NEW DATA ON THE GENETICS OF POLYMORPHISM IN THE SNAIL CEPAEA NEMORALIS L.

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A REVIEW of the remarkable polymorphism in the European land snail *Cepaea nemoralis* L. and of the various interpretations based on it has been given in a previous issue of this journal (CAIN and SHEPPARD 1954). Since the adaptive and evolutionary significance of the polymorphism is the subject of active research, a considerably better knowledge of its genetics is desirable. Subsequently, LAMOTTE (1954, 1959), and CAIN and SHEPPARD (1957) have provided more data. The purpose of this paper is to present further information from the breeding program being carried out at Oxford and to consider the significance of the dominance relations revealed.

Orange bands

This form is characterized by having both bands and lip, i.e. all parts normally with dark pigment, a brownish orange instead of dark brown or black. (This orange color is often found in the shells of snails with normally colored bands which have been badly scorched in grass fires, and must not be mistaken for the genetically orange form). The orange pigment may be missing in young individuals, so that they seem like hyalozonates (with unpigmented bands), but they develop the characteristic orange-brown pigment later in life. We have found this form only in one small locality in the Oxford district (in which it is not uncommon). One specimen which looks the same was seen in a sample from Bundoran, Western Ireland, very kindly shown to us by DR. A. COMFORT.

This form is recessive to normally-pigmented bands, since in mating ES 1 (Table 1) one normal-banded parent and one orange-banded gave only normally-banded progeny. This conclusion is confirmed by EX 1, in which no orange-bandeds were produced among 19 individuals, all of which are progeny of the orange-banded adult. The form is not phenotypic modification since it segregates from an orange-banded parent in EM 1. E 2 was set up with adults taken from the wild, but all eight progeny are orange-banded, and therefore must be the result of a mating between them.

All the orange-bandeds we have seen in the wild have been pale yellows, never pinks, although the pink allelomorph is common in this population. This suggests that there is linkage between shell color (pink and yellow) and color of banding, unless the gene producing the paler bands is also removing the pink or yellow pigment from the shell, producing pale yellows. Alternatively, the gene may not exert any effect in the presence of the allelomorph for pink.

TABLE 1

*General list of broods**

Brood no.		Parents		Progeny			
E	2	w	10345 ob Ad	Yw	12345 ob	8	
		w	12345 ob Ad				
EM	1	w	00300 ob Ad	PP	00300	1	
				PP	12345	1	
				Yw	00300 ob	2	
				Yw	10345 ob	1	
ES	1	Yw	12345 ob	Y	12345	15	
		Y	12345				
EX	1	w	12345 ob Ad	PP	00300	2(2)	
		PP	00300	PP	12345	3(1)	
				Y	00300	6(1)	
				Y	12345	3(1)	
L	1	Y	00000	DP	00000	8	1957 item 13 with additions.
		DP	12345	DP	12345	11	
				PP	00000	4	
				PP	12345	9	
L	2	DY	00000	DP	00000	9	1957 item 14 with additions.
		DP	12345	DP	00300	6	
				DP	12345	5	
				PP	00000	11	
				PP	00300	3	
				PP	12345	4	
L	4	B	00000	B	00000	1	1957 item 15
		B	00000	PP	00300	1	
L	5	Y	12345	PP	00300	1	
		PP	00300				
L	9	B	00000 } sibs,	MB	00000	2	
		PP	00300 } prog. L 4	PP	00300	1	
L	10	PP	00300 } sibs,	PP	00300	12	
		PP	12345 } prog. L 2	PP	12345	21	
				PY	00300	4	
				PY	12345	6	
L	11	DP	00300 } sibs,	DP	12345	1	
		DP	12345 } prog. L 2	PY	00300	1	
				PY	12345	1	
L	12	DP	00000 } sibs,	DP	00000	38	
		DP	00000 } prog. L 2	DP	00300	3	
				DP	12345	9	
				DY	00000	6	
L	13	PP	00000 } sibs,	PP	00000	18	
		PP	00000 } prog. L 2	PP	12345	9	
				DY	00000	7	
LE	1	PP	00300 prog. L 5	PP	12345	3	
		Y	12345	Y	00300	1	
M	2	P	12345	PP	00300	22	1957 item 3.
		PY	00300	PP	12345	10	
M	3	P	12345	DP	12345	2	1957 item 4 rescored as far as possible, with additions.
		Y	00300	MP	00300	1	
				MP	12345	9	
				PP	00300	8	
				PP	12345	6	
				PP	02345	1	
				PP	00345	1	

