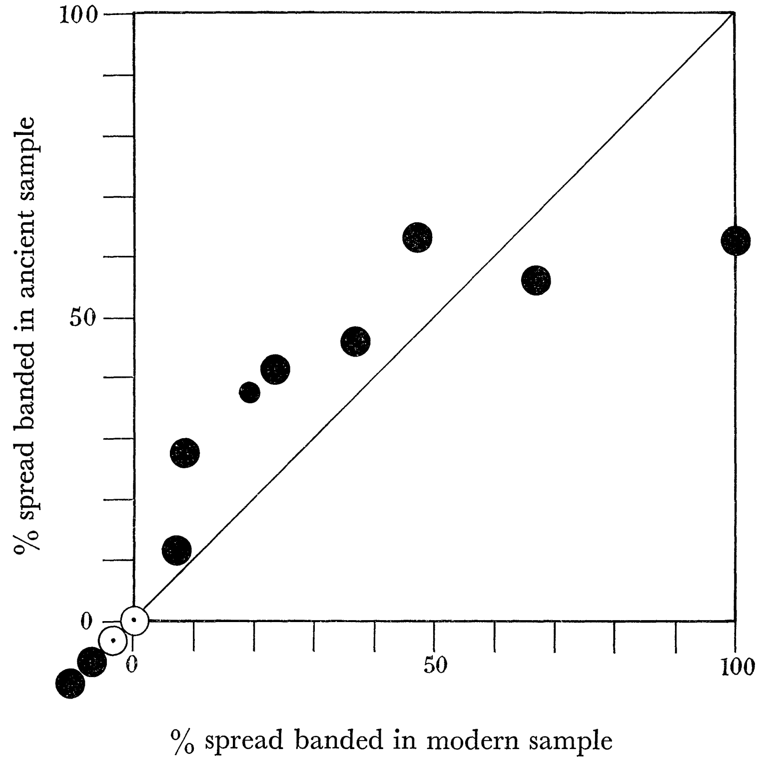

FIGURE 5. *Cepaea nemoralis*. Percentage spread banded in Iron Age or later and corresponding modern samples. Symbols as in figure 4.

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high frequency of unbandeds and mid-bandeds. For example, in the Oxford district (Cain & Sheppard 1954; Cain & Currey 1963 *a*) all 67 samples have more than 20% five-banded shells. In a district of south Warwickshire (Currey, Arnold & Carter 1964) one out of 36 samples has less than 20% five-bandeds.

(ii) In upland areas (Marlborough Downs, Lambourn Downs, Cain & Currey 1963 *a*; Salisbury Plain, Cain & Currey 1963 *c*; Purbeck Hills, Carter, this volume, p. 418; South Downs, Arnold, in preparation; Derbyshire limestone district, Greenwood, in preparation) morph frequencies remain rather constant irrespective of habitat over definite areas, sometimes changing very abruptly at their borders. The resulting types of geographical distribution of morph frequencies are called area effects. They have been described involving high frequencies of five-bandeds, mid-bandeds and unbandeds.

If we have a single sample with no information on its habitat, it is likely to belong in an area effect if it has a low frequency of five-bandeds. If it has a high frequency of five-bandeds, nothing can be said about the selection régime without further information. The two régimes are not exclusive (Carter, this volume, p. 423). In intermediate areas there can be an overlap, with some morphs showing area effects and others apparently still responding to visual selection, or showing a small difference between habitats in the directions to be expected from visual selection but with a mean frequency value appropriate to an area effect. Having ourselves found area effects to be associated with uplands or strong topographical features such as the scarp face of downland or limestone hills, we have taken all upland sites as more likely to be in area effects, defining upland as over 500 ft. in altitude or in association with a strongly marked gradient. Sites are correspondingly shown as upland or lowland in the triangle diagrams (figures 2 and 3).

