Cepaea genetics - what we think we know and what we don't know

The following technical notes on *Cepaea* genetics are kindly provided by Dr Laurence Cook. They are not intended for use by school pupils, but will give you the low-down from the man at the top!

Introduction

The polymorphism in *Cepaea* was shown to have a Mendelian basis at the end of the 19th C. (Lang, 1904, 1908). It thus became one of the standard early genetic examples. Like most others, however, simple segregation rules do not describe all the complexities of the system (Darbishire, 1905; Stelfox, 1918; Pelseneer, 1920). The current picture is due to extensive breeding by Lamotte (1951, 1954) and Cain & Sheppard (Cain *et al*. 1960, 1968) plus a few others. It is reviewed by Murray (1975), who gives references. Table 1 is modified from his review.

Nomenclature

The nomenclature was established by Cain, based on previous usage, and should be used in formal discussion (see Cain, 1988). However, it is inconvenient to type (the superscripts in Table 1 should actually be italicised) and there seems little objection to sometimes using, for example, Pb and yU for pink banded and yellow unbanded or M3 for mid-banded (what do you think?).

Banding

The basic banding pattern consists of five bands. Conventionally, at least since Taylor (1914), these are numbered from the top of the whorl to the bottom and represented by a zero if a band is missing, so that 12345 is the standard full-banded pattern, 10345 has band 2 missing, 00300 is mid-banded etc. Partial bands are represented by a colon (:) instead of a zero. Adjacent bands can sometimes be fused, represented by enclosing the numbers in parentheses (so 1(23)45 has bands 2 and 3 fused, (12345) has them all attached to each other). Spread bands (S) is a distinct condition which has the appearance of leakage of pigmentation into the intervening ground colour areas. Bands are formed by loss of ground colour pigmentation from the band positions and replacement by brown pigment. In the P series of alleles ground colour is removed but deposition of the brown pigment is variously reduced.

Non-segregating band variation

Variation in band width, band fusion and loss of odd bands is said to be ‘under multifactorial control’, as distinct from the segregating U and T loci. This is no doubt correct, but there is no information on heritability or size of the environmental component. Frequency of fusions has sometimes been scored but I do not know of longitudinal studies of how fast the frequency may change.

Ground colour

The Table shows ground colour alleles that have been identified in breeding tests. Pink is sometimes called red (Wolda. *Rot*, Boettger) or *rose* (Lamotte). It is usually difficult to separate morphs such as pale pink and faint pink in field-collected samples and best to score samples simply as brown, pink or yellow. However, the alleles present within categories are

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probably quite variable from place to place. Where there is a problem separating the three main categories it has been the practice to scrape the periostracum from the body whorl near the umbilicus and examine the shell colour beneath. Browns tend to have a violet hue, pinks are definitely pink and yellows a more acid yellow colour. The genetics of brown is not properly investigated. In most of Britain there is a dark brown phenotype, which is almost always bandless. The reason why is unknown (epistasis?, metabolic incompatibility?), but this means that frequency of banding has to be estimated for pinks and yellows only. Some colonies, especially in Ireland, have pale brown or faint brown individuals, however, which are commonly banded. These may be very difficult to distinguish from pinks (e.g. see Clarke, Diver & Murray, 1967). It is evident that in all three hue categories there is variation in saturation that in extreme cases can lead to an almost white shell; these, of course, converge in appearance (and it is possible that very pale brown is dominant to dark pink, reversing the usual relation between the main colour classes). For most of our region this should not present a problem with fresh material. Colour tends to fade in stored shells.

Linkage

Cepaea grows to a fixed adult size, at which point a clearly defined lip is formed on the shell. It is natural to assume that sexual maturity occurs at the same time. When the animals start breeding spermatophores are exchanged before eggs mature, and it is possible that exchange can take place before lip formation. Sperm storage can take place, so that a brood is derived from more than one mating. These facts possibly have a bearing on some of the breeding results from which linkage has been measured. The greatest amount of information is available on linkage of ground colour to banding. Various types of cross that produced a total of 1094 progeny suggest a crossover value of 0.0021 ± 0.0015. This provides an upper 95% confidence limit of 0.5% (Cook & King, 1966). Three crosses, one published by Fisher & Diver (1934) the other two from the same stock bred by Cain *et al*. (1960), give the significantly different result of ca. 20% crossing over. Both sets of authors would probably have been indignant to think that their rearing technique was questioned. Either something has gone wrong or there are at least two ways in which the pair of loci is inherited. Stelfox was perhaps not quite so careful in his breeding programme but was nevertheless aware of the problem of multiple mating. His results suggest a linkage distance of less than 3% between punctuate and the colour/banding complex, and about 10% between the latter and the P (hyalozonate) locus (Cook, 1967). In terms of collecting new data it is essential to distinguish browns from the others and to score the remaining four colour/banding classes separately. Mid/non-mid banded in pinks and yellows is also a must, for comparison of a linked with an unlinked pair. Punctate, trifasciate (T) and the P locus would also be nice, although the latter is quite a complicated locus to deal with.