M	5	PP	00000	PP 00000	1	1957 item 5.
		Y	12345	PP 12345	3	
M	6	PP	00000	PP 00000	26	1957 item 6.
		Y	12345	PP 12345	15	
M	7	P	00000	PP 00000	36	Revision of extant material: all were MP in 1957 item 7.
		Y	12345	PP 00300	13	
				PP 12345	18	
M	8	B	00000	B 00000	2	1957 item 11: pinks there shown as MP.
		DP	12345 db	DP 12345	1	
				PP 12345	2	
M	14B	PP	00300 sibs,	PP 00300	4	
		PP	00300 prog. M 2	PP 12345	2	
				PY 00300	1	
				PY 12345	2	
M	15	B	00000 sibs,	B 00000	2	
		PP	12345 prog. M 8	PP 12345	2	
M	16	PP	12345 sibs,	DP 12345	7	
		DP	12345 prog. M 8	DP 12345 db	1	
				PP 12345	10	
				PP 12345 db	4	
M	17	PP	00300 sibs,	PP 00300	7	
		PP	00300 prog. M 3	PP 12345	3	
				Y 00300	2	
M	18	PP	00000 sibs,	PP 00000	12	
		PP	00000 prog. M 7	Y 00300	1	
				Y 12345	1	
ME	1	PP	00300 db prog M 3	PP 00300	10	
		Y	12345	PP 12345	4	
				Y 00300	10	
				Y 12345	5	
ME	2	PP	00300 prog. M 2	PP 00300	1	
		PY	12345	PY 12345	5	
ME	4	PP	00000 Ad? prog. M 7	PP 00000	11	
		Y	12345	Y 12345	13	
ML	1	DP	00000	DP 12345	20	1957 item 16 with additions: MP all rescored as DP.
		Y	12345	PP 00000	21	
ML	2	MP	12345 probably DP but faded: prog. M 3	DP 00000	11	
				DP 12345	5	
				PP 12345	9	
		PP	00000 prog. L 2	DY 00000	7	
ML	3	DP	12345 prog. M 3	DP 12345	26	See Table 2 for details.
		DP	12345 prog. L 2	DY 12345	11	
MP	1	Y	00300 hz Ad	DP 00000	3	Progeny of either parent.
		DP	00000	DP 00300	1	
				Y 00300	17	Progeny of Y only.
MR	1	PP	00000	PP 00000	42	1957 item 8.
		Y	12345			
MR	2	Y	00000	PP 00000	15	1957 item 9 with additions.
		PP	12345	PP 12345	10	
				Y 00000	9	
				Y 12345	15	
MR	3	DP	00000	DP 00000	45	1957 item 10.
		Y	12345	Y 00000	33	

TABLE 1—Continued

*General list of broods**

Brood no.	Parents	Progeny	
MR 4	PP 0000t0 B 00000	B 00000 9 B 000t00 1 PP 00000 7 PP 0000t0 1 Y 00300 2 Y 12345 3	1957 item 12: trace bands not then scored.
MR 23	PP 00000 prog. MR 1 Y 12345 prog. MR 2	PP 00000 41 Y 12345 48	
MR 28	PP 00000 } sibs, Y 00300 } prog. MR 4	PP 00000 3	
MR 30	DP 00000 prog. MR 3 Y 12345 prog. MR 4	DP 00000 36 Y 12345 22	
MR 31	DP 00000 prog. MR 3 Y 12345 prog. MR 4	DP 00000 16 Y 12345 19	
MR 32	B 000t00 prog. MR 4 Y 00300 S prog. R 5	B 00300*S 1 B 00300 1 Y 00300 2 Y 00300*S 1 Y 02345 S 1	Very thin band. Too small for S.
MR 34	DP 00000 prog. MR 3 Y 00300 prog. R 5 Y lost: not scored for S	DP 00000 8 DP 00300 S 4 Y 00000 1 Y 00300 S 3 Y 00300 5	
MR 35	DP 00000 prog. MR 3 Y 00300 prog. R 8	DP 00000 9 DP 00300 2 Y 00300 11	
MR 36	PY 00000 Ad PP 00000 prog. M 6	DP 00000 16 PP 00000 7 Y 00300 6	
MR 38	PP 00000 prog. MR 1 DP 00000 prog. MR 3	DP 00000 10 PP 00000 7 Y 12345 1	
MR 39	PP 00000 prog. MR 1 DP 00000 prog. MR 3	DP 00000 13 PP 00000 4 Y 12345 6	
P 1	Y 00000 al Ad PP 00300	PP 00000 2 PP 00000 nl 1 Y 00000 1 Y 00000 al 2	Probably progeny of Y 00000
P 2	DP 00000 rl } sibs, DP 00000 } prog. PH 1	DP 00000 18 DP 00300 2 Y 00000 5	
PH 1	PP 00300 rl Ad	DP 00000 nl 1 DP 00000 rl 1 PP 12345 nl 1	

PLN	1	PP	00000 prog. P 1	PP	00300	1	
		Y	00300 hz	PP	12345	1	
				Y	00000	2	
PM	1	PP	12345 prog. M 5	PP	00000	4	
		Y	00000 al prog. P 1	PP	00300	4	
				Y	00000	4	
				Y	00300	2	
POE	1	PP	00000	PP	12345	30	
		Y	12345	Y	00000	28	
R	1	B	00000	B	00000	18	
		B	00000	DP	00000	2	
R	4	B	00000	B	00000	7	1957 item 2, with additions.
		B	00000	DP	00300	3	
R	5	B	00300 S at end	B	00300	18	Indistinct band.
		Y	00300	Y	00300*S	19	
				Y	00300	1	Not scored for S (MR 34)
R	8	B	00300 Ad	B	00000	1	prog. B 00300.
		B	00300 Ad	B	?	1	
		P	12345	B	00300	2	
				P	00300	1	
				Y	00300	1	
				B	00300	11	prog. P 12345.
				P	00300	3	
				Y	00300	7	
RE	1	B	00300 prog. R 8 B 00300	MB	00300	11	
				PB	00000	2	
		Y	12345	PB	00300	1	Indistinct band.
				PB	00300	4	Full band.
				Y	00300*S	17	
RE	3	MB	00300 prog. R 8	PB	12345	1	
		Y	12345	PP	00300	4	
				PP	12345	1	
RL	2	MB	00000	B	00000	15	1957 item 1.
		Y	00300	PP	00300	24	
T	2	MB	00000	DB	00000 nl	1	
		PP	00300 rl, band hz or pale	PP	00300 al	1	pale band.
				PP	00300 hz?	1	small.