In one district we have a definite example of an ancient area effect, namely in the south-west corner of the Marlborough Downs. Since our description of the area effects in the south-west area (Cain & Currey 1963 *a*) two subfossil samples from there have been obtained (Down Barn and West Overton Barrow, in the present paper). Figure 6 shows a map of the area with both ancient and modern sites. The ancient distribution of *nemoralis* appears to have been more extensive, stretching down into the valleys (Sanctuary, Silbury, Avebury) and the ancient samples show (with the exception of a single shell) nothing but unbandeds in a total of 1964 shells. At present the main distribution of *nemoralis* is higher on the Marlborough Downs, with many unbandeds and some mid-bandeds; the scattered populations that remain at rather lower altitudes to the west have quite high proportions of five-bandeds. Knoll Down is higher than the others and has no five-bandeds. Here, then, is a present-day area effect involving unbandeds which was formerly more intense and more widespread, extending over lower ground on which at the present day, where *C. nemoralis* persists, there has been a considerable change towards five-bandeds. Snail Down, also a pre-Iron Age sample, has many unbandeds and is apparently (from the modern sample) in a similar area effect today, but with an increase of mid-bandeds. The Brook sample, at the base of the North Downs, has changed from being extremely unbanded to extremely five-banded, and collections nearby show that it is now in a five-banded area effect. Conderton, on Bredon Hill, an outlier of the Cotswolds, has changed from being very mid-banded to entirely five-banded. On Bredon Hill the proportions of five-bandeds are very high, even in a small beechwood. Visual selection may have a little

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Table 2. Scores of subfossil and modern samples of *Cepaea hortensis*

locality	period	0	5	5fus	total
Blashenwell	VII *a*	6	28	14	48
	modern	6	44	15	65
Devil's Kneading Trough, Brook	VII *a*	6	36	—	42
Wateringbury	VII *a*	5	2	—	7
	modern	9	8	2	19
Tilekiln Green	VII *a*	—	5	—	5
	modern	8	10	—	18
Great Offley	VII *b*	2	4	—	6
	modern	13	18	11	42
Avebury	Neolithic	—	7	—	7
	modern	11	45	22	78
Windmill Hill	Neolithic	12	12	6	30
	modern	11	29	6	46
Wayland Smith's Cave	Neolithic	3	10	16	29
	modern (1)	38	16	—	54
Abingdon	Neolithic	29	13	21	63
	modern (2)	43	50	4	97
	modern (3)	53	21	1	79
The Sanctuary, West Kennet	Neolithic	3	10	3	16
	modern (4)	1	11	9	21
Easton Down	Neolithic	—	22	31	53
	modern	6	21	13	40
City Farm, Eynsham	Middle Bronze Age *c.* 1450 B.C.	—	3	—	3
	modern (5)	3	30	11	44
Ham Hill	Iron age and Roman	15	10	3	28
	modern	24	45	5	74
Maiden Castle	Early Iron Age (lumped except sample below)	10	61	14	85
	Early Iron Age	4	26	70	100
	modern (east and west)	5	1	20	26
Shakenoak Villa, N. Leigh	Romano-British	36	11	4	51
	modern	20	29	17	66
Bagendon	Iron Age, Belgic	—	14	2	16
	modern	12	3	8	23
Shenbarrow Stanton	Iron Age	7	3	—	10
Barnsley Park	Roman	2	3	—	5
	modern (6)	5	24	—	29

Note: Map references are as in table 1 except for the following: (1), SU 283854; (2), SU 487993; (3), SU 469978; (4), SU 118679; (5), SP 435115; (6), SP 081064. 0 = unbanded, 5 = plain five-banded (plus slight modification), 5fus = five-bandeds with some fusion of adjacent bands. All samples seen are recorded here.

effect here on modifications of five-banded (Cain & Currey 1963 *a*, p. 37) but there seems to be a definite area effect for five-bandeds, unbandeds and mid-bandeds being few. We can say nothing about those ancient samples which had a high proportion of five-bandeds except that they have perhaps moved less in frequency to the present than have the less banded samples. The conclusion that can be drawn from the pre-Iron Age upland samples is that as far as the evidence goes, samples that were in ancient area effects are likely to be in area effects now, though not necessarily of the same type.