Dominance and epistasis

For all but two cases alleles are dominant or recessive to one another. In some ground colour crosses, heterozygotes display their genotype in the colour of the tip (early growth) of the shell (Cain *et al*., 1960). It is not practical to use this information in scoring wild samples, however. White lipped heterozygotes appear to be paler that brown lipped homozygotes (Cain *et al*., 1968) and there is evidence from the field to suggest that expressivity may be very broad (Cook, 2003). Unbanded is, of course, epistatic to all the band-modifying genes.

Conclusion

When I got the *Handbook of Genetics* out of the Library the chap behind the desk said ‘Cor, a lot must have changed since that was written’. To which the reply might well be ‘Up to a point, Lord Copper’.

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References

This is a short list of references cited By Laurence Cook in his summary of *Cepaea* genetics.

Cain, AJ. 1988 The scoring of polymorphic colour and pattern variation and its genetic basis in molluscan shells. *Malacologia* 28, 1-15.

Clarke, B, Diver, C & Murray, J. 1967 Studies on *Cepaea*. VI. The spatial and temporal distribution of phenotypes in a colony of *Cepaea nemoralis* (L.). *Phil. Trans. R. Soc. Lond. B* 253, 519-548.

Cook, LM. 1967 The genetics of *Cepaea nemoralis*. *Heredity* 22, 379-410.

Cook, LM. 2003 A colony of pale-lipped *Cepaea nemoralis.* J. *Conchol*. 38, 73-78.

Cook, LM & King, JMB. 1966 Some data on the genetics of shell-character polymorphism in the snail *Arianta arbustorum. Genetics* 53, 415-425.

Fisher, RA & Diver, C. 1934 Crossing over in the land snail *Cepaea nemoralis* L. *Nature, Lond*. 133, 834.

Murray, J.1975 The genetics of the Mollusca. In King, RC. (ed.) *Handbook of Genetics. Vol. 3. Invertebrates of genetic interest*. Plenum, New York 3-31.

Taylor, JW. 1914 *Monograph of the land and freshwater Mollusca of the British Isles. Vol. 3. Zonitidae, Endodontidae, Helicidae*. Taylor, Leeds.

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Table 1. Loci and alleles of *C. nemoralis*.

Loci and alleles of *C. nemoralis*. Modified from Table 2 of Murray (1975). Information on genetics is from Cain and Sheppard (1957), Cain, King & Sheppard (1960), Cain, Sheppard & King (1968), Cook (1967, 1969), Darbishire (1905), Lamotte (1951, 1954), Lang (1904, 1908, 1911, 1912), Murray (1963), Stelfox (1918), Wolda (1969). Alleles are listed in order of decreasing dominance. The dominance relationships of P^L and P^A have not been established.

	Locus	**Alleles**
C	Ground color of shell	C^B Brown C^{DP} Dark pink C^{PP} Pale pink C^{FP} Faint pink C^{DY} Dark yellow C^{PY} Pale yellow
B	Presence or absence of bands	B^0 Unbanded B^B Banded
I	Punctuate bands	I^I Punctuate I^- Unmodified
S	Spreading of band pigment	S^S Spread bands S^- Unmodified
P	Pigmentation of bands and lip	P^N Normal (dark brown) bands and lip P^L Light brown bands and lip P^A White lip and normal bands (albolabiate) P^T White lip and transparent bands (hyalozonate)

The above 5 loci are linked, those below are unlinked to them or, so far as information is available, to each other.

	Locus	**Alleles**
U	Suppression of bands 1, 2, 4, and 5	U^3 Mid-banded (00300) U^- Unmodified
T	Suppression of bands 1 and 2	T^{345} Bands 1 and 2 suppressed (00345) T^- Unmodified
D	Dermal pigmentation	D^R Reddish dermal pigment D^G Gray dermal pigment
Q	Quantity of dermal pigment	Q^M Medium gray Q^P Very pale (yellowish)
R	Darkening bands	R^- Unmodified R^D Bands gradually darken from apex to lip
O	Orange bands	O^- Unmodified O^O Orange bands and lip

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