* Key:

Column 1: Brood number consists of letters giving provenance of stock followed by a serial number. E=Eynsham road, near Oxford; H=Hackpen, Wiltshire; L=My Lady's Seat, Wytham, Berkshire; LN=Lambourn, Berkshire; M=Marley Wood, Wytham, Berkshire; P=Pentridge, Dorset; PO=Portnoo, Donegal; R=Rockley, Wiltshire; S=Swindon road, Wiltshire; T=Thruxton, Hampshire; X=Uncertain origin.

Columns 2 and 3: B=Brown; P=Pink; Y=Yellow; (With prefix D (Dark), M (Medium), P (Pale). If the depth of color is uncertain, no prefix is given.); Yw=Very pale, whitened Y; w=White shell, color not ascertainable.

00000=Unbanded (0[t] means a trace of that band occurs near lip of shell); 00300=Mid-banded; 12345=Five-banded—i.e., with no band completely absent in the adult, unless otherwise specified. Fusions are ignored in this table.

al=Albolabiate; rl=Roseolabiate; db=Darkening bands; ob=Orange bands; hz=Hyalozonate; S=Spread bands. The absence of a symbol indicates that this character is normal. But with al or rl in column 2, the absence of a symbol or comment in column 3 means that the character is as yet unscorable in the progeny: where lip is known and normal, nl is used.

* Includes individuals which have parts of bands other than band 3 present, although carrying the gene controlling 00300.

Ad=Adult when mated; could have been fertilized already; Ad?=Adult; possible, but unlikely that it had been fertilized; prog. followed by brood number=parent is progeny from this brood.

Plain figures in column 3 are for progeny of the mating as stated; figures in parenthesis are of dubious parentage.

Hyalozonate bands ("albino" of several authors)

Of 18 banded offspring from the adult yellow hyalozonate in MP 1, not one was hyalozonate. This shows that hyalozonate is recessive to normal bands, as previously reported by LANG (1911).

Darkening bands

This form is characterized by the presence of bands which are not fully pigmented when they are first laid down, and consequently appear on the upper whorls of the shell as medium brown instead of deep brown or black. This dilution of pigment continues until the animal is approximately half-grown; thereafter, increasing amounts of dark pigment are laid down as successive additions to the shell are made, until on the last parts to be formed—next to the lip—full pigmentation is found. Even on the uppermost whorls, the bands are always much darker than in the orange-banded form.

Care must be taken in scoring this character when either the bands are very narrow, or there are varices present. In the first case, if the band is thin enough to be interrupted in places, it can be seen to be much paler close to the interruptions, where its width is least, than a little farther away; such very narrowed and often interrupted bands are what LAMOTTE (1951) has called "bandes pâles." He has shown them to be dominant to bands of normal width. Darkening bands are of normal width, or rather, the gene can affect bands irrespective of width, but its presence cannot be observed in bands which are so narrow as to be pale anyway. In the second case, it is well-known that if the animal stops making additions to the shell for a time, a line, or ridge, termed a varix, remains to show the limit of the shell before the pause, even after much more has been laid down. Such a pause often occurs when the animal is half-grown and hibernates in its first winter. When it starts in the spring, leaving a varix to mark the limit of the shell in that winter, the new part of the shell is often paler in ground color, and also in the pigmentation of the bands. The tone produced in the bands is often almost identical with that in a half-grown animal with darkening bands. As far as the bands visible on the last whorl are concerned, an adult animal with such a history looks like a very marked example of darkening bands; but just inside the mouth will be found a varix, and beyond that, the bands will be normally colored.

In M 8 a darkening-banded five-banded dark pink was mated to an unbanded brown, giving one dark pink five-banded and two pale pink five-banded, all with fully colored bands, (also two unbanded browns). One pale pink was sibmated to a dark pink (M 16), and gave the progeny shown, in which there is a clear 3:1 segregation for normal *vs.* darkening bands. Since dark pink and pale pink are allelomorphs (see below) and darkening bands appear in both dark pink and pale pink progeny, it cannot be controlled at the pink locus, and this brood gives evidence that the two loci responsible are not (or not very closely) linked. That darkening bands is recessive, as indicated by M 16, is confirmed by ME 1, in

which a normal-banded and a darkening-banded parent gave 29 offspring, all normal-banded.

Brown

That brown shell color is determined by an allelomorph at the locus controlling pink and yellow, and is dominant to these other colors (as already suggested by CAIN and SHEPPARD 1957) is supported by our additional breeding data.

Not only do broods L 4 (1957, item 15), R 1, and R 4 (1957, item 2) when summed give a 3:1 ratio, but whenever two heterozygous browns or one such brown and a yellow are mated (MR 32, R 5, RE 1, RE 3, RL 2 (1957, item 1)) only browns and one other color class segregate among the offspring. If brown were not an allelomorph at the locus controlling pink and yellow (nor extremely closely linked to it), both these colors as well as browns should appear in some broods, as they do in the brown × pink mating (MR 4). Furthermore, despite a slight epistatic effect of brown on banding (see below), it is clear from broods L 4, L 9, M 8, M 15, MR 4, R 4, and RL 2 that the locus determining the presence or absence of brown is very closely linked to that controlling banding, as is the locus controlling pink or yellow shell color (see below).

Spread bands and penetrance of banding in browns

The form 'spread band' has a wide middle band, often unusually heavily pigmented, with to either side of it, on the upper parts of the shell, traces of the other four bands, which may so extend and fuse farther down the shell as to give the appearance of a five-banded shell with complete fusion of all bands. In this case, the predominance of the middle band is still usually evident right up to the lip.

