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# SUPERGENES IN POLYMORPHIC LAND SNAILS
## I. *PARTULA TAENIATA*

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SUMMARY

The general colour of the shell in *Partula taeniata* is controlled by at least two loci. One of these (*C*) has a series of six alleles which determine the yellow (Y) and neutral brown (N) series of colours. Alleles for darker colours are dominant to those for lighter colours, but dominance is not always complete. The pink (P) colours are determined by a second locus (*P*) which modifies the expression of the lighter alleles of the *C* locus. Orange shell colour segregates with yellow but its allelic relationship is unknown. Colour of the lip is controlled by a locus (*L*) with pink lip dominant to white lip. The colour of the spire is determined by a locus (*S*) with dark (N4) spire dominant to light spire. An intermediate spire colour shows the same pattern of inheritance and may represent the effect of another allele. Banding of the shell is dominant to absence of bands, with two loci (*B*1 and *B*2) determining the type of banding. An allele at *B*1 produces the frenata pattern; an allele at *B*2 produces zonata; together they produce lyra. All the loci for which linkage data are available are linked so strongly that the whole array may be considered a supergene.

Self-fertilisation takes place primarily during early reproductive life. About 20 per cent of the young of the first mating of an individual are produced by selfing, but over the whole reproductive span the frequency is only about 2·5 per cent. There is inconclusive evidence for heterozygote advantage of banded individuals.

## 1. INTRODUCTION

THE polymorphic land snail *Partula taeniata* Mörch has provided material for several studies of variation in natural populations (Crampton, 1932; Lundman, 1947; Bailey, 1956; Murray and Clarke, 1968*a*; Clarke and Murray, 1969). A clear understanding of this variation requires a knowledge of its genetic basis. In earlier papers (Murray and Clarke, 1966, 1968*b*) we have given an account of the breeding biology of *Partula* and have reported some preliminary results of our breeding experiments.

*P. taeniata* is hermaphroditic, usually producing young by means of cross-fertilisation, but capable of self-fertilisation. During courtship one partner behaves as a male and the other as a female, although a successful courtship is often followed by an immediate reversal of roles and hence mutual fertilisation. *P. taeniata* is ovoviviparous, producing single young at intervals of about 19 days. Maturity may be reached in 4 months, but usually takes 6 months to a year.

In this paper we present new information about the inheritance of polymorphisms in shell colour and pattern. We have identified six loci, controlling shell colour (two loci with six and three alleles respectively), lip colour (two alleles), spire colour (two alleles), and banding pattern (two loci with two alleles each). In addition, we describe the linkage relationships that apparently allow the whole polymorphic system to function as a supergene.

## 2. Methods

A general account of the laboratory care of *P. taeniata* is given in Murray and Clarke (1966). Our experimental animals were kept in plastic boxes lined at the bottom with moistened toilet-paper and were fed on a diet of oatmeal, lettuce and powdered natural chalk.

The shells were scored for the colours of the major body whorl, of the spire and of the lip. They were also scored for the presence and type of banding. We used a two-dimensional classification of shell colour, with letters indicating the hue and numbers (from 1 to 4) indicating the saturation and intensity of pigmentation. The following classes were recognised:

W—White, the point of divergence of all series.
N1 to N4—Neutral brown with increasing intensity of a purplish hue.
Y1 to Y2—Yellow of increasing intensity.
P1 to P3—Pink of increasing intensity.
O1 to O3—Orange of increasing intensity.

The spire of the shell may be similar in colour to the rest of the shell or it may be significantly darker. Spire colours were scored on the same scale, but were recorded only if they differed from the colour of the rest of the shell. The lip colour in *P. taeniata* is usually white, but other colours do occur. They have been scored by hue alone.

Three principal banding types have been recognised, frenata, zonata and lyra (according to the terminology of Crampton, 1932, q.v. for illustrations; also Murray and Clarke, 1966). Frenata bears two narrow longitudinal lines darker than the background colour of the shell; zonata has a broad central darker band, flanked by lighter areas; lyra has three narrow longitudinal bands darker than the background.

## 3. Breeding results

Table 1 records the progeny of the experimental matings. Some of the crosses recorded in our earlier paper (Murray and Clarke, 1966) are also included here if significant numbers of additional offspring have been produced or if the mating is crucial to the genetic interpretation. Loci and alleles that have been identified are listed in table 2.

### (i) *Locus* C*: the N-Y-W series of shell colours*

The general colour of the shell is determined by a series of apparent alleles. We have been able to identify six, and it is likely that there are more. These alleles control the yellow (Y) and the neutral brown (N) series of colours, producing various degrees of intensity. As a rule, alleles giving greater intensity of colour are dominant to those producing lighter shades, although, as we shall show, dominance is not always complete.

*Allele* $C^{N4}$. Among the alleles determining colours in the N series, there is one ($C^{N4}$) that produces an intense purplish-black (N4) in both homozygotes and heterozygotes. Its inheritance may be followed in the lineages derived from matings 2 and 4. There are $F_2$ segregations in matings 56, 167 and 168 and backcrosses in matings 2, 57 and 64.