Of the pre-Iron Age lowland samples, Blashenwell was obviously in an area effect and might be in one now. It is from a tufa near Corfe (Dorset), from a geologically very mixed district; no other modern populations could be found nearby because of acid soils. Abingdon and City Farm are near Oxford and adjacent to the classic visual selection district described by Cain & Sheppard (1954). Nowadays they have morph frequencies appropriate to their backgrounds but the ancient samples are very different, and look as if they were in area effects. Here again, then, where any conclusions can be reached, it seems that area effects were present before the Iron Age, even in a district now subject to visual selection.

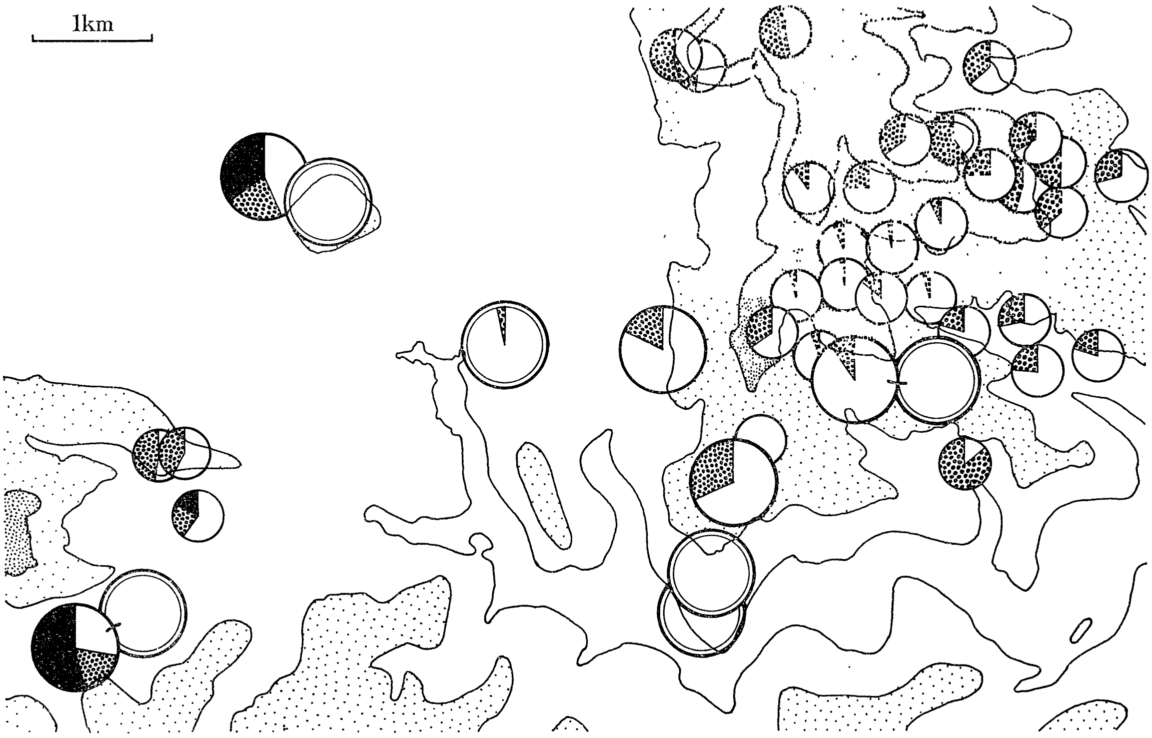

FIGURE 6. The Avebury district. Contours at 100 ft. intervals. Land over 700 ft. heavily stippled; between 600 and 700 ft. lightly stippled. Small circles, modern samples of *C. nemoralis*, with percentage unbanded (white), mid-banded (stippled) and five-banded (black) in all colour morphs added together. Large circles, subfossil samples and nearest modern ones, showing percentage unbanded, mid-banded and five-banded (same convention). Double-ringed circles show the subfossil samples, all pre-Iron Age except furthest on the right (Romano-British). Circles tied are of samples taken within 200 yards. Of the two northernmost, the modern has been displaced north-west for clarity.