In R 5, the yellow parent had a strongly pigmented middle band, not unusually wide; the brown parent had a markedly widened middle band with a spread only at the mouth but with occasional traces of the other bands further back. The yellow offspring all have a very heavy middle band and all those scored have a definite spread on either side of it. The brown offspring have only an indistinct middle band, devoid of a spread and in some hardly visible. From these progeny were set up MR 32 and 34. In both, the spread-banded character has reappeared; in MR 34 it is segregating in the yellow class, and appears also in the pinks.

Since only one of the parents of R 5 had spread bands, and it reappears only in its yellow offspring, the character would appear to be dominant, with its allelomorph carried on the yellow chromosome of the brown parent.

In MR 32, the brown parent came from MR 4 which gave no spread bands in five yellow bandeds. The yellow parent came from R 5, had spread bands, and produced spread bands in the two scorable yellow progeny and in one brown. This suggests again that spread bands is dominant and exerts its effect in brown as well as yellow. The other of the two brown progeny is as yet too small for a certain score of banding, but is not as heavily banded as the first, and may even be not banded at all; this suggests segregation within the brown class, as might

be expected. The banded brown is apparently genetically abnormal in other respects (see below).

It might be objected that there is some interference between brown and the expression of the gene. The brown parent of R 5 supports this suggestion. If this is so, the spread-banded character is still dominant, but its linkage relationships remain undetermined. In RE 1, since the allelomorph is a dominant and appears in all the yellow progeny, one of the parents must be carrying it. The yellow parent is a normal five-banded; the brown has an exceptionally wide band but no traces of the other bands. The brown progeny have bands varying considerably from nearly normal width to very narrow, and correspondingly from fairly well-pigmented to very faint, and there are two which have no trace of any band. This appears to be a continuous variation. RE 1 also suggests from the appearance of the brown parent that the gene has sometimes a less marked effect in browns than in yellows. Since the brown progeny in both R 5 and RE 1 tend to have narrow or very narrow bands, not resembling the broad bands of the brown parents, it appears that they are not carrying the spread gene, which therefore is most likely to be linked with color, as suggested above. In RE 3, a mating between a brown narrow-banded 00300 from R 8 and a normal yellow five-banded, exactly as in RE 1, no spread bands appear in six progeny, and since no yellows appear, but brown and pink segregate, the brown could not have been carrying the spread gene, if as suggested the latter is linked to yellow. This mating, therefore, supports strongly the suggestion of linkage.

The suggestion that spread bands has less expression in browns is supported by the observation that normal middle bands is also reduced in browns. In RE 1, the two banded parents produced 35 offspring, of which two are phenotypically unbanded. From the known dominance of unbanded to banded, this is impossible; and in fact, these two seem to be only at one extreme of the continuous variation in the brown progeny, in many of which the band is markedly narrow, especially when compared with the yellows of the same brood. There is no doubt, therefore, that in this brood, the penetrance of midbanded in the brown class is not perfect. Similarly in R 5 the banding is weak in the brown class; in fact, when this brood was scored in November, 1958, five had no trace of a band. One developed a trace later, but this and the other four died when still rather small, and as they might or might not have developed bands they are not included in the table of broods. However, one of the RE 1 apparently unbanded browns is now over half-grown, and still has no trace of banding. The other is about one third grown. On the other hand, in R 8 (in the progeny of the pink 12345) the 11 browns all have well-marked bands, as expected. Similarly, in RE 3, the only brown offspring is banded as expected. The total number of browns expected to be banded is 50, of which two are unbanded.

Spread bands, therefore, appears to be a dominant, linked with color (in the matings reported, to yellow) and fully expressed in yellows. In browns, the expression of banding including spread bands, is sometimes reduced. Narrow band-

ing in browns may perhaps be a different allelomorph at the same locus, or only normal banding interfered with in browns.

The brown parent in MR 32 is unbanded with a very slight trace of band 3 almost at the lip. It was produced by MR 4, the brown parent in which was unbanded. However, it has given rise to two browns, one of which (the abnormal one mentioned above) is most remarkable in that the first few whorls are yellow 00300, and then change abruptly to brown with spread bands. Banded browns would not be expected at all in the progeny of this mating, unless there had been a crossover, or the brown parent is really banded genetically (as might be indicated by the trace of band 3). The change from yellow to another color in animals up to one quarter grown is shown by many yellow-spired individuals heterozygous for yellow, and this condition appears to be connected by continuous variation with ordinary yellow tip (see below). Until more offspring can be obtained from this mating, little more can be said about the penetrance of banding in browns.

Fusions and width of bands within the 12345 class

Mating ML 3 was between a :2345 dark pink and a 12345 dark pink. The progeny are shown with detailed scorings for banding in Table 2. The result

TABLE 2

Fusions and reductions of bands in brood ML 3

Parents: DP : $_{2345}$ × DP $_{12345}$			
Progeny:			
DP		DY	
12345	3	$_{123}45$	1
$_{1}2345$	3	$:_{23}45$	1
$_{12}345$	2	$:_{2}3_{45}$	1
$_{1}234_{5}$	2	$0^{t}:_{345}$	1
$_{12}34_{5}$	3	$0:34_{5}$	1
$:_{2}34_{5}$	1	$::_{3}(4_{5})$	1
$:_{2}3_{45}$	1	$_{123}(45)$	1
$0:_{2}4_{5}$	1	$:_{23}(4_{5})$	1
1(23)45	1	$(_{12})_{3}(45)$	1
1(23)(45)	1	$(:_{2}3)(4_{5})$	1
$_{1}$(23)(45)	1	$(:_{23}(4_{5}))$	1
$_{1}(_{2}3)(45)$	1		—
$(_{1}(23)(45))$	1		11
$:((_{2}3)(4_{5}))$	1		
:(2345)	1		
$:(_{2}3)(4_{5})$	1		
$(:234_{5})$	2		
	—		
	26		

Key: 12345 Full bands $1_{2}345$ Reduced band 2
1:345 Intermittent band 2 $10^{t}345$ Trace of band 2
123(45) Fusion of bands 4 and 5 (1(23)(45)) Fusion of 2 and 3, 4 and 5, with later fusion of all.
Fusions of bands are scored as at three-fourths grown; in adults this is therefore the condition at the level of the lip on the penultimate whorl.

demonstrates that both fusion of bands and the width of bands, and their reduction to almost absence in the case of bands 1 and 2, are multifactorially controlled, with no clear-cut segregation. The time of onset of fusions is also continuously variable. It is noticeable, however, that in none of the progeny (with two exceptions which are still very small) was any band clearly and wholly absent, a condition which, for some combinations at least (00300, 00345) is known to be controlled at a single locus.

Depth of pink

Previously (1957) we distinguished three shades of pink, dark, medium and pale. Although this classification is valid on color alone, the medium pinks include both individuals which are genetically dark, and some which are genetically pale. Our previous difficulties can now be cleared up.

The pink parents of both L 1 and L 2 (previously reported as items 13 and 14 (1957) now reported with additional progeny) judging from their offspring must be homozygous pink, and are dark. Both produced a segregation (1:1) of dark and pale pink. Consequently, either dark is dominant to pale pink, or pale is controlled by a modifier of pink at a different locus, brought in from the yellow parents. But in this latter case, either pale pink or dark pink must be heterozygous for the modifier in the progeny, but not both. However, the sib matings L 10, 11, 12 and 13 disprove the hypothesis of modifiers, since there is no segregation of dark and pale pink in broods with either both parents dark or both pale. Since all these parents were heterozygous for yellow, and the hypothesis of modifiers is disproved, dark and pale pink must be allelomorphs. The broods from L 12 and 13 demonstrate linkage between both shades of pink and banding. M 16 shows a backcross for pale and dark pink. On rescoring the previously reported offspring when they were more nearly full-grown, and by comparing them with the undoubted darks and pales of L 1 and L 2, we find that in the broods previously stated to have produced only pale pinks from a medium pink parent (M 5, M 6 and MR 1; items 5, 6 and 8 in our previous paper), the parents were in fact pale. There is no reason, therefore, to doubt the allelomorphism. In ML 1 (previously reported as item 16), the medium pink parent is in fact dark, and is producing a segregation for dark and pale, which confirms the allelomorphism since all are heterozygous for yellow; and the pale pink allelomorph is linked with unbanded, the dark pink with five-banded. The medium parent is dark also in MR 3 (reported as item 10). In M 8 (item 11) the progeny are one dark and two pale pinks.

In L 13, all the pale pink unbandeds are heterozygous for yellow, all the pale pink bandeds are homozygous. It is often observed that the presence of banding is correlated with a lightened ground color of the shell. Nevertheless, inspection of the homozygotes and the heterozygotes in L 13 shows that the heterozygotes are lighter in tone, and a more orange pink, while the homozygotes are darker and a more bluish, less orange pink. Presumably, if the homozygotes had been unbanded, the difference would have been greater. It is possible, therefore, that

some confusion might be caused by homozygous pale pinks looking as dark as a rather pale or somewhat faded dark pink. Dark pink heterozygotes seem to be dark; this explains the excellent segregations between dark and pale pinks in the progeny of L 1 and L 2.

It appears, then, that when whole broods are taken into consideration, there is no difficulty in scoring dark and pale pinks; but the scoring of unrelated individuals may not always be straightforward, and we find that living dark pinks may fade perceptibly over a period of a few years, so as to cause some confusion.

Color of tip in the pink and brown classes

In L 1 and L 2, all pink individuals in the progeny are heterozygous for yellow. The dark pinks all have a pink tip to the shell. By tip is meant the shell as possessed by the newly hatched young, plus about one successive whorl. The pale pinks mostly have yellow tips (and in fact the yellow may extend much further down the shell, but this is not a character in question here). In L 12 (dark pink × dark pink) we know that the pinks which are heterozygous for yellow are unbanded, those homozygous for pink are banded, because there is very close linkage between color and banding (see also below). All the progeny of this mating have pink tips. In L 13 (pale pink × pale pink), in which we have the same situation with regard to heterozygosity and banding, the nine homozygotes have pink tips, while 17 of the 18 heterozygotes have yellow tips, the remaining one having a pink tip. This strongly suggests that although heterozygotes cannot be recognized by tip-color in the dark pink class, in pale pinks the heterozygotes for yellow often have a yellow tip. This is amply confirmed by the rest of our data. The pink parents of M 5, M 6, and MR 1 have pink tips and are known to be homozygous pale pinks by their progeny. The pink parent of MR 2 is yellow-tipped and heterozygous. In M 16, in which the pale pinks are almost certainly homozygous, none out of 14 have yellow tips. For the pink progeny available in good condition for scoring and known to be heterozygous, the color of the tip is shown in Tables 3–5. Table 6 gives corresponding data for brown shells. Some tips are almost whitish, and cannot be described with certainty as pink or yellow. These are shown as pallid.