Of the Iron Age and later samples, which show little movement, the following are known to be at present in some kind of area effect: Down Barn (Marlborough Downs), Bury Wood, Bagendon, Crickley Hill (all Cotswolds). Barnsley Park (Cotswolds) and Maiden Castle (Dorset) are probably in area effects. About the others we either have no information or know that they are in visual selection areas. So far as our information goes, it seems that area effects have been rather constant from the Iron Age samples to now.

The data presented in this section show: (i) that districts that show area effects now probably showed them in ancient times, though not necessarily with the same morph frequencies;

(ii) that area effects were probably more widespread before the Iron Age than they are now, and (iii) that area effects in general have remained in being with roughly similar morph frequencies from the Iron Age onwards.

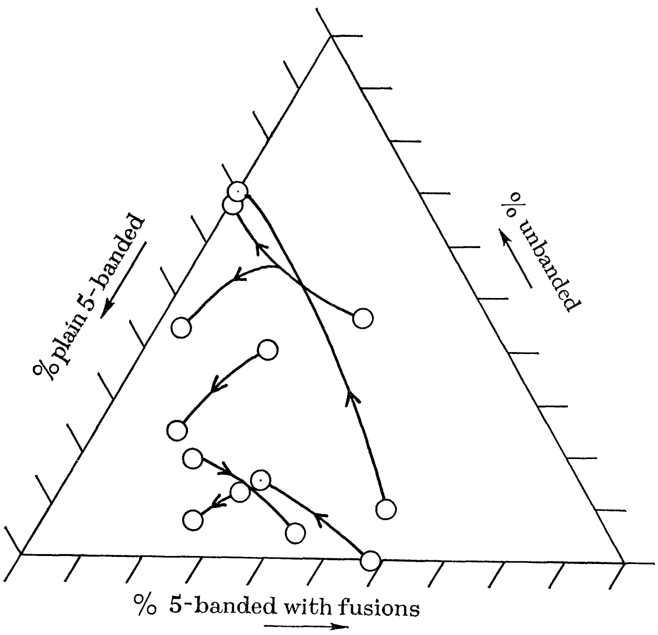

FIGURE 7

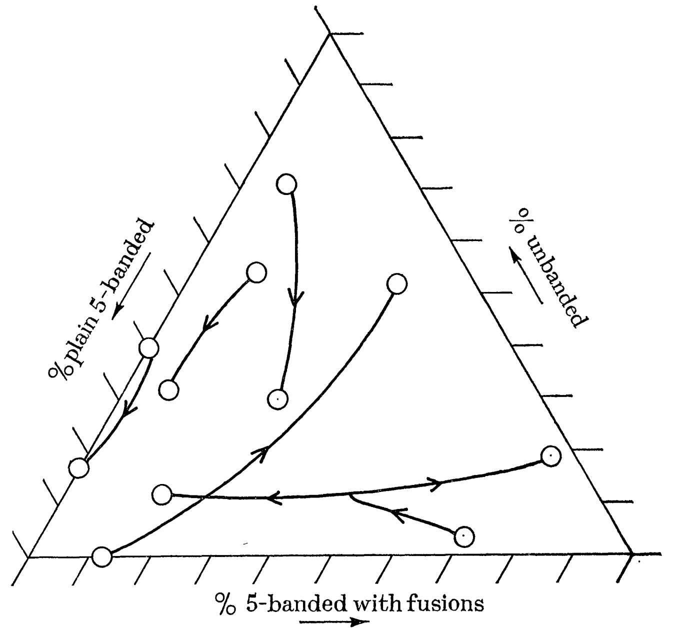

FIGURE 8

FIGURE 7. *Cepaea hortensis*. Pre-Iron Age and corresponding modern samples. Triangle diagram for percentage unbanded, plain five-banded, and five-banded with fusions of bands. Arrowheads point from ancient to modern samples.