The breeding data agree well with the hypothesis that browns or pale pinks are heterozygous for yellow if they have a yellow tip. Table 3 shows that about two thirds of the pale pink/yellow heterozygotes can be recognized. The noticeable heterogeneity between broods suggests that different combinations of modifiers of dominance and/or different allelomorphs are found in the various stocks. Browns with a pink tip are heterozygous for pink. Pale pinks with a pink tip are usually, but not always, homozygous for pale pink. We find that our dark pinks seem to have a pink tip, whether heterozygous or homozygous, except in MR 36: in this brood, of 16 dark pink progeny, eight had a pallid and eight a yellow tip; the tips of the pale pinks were two pallid, five yellow. Both in pale pinks and in browns, there are a number which cannot be classified, the tips being pallid or brown. Apparently, dominance is often incomplete in browns (for both yellow

and pink) and usually in pale pinks (for yellow), but it is complete, as a rule, in dark pinks (for both pale pink and yellow). Brown heterozygotes (for pink or yellow) and pale pink heterozygotes (for yellow) can therefore be identified when wanted to set up matings.

These suggestions are confirmed by observation of random samples taken from

TABLE 3

Color of tip in pale pink/yellow heterozygotes

No.	Pink	Pallid	Yellow	Total
EX 1	..	3	5	8
L 1	..	..	13	13
L 2	..	5	4	9
L 5	..	1	..	1
L 13	1	..	17	18
LE 1	..	..	2	2
M 5	..	..	2	2
M 6	..	4	9	13
M 7	..	1	46	47
ME 1	3	4	7	14
ME 2	..	..	1	1
ME 4	..	..	11	11
ML 1	..	.	4	4
ML 2	1	5	3	9
MR 1	..	..	42	42
MR 2	7	..	..	7
MR 4	1	..	5	6
MR 23	..	11	20	31
MR 28	..	..	3	3
MR 36	..	2	5	7
MR 38	..	..	7	7
MR 39	..	..	4	4
PM 1	..	..	2	2
POE 1	14	12	..	26
RL 2	..	..	20	20
	27	48	232	307

In this table, and in Tables 4, 5 and 6, the brood totals do not always agree with the figure in Table 1: this is because Table 1 includes old records of dead progeny which are now faded and not scorable for tip color.

TABLE 4

Color of tip in pale pinks of broods known to have both homozygous pale pinks and pale pink/yellow heterozygotes

No.	Pink	Pallid	Yellow	Total
L 10	6	7	20	33
M 17	4	2	2	8
M 18	..	7	4	11
	10	16	26	52

All 2:1 segregations.

TABLE 5

Color of tip in pale pink homozygotes

No.	Pink	Pallid	Yellow	Total
L 13	9	..	..	9
M 16	9	5	..	14
	18	5	..	23

TABLE 6

Color of tip in browns of known constitution

No.	Brown	Pink	Pallid	Yellow	Heterozygous for:
MR 4 parent	..	..	..	1	yellow
MR 32 parent	..	..	..	1	yellow
MR 32 offspring	..	..	..	2	yellow
R 5 parent	..	..	.	1	yellow
R 5 offspring	..	..	3	15	yellow
R 8 offspring	..	5	..	4	pink and yellow (1:1)
RE 1 parent	..	..		1	yellow
RE 1 offspring	..	..	5	13	yellow
RE 3 parent	..	1	..	..	pink
RE 3 offspring	..	..	1	..	yellow
RL 2 offspring	..	..	..	15	yellow

the wild in which we have scored tip color in browns and those pinks that are undoubtedly pale. Since in the brown class, many known by calculation to be heterozygous do not show either pink or yellow, the observed ratio of pink and yellow tips must be compared with that expected from a calculation of the frequencies of the pink and yellow genes in that sample based on the observed phenotype ratios of pink, yellow and brown. The results are given in Table 7. It will be seen that there is excellent agreement between the observed and calculated ratios. This suggests that the penetrance of pink and yellow in browns is approximately equal, i.e., that an unscorable brown heterozygote, as far as penetrance is concerned, is equally likely to be heterozygous for pink or yellow.

Pale and dark yellow

Mating L 2 is of a deep yellow unbanded with a dark pink five-banded known from the progeny to be heterozygous for pale pink. Matings L 12 and L 13 from this progeny segregated out deep yellow unbandeds, in L 12 from dark pink unbanded parents and in L 13 from pale pink unbandeds. In L 10 and 11, pale yellow bandeds segregated out from pale pink banded and dark pink banded parents respectively. By far the most likely explanation is that dark and pale yellow are allelomorphs at the locus controlling the pink shades, and that the unbanded chromosome was carrying the allelomorph for dark yellow, the banded one that for pale yellow. Then from L 2, dark yellow is dominant to pale. If the

TABLE 7

Color of tip in random samples from the wild

Locality	Shell color	Tip color			Phenotypes of sample		
		Indeterminate (brown or uncertain)	Pink	Yellow	Brown	Pink	Yellow
Rockley East	Brown	42	19(19)	27(27)	88	83	42
	Pale pink	2 (pallid)	6	9			
Rockley 4	Brown	13	6(7)	20(19)	39	32	40
	Pale pink	2	7	9			
Rough Down	Brown	4	1?(0)	11(12)	16	1	28
Wytham Lane	Brown		2(2)	9(9)	11	16	26

The expected values are in parenthesis next to the observed value for brown shell with pink or yellow tips.

difference were due to a modifier of yellow unlinked with banding, broods ML 2 and M 14B, from L 2 and M 2 respectively, might well have disproved the hypothesis of allelomorphism, but neither did. In ML 2, the yellow offspring have the chromosome carrying unbanded from L 2; they must therefore all be dark yellow on the allelomorphism hypothesis, and the appearance of any pale yellows at all would have shown the existence of a modifier. The seven progeny were all dark yellow. In M 2, a pale yellow mated with a homozygous pink produced nothing but pinks, and two of these in mating M 14B produced pinks and three yellows, all pale. Again, the occurrence of a single dark yellow would have disproved allelomorphism. Further support is given by ME 2, in which a pink from M 2, heterozygous for pale yellow on this hypothesis, was mated to a pale yellow, and segregated pinks and pale yellows (five), as would be expected.

The pale yellows in these matings have quite dark yellow tips; it is not possible, therefore, to separate dark yellows heterozygous for pale yellow by tip color.

Viability

Before crossover values can be calculated, the data must be examined for evidence of differences in viability disturbing segregation ratios. Moreover, since a stable polymorphism is in question, which is maintained despite visual selection in many localities for monomorphism, CAIN and SHEPPARD (1954) have pointed out that there is almost certainly strong heterosis acting to preserve it. Such physiological selection may be operating even under a careful breeding regime (although not necessarily in exactly the same direction as in the wild).

The data (Table 1) are unfortunately not sufficient to show small viability

effects which would be very important in the wild. Our findings can be summarized as follows:

Color:	
Pink/yellow heterozygote	Backcrosses to yellow, no significant departure from 1:1, nor heterogeneity between families. F_2, a nonsignificant deficiency of the recessives (yellows), no marked heterogeneity between families.
Brown/not brown heterozygote	Backcrosses, no significant deficiencies, nor heterogeneity. F_2, no significant deficiencies, a possibility of heterogeneity (R 1) but the numbers are small.
Banding in pink and yellow:	
All banding/unbanded heterozygote	Backcrosses, no significant deficiencies, nor heterogeneity. F_2, there is a not quite significant deficiency of the recessives (bandeds) but as this locus is linked with color, the deficiency could be due in part to that of yellows noted above.
00300/banded heterozygote	Backcrosses, no significant departures from an over-all 1:1 ratio, but considerable heterogeneity between families ($P<0.01$). F_2, not sufficient data.

(No test of banding in browns has been made since the degree of penetrance is in doubt.)

The heterogeneity between families in 00300/banding segregation is remarkable, the more so since there is no significant heterogeneity when all types of banding taken together are compared with unbanding, although this includes several families segregating unbanded and 00300. The heterogeneity could be due to linked semilethals, sometimes in coupling and sometimes in repulsion, or the allelomorph controlling 00300 may be particularly sensitive in viability to differences of conditions in the different breeding pots. It cannot be due to differences in penetrance, since at least part of it is caused by an excess of 00300, and part by a deficiency, whereas with incomplete penetrance a departure in one direction only would be expected. The occurrence of phenocopies is highly unlikely since the phenotypes are clear-cut, and 00300 never occurs in families in which both parents are known by inspection of their parents and siblings not to be carrying the gene for 00300.

Independence of 00300 and color

Broods EX 1, LE 1, ME 1 and ME 2 give no evidence of linkage between color and the gene for 00300. ME 1 and 2 are of particular importance, since if there were linkage, the allelomorph for 00300 must be on the chromosome carrying the allelomorph for yellow. The results of the two broods can therefore be

summed, and give an excess of the putative crossover classes pink 00300 and yellow 12345. This confirms our previous findings and those of LAMOTTE (1954) that 00300 and color are not, or are only loosely, linked.

Crossing over between color and banding

The following matings show that crossing over is extremely infrequent: ME 4, MR 23, 30, 31, 34, 35 (backcross coupling); PLN 1, POE 1 (backcross repulsion); M 18, MR 38, 39 (F_2 coupling); L 12, 13, P 2 (F_2 repulsion); ML 2 (single backcross repulsion). In fact, there is no evidence for it at all, except in MR 34 and 35. In both of these matings, the parent in which crossing over occurred came from MR 3. Because of the suggestion of a disturbed segregation ratio in the F_2, it is convenient to calculate crossover values from backcrosses only. The crossover value calculated from the backcross data is about 2.25 percent. Since no crossovers appeared in the F_2 families, the real crossover value is probably lower than this. FISHER and DIVER (1934) have reported differences in crossover value between families, but, as LAMOTTE (1954) has pointed out, they were using adult snails which might have been previously fertilized. Since all our crossovers occurred in only two matings in which the heterozygous parents were sibs, there is almost certainly heterogeneity in our data, and large differences in crossover value between different individuals.

Dominance relationships

The results so far obtained of genetical work on this snail have revealed a series of allelomorphs at the color locus, with a dominance hierarchy, in the order: brown, dark pink, pale pink, dark yellow, light yellow. In this, every form is dominant to all those to the right of it (except for tip color). It is remarkable that the series is also in order of decreasing darkness from left to right. If, as seems possible, orange bands is dominant to hyalozonate, there will be a similar series for the color of the band pigment, in the order full pigment (nearly black), orange bands, unpigmented bands (hyalozonate). These seem to be linked with the color locus. The modifications 00300 and 00345 of five-banded, however, are dominant, and unlinked with color, and LAMOTTE's "bandes pâles" is also a dominant to normal banding and unlinked with color. Since 12345 is linked very closely with color, it is perhaps not surprising that modifications of the width of the bands, and modifications removing some of the bands, are not linked, since they can appear only in the five-banded form 12345, and therefore cannot help but behave in part phenotypically as though linked with color. Thus in a locality in which pink unbanded was at an advantage to pink 00300 but yellow 00300 was at an advantage to yellow 00000, the population could become almost completely composed of P 00000 and Y 00300 by selection for the chromosomes P 00000 and Y banded, despite the fact that 00300 is not linked to color. Selection to increase the linkage between 00300 and color, therefore, would have little effect. Linkage of banding with color, however, is to be expected, since different combinations of bandings and colors have very different selective values against different backgrounds (CAIN and SHEPPARD 1954).