FIGURE 8. *Cepaea hortensis*. Iron-Age and later samples and corresponding modern samples. Conventions as in figure 7.

3·2. *Cepaea hortensis*

In this species mid-banded is exceedingly rare, and for the triangle diagrams (figures 7, 8) we take unbanded, plain five-banded, and five-banded with fusions between the adjacent bands (Clarke 1960). The samples obtained are very much smaller (table 2); only those with 10 shells or more are shown on the diagrams. The pre-Iron Age *hortensis* show much difference from the present day, but, in contrast with *nemoralis*, no sign of overall trend. Those of the Iron Age onwards show much more difference from the present day than do the corresponding ones of *nemoralis*, again with no special trend. As yet, too little is known about the morph frequency variations of *hortensis* over large districts for any interpretation in terms of variation and selection régimes to be attempted, but it is clear that, as in its response to visual selection (Clarke 1960), *C. hortensis* is behaving very differently from its sibling *nemoralis*.

4. DISCUSSION

The sites for which we have samples are scattered over southern England in a good variety of places topographically, some at the foot of a chalk scarp, others on chalk or limestone uplands, two on calcareous gravels, some on isolated hills, others in valleys, others on gently undulating plains. All they seem to have in common beyond a calcareous or very calcareous soil is the general climate. It is known that over this large region (and

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indeed the rest of the British Isles) there have been considerable changes of climate since the height of the last glaciation, and if there has been a general trend in morph frequency over such a diversity of places, climate is naturally the first possible selective agent to be tested. Cain & Sheppard (1954) originally pointed out that there was some evidence of relation between morphs of *C. nemoralis* and climate in the extensive data of Lamotte (1951) for colonies scattered over France. Lamotte (1959) has since stated that there are associations between morph frequency and climatic conditions generally and has made experiments, as has Sedlmair (1956), which indicate that certain aspects of climate, especially temperature, are important as selective agents. Carter (in preparation) has confirmed Lamotte's results on juveniles. In particular, unbanded is stated to be more resistant to extremes of temperature than banded. At the present time, there is evidence that unbanded and mid-banded are more frequent in southern and central than in northern France (Lamotte 1954). The frequencies given are higher than those found in England generally. There is some evidence therefore, at the present day that unbanded and mid-banded may be associated with warmer summers, and five-banded with cooler ones.

A summary of work on the time-scale and climatic changes of the Holocene in Britain is given by Godwin (1956) as a framework for his account of floral changes in that period. There has been much subsequent work, which has not changed the major results, all that need concern us here, but references can be found in Johnson & Smith (1966). From the end of the Late-glacial period (pollen zones I, II and III, ending about 8000 B.C. according to Godwin & Willis 1959) there seems to have been a fairly steady improvement of mean temperature during the pre-Boreal and Boreal periods (zones IV, V and VI) culminating in the so-called 'climatic optimum' or hypsithermal of the late Boreal and early Atlantic periods (*ca.* 5500 to 4000 B.C.) when the mean summer temperature may have been 2·5 °C (4·5 °F) higher than at present. In the early Atlantic period the climate became distinctly wetter than in the Boreal, and Kerney, Brown & Chandler (1964) ascribe the formation of the tufa in the Devil's Kneading Trough (Brook, Kent) to this time; they quote a radiocarbon date of 4490 ± 150 B.C. (early VII *a*) for the tufa at Blashenwell, which is associated with a mesolithic industry. Our earliest samples of *Cepaea* are from these and other tufaceous sites. After the hypsithermal, pollen analysis indicates a rather drier climate and cooler summers (sub-Boreal period, zone VII *b*) although warmer than at present. The Neolithic and Bronze ages in South Britain fall into this period. About 400–500 B.C., in the early Iron Age of Britain, there was a marked deterioration (Godwin 1956, 1960) after which (Subatlantic period, zone VIII) the climate was as damp and cool as now. Of course there have been fluctuations throughout the periods as at the present day, but the major trends of temperature and dampness were as just described.

We have a few samples from the time of the hypsithermal, a number from Neolithic and Bronze age sites, and a number from Iron Age ones (Belgic, Romano-British and Anglo-Saxon) too few as yet to warrant further subdivision. The most useful grouping to test association with well-known change of climate is into pre-Iron Age and Iron Age as earlier in this paper. The pre-Iron Age samples compared with present-day ones show a significant change (p. 487 above) in the direction we expect from the evidence of present-day distributions and of experiments in relation to climate, there having been overall considerably more unbandeds (and perhaps mid-bandeds) when the climate in southern England approached more closely to that in present-day southern France. If morph frequencies were being determined by sampling drift, we should expect the directions of the changes within each pair of ancient and modern samples to be at random over the diagram (figure 2), which these clearly are not (p. 487). Drift could, however, produce the appearance of a directed change if all the populations began at one extreme or other of possible frequencies, since then there could be alteration only in one direction. Again, figure 2 shows that this is not the case with our pre-Iron Age samples. It is true that four are completely unbanded. If these are excluded on the grounds that only change in one direction is possible, we are left with two that have increased in unbanding and eleven that have decreased, which has $P = 0{\cdot}022$. Therefore the relationship between the present-day and pre-Iron Age samples can hardly be explained by sampling drift. Climatic selection is much the more likely explanation of our data and suggests that the selective agent bringing about the overall change in banding morph frequencies since the 'climatic optimum' is mean or maximum summer temperature. We have evidence (Cain & Currey, this volume, p. 461) that provided there is a snow cover, adult *Cepaea* in hibernation are unaffected by even severe winters, and considerable changes in winter temperature are not likely to affect these species.

The similarity between the Iron Age and present-day samples can also be explained by climatic selection, since over the period they span there has been no change of climate comparable with that before 450 B.C. Climatic selection, therefore, could be expected to stabilize the morph frequencies over the period since 450 B.C., or, without stabilizing, to have no net effect. However, we know nothing of population sizes at our sites, and it is conceivable that the climate in southern England in the last 2000 years has been such as to exert no selection upon any of the banding morphs, and the genes have been effectively neutral. Then, over a period of 2000 years, which is only about 500 generations, with large populations, it is possible that drift has had only a slight effect and overall, samples from the same site are more similar than one would expect by chance. The likelihood that genes with major effects such as these (and no doubt others not yet identified) should remain effectively neutral for 2000 years seems slight; and in fact, Clarke & Murray (1962) have shown a mean selection on 00300 of at least 0·05 over 30 years, within, of course, the period (Iron Age to the present) under discussion.

Drift has been supposed to act in *Cepaea* populations in relation to area effects. Goodhart (1963) and Wright (1965) have suggested that initial chance differences in morph frequencies in founding populations of *C. nemoralis* have been perpetuated through the development of genotypes in each adapted to that particular frequency, with consequent hybrid breakdown when the populations spread and meet, providing a barrier to their merging. The large changes in morph frequency between pre-Iron Age populations and modern ones on the same site together making a significant trend suggest either (i) that morph frequencies can change in the same persistent population subject to area effects under the influence of selection regardless of co-adaption in the genotype generally, or (ii) that co-adapted genotypes in different populations are themselves selected in competition with one another when the populations spread and meet as we have suggested (1963*d*) and the result will be determined mainly by selection in relation to the environment. Either way, the importance of environmental selection is clear.

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