The dominance relationships in the series of allelomorphs at the color locus need explanation. It is not sufficient to say that a more intense pigment (e.g. deep pink, or the violet that is found in the calcareous layers of the shell in browns) will overpower a lighter or less intense pigment (e.g. pale pink or yellow) and that therefore the hierarchy is what would be expected if there were no dominance. One would expect the heterozygote between dark pink and dark yellow to be a *very* yellowish orange, even supposing the heterozygote to produce as much pink pigment as the homozygous dark pink, but the two are indistinguishable. Moreover, there is nothing in darkness or intensity of pigment as such that must be correlated with dominance; both dominant and recessive melanics are well-known in various sorts of animals. Nor can the difference between brown, pink and yellow be a simple dosage effect since the different colors must be produced by different pigments and not by a dilution of the same pigment (SHEPPARD 1958, p. 142).

In cases of polymorphism maintained by mimetic resemblance, a new allelomorph or gene affecting the visible appearance of the mimetic forms will not spread by visual selection unless either (1) it improves the present mimicry or (2) it produces a new phenotype which has a sufficient, although no doubt rudimentary, resemblance to a model not thus far exploited by this species of mimic. The visible influence on the new form of the genes mediating the already existing polymorphism will be eliminated in order to improve the new mimic, and thereby dominance will be evolved. Consequently, there will be a dominance hierarchy in mimetic polymorphisms in respect of all those allelomorphs that coexist in the same population. This has been demonstrated in detail by CLARKE and SHEPPARD (1960) in *Papilio dardanus*.

It seems not impossible that the polymorphism in *Cepaea nemoralis* can be regarded as a cryptic polymorphism analogous to the mimetic polymorphism in *Papilio dardanus*. It has been shown (CAIN and SHEPPARD 1950, 1952, 1954; SHEPPARD 1951, 1952) that yellow shells are at an advantage in green situations, pink ones in leaf litter, and brown ones in beechwoods with their frequent expanses of blackish soil. It is certainly true, at least in Britain, that plants at ground level are either green and growing or brown and decaying. Intermediates are not common, or common only for a short time in the year. If yellow shells are imitating the green elements in the background, and pink and brown ones the brown elements, it is understandable that intermediates between the yellows and the other colors which would be bright or dull orange, might nearly always be at a disadvantage. This sort of explanation might also apply to the difference between the pinks and browns, since dead vegetable matter is certainly often either straw-colored or blackish brown, but this point needs further investigation. It is therefore likely that there are fewer optimal phenotypes in Cepaea than there are possible combinations of the allelomorphs necessary to produce these phenotypes. When there is more than one optimal phenotype, polymorphism may evolve by disruptive selection (MATHER 1955). We can generalize the argument just given, and say that when the number of optimal

phenotypes is less than the number of genotypes necessary to produce them, a dominance hierarchy will also be evolved, with the ancestral form very low in the hierarchy.

It is quite possible that the bright sunshine and comparative aridity of much of France, especially in the south, by producing mainly pale backgrounds, favors yellows above the other colors, and that dark browns are confined to northern Europe because sodden blackish elements are far more frequent in the backgrounds there, although other causes may also be active. The hierarchy would also suggest that, irrespective of their present distributions, the allelomorphs dominant to yellow are later than it, brown being the latest of all, and that the original habitat of Cepaea was green places, perhaps grassy limestone pavements, in a warm climate, the animals probably aestivating in the height of the summer when the vegetation might be parched.

SUMMARY

1. The following genes are described:
(a) Orange banded, recessive to normal pigmentation of bands, probably linked with shell color.
(b) Darkening bands, recessive to normal pigmentation of bands, not closely linked with shell color.
(c) Spread bands, dominant in the 00300 phenotype, almost certainly linked with shell color.
(d) Dark versus pale yellow, allelomorphs at the pink/yellow locus, with pale yellow recessive.
2. The recessiveness of hyalozonate to normal bands is confirmed and the independence of 00300 and shell color is strongly supported. Pale pink (recessive) is allelomorphic to dark pink. Further evidence is presented that brown is allelomorphic with and dominant to pink and yellow.
3. Fusions and reductions (but not absences) of bands in the 12345 phenotype are multifactorially controlled.
4. There is an epistatic effect of brown on banding, reducing the expression of banding, so that it is even absent in a few cases.
5. Dominance is incomplete in many brown/pink and brown/yellow heterozygotes, and in most pale pink/yellow heterozygotes, but appears nearly complete in dark pink/yellow heterozygotes.
6. A striking heterogeneity between families in 00300/12345 segregation ratios is reported.
7. Data confirm that pink and banded are very closely linked. A few crossovers have been observed, but only in the progeny of two full sibs, which suggests heterogeneity in crossover value.
8. The significance of the dominance relationships at the shell color locus in this polymorphic snail is discussed. It is suggested that in polymorphisms whenever the number of optimal phenotypes is less than the minimum number of combinations of the major genes necessary to produce them, dominance will be evolved.

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