*Allele* $C^{N3}$. A second allele of the N series ($C^{N3}$) segregates from mating 9, yielding an N3 or slightly lighter phenotype when heterozygous with alleles for paler colours. In subsequent matings, 165 and 182, the allele is recovered in homozygous condition. The phenotype is as dark as that of the $C^{N4}$ homozygotes in lineages 2 and 4. The dominance of $C^{N3}$ is thus incomplete.

*Allele* $C^{N2}$. Incomplete dominance is also shown by the next allele in the series, $C^{N2}$. Mating 10 is a backcross in which this allele produces an intermediate brown (N2) phenotype when it is heterozygous with alleles for paler colouration. Mating 74, an $F_2$ segregation from the offspring of mating 10, produces a range of phenotypes, the darkest being considerably darker (N4/N3) than the parents. The hypothesis of intermediate dominance is confirmed by matings among the offspring of 74. Mating 121, between two of the darkest offspring, does not show any segregation, indicating that the parents are indeed homozygotes. The paler (N2) offspring from 74 are heterozygotes, producing three phenotypes in the ratio of 1 : 2 : 1, as in mating 123. Other matings in the lineage (146, 147, 129 and 130) are consistent with this interpretation, as are the crosses derived from mating 8. In an earlier paper (Murray and Clarke, 1966) we suggested that the phenotypes among the offspring of mating 74 might be the result of recombination in a polygenic system. In the light of the results reported above it no longer seems necessary to postulate recombination in order to account for the major variations in the lineage of this mating. However, it seems likely that modifying loci are responsible for the minor variations in colour to be found in the offspring of matings 121 and 129 and in other lineages.

*Allele* $C^{N1}$. An allele producing a much paler colour (N1) segregates in the offspring of several matings such as 11, 17, and the lineage of mating 6. Homozygotes for this allele, such as the N1 offspring of 166 and 187, appear to be no darker than individuals heterozygous for alleles determining light yellow or white, as in 65, 66 and 67.

*Allele* $C^{Y1}$. The pale yellow phenotype (Y1) is determined by an allele ($C^{Y1}$) that is recessive to all others except white. It has been so widely used in these crosses that its behaviour may be seen in almost every lineage.

*Allele* $C^{W}$. The allele that produces a white shell in the homozygous condition appears to be recessive to all the others. This behaviour can be seen in the lineage of mating 7. Whites are recovered among the offspring of one of the $F_2$ crosses (61) but not from the other two (135 and 136). The interpretation of the white phenotype is complicated by the observation, discussed below, that light yellow shells, especially on living animals, tend to fade to white.

*Allelism.* Our interpretation of these colour forms as the expression of a series of alleles must be viewed with some caution. It is, of course, impossible to exclude more elaborate hypotheses invoking multiple loci. Our hypothesis is, however, supported by several lines of evidence. First, the segregations involve a graded series of phenotypes. Second, there is no evidence of crossing over between pairs of alleles in this series. Third, there are no cases in which backcrosses produce more than two colour types among the

TABLE 1

*Matings of* Partula taeniata *and their progeny. Names of localities are from Crampton (1932). " Prog. 2 " indicates that the parents of that mating are the progeny of mating 2. Phenotypes are explained under " Methods ". The asterisk (*) indicates that those offspring may have been produced by either of the two parents. Matings mentioned in the text and not included here will be found in Murray and Clarke (1966)*

| Mating No. | Provenance | Parents: Phenotype | Parents: Inferred genotype | Progeny: Phenotype | Progeny: No. | Notes |
|---|---|---|---|---|---|---|
| 2 | Faatoai | N4 | $C^{N4}/C^{Y1}$ | N4 | 33 | |
| | | | | Y1 | 33 | |
| | Faatoai | Y1 | $C^{Y1}/C^{Y1}$ | N4 | 47 | |
| | | | | Y1 | 49 | |
| | | * | | N4 | 2 | |
| | | | | Y1 | 1 | |
| 4 | Faatoai | N4 | $C^{N4}/C^{N4}$ | N4 | 62 | |
| | | | | Y1 | 0 | |
| | Faatoai | N1 | $C^{N1}/C^{Y1}$ | N4 | 50 | |
| | | | | Y1 | 1 | |
| | | * | | N4 | 1 | |
| 6 | Faatoai | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N1}B1^-B2^-$ | Zonata (N4) | 37 | |
| | | | | N1 | 35 | |
| | Faatoai | Y1 | $C^{Y1}B1^-B2^-/C^{Y1}B1^-B2^-$ | Zonata (N4) | 57 | |
| | | | | N1 | 49 | |
| 7 | Faatoai | Zonata (N2) | $C^{N2}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N2) | 24 | (1) |
| | Faatoai | W | $C^{Y1}B1^-B2^-/C^{W}B1^-B2^-$ | Zonata (N2) | 59 | (2) |
| | | * | | Zonata (N2) | 1 | |
| | | | | Y1 (N2 spire) | 1 | |
| 8 | Faatoai | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{N1}B1^-B2^-$ | Lyra (N2) | 23 | |
| | | | | N2 | 10 | |
| | | | | N1 | 10 | |
| | Faatoai | N2 | $C^{N2}B1^-B2^-/C^{N1}B1^-B2^-$ | Lyra (N2) | 5 | |
| | | | | N2 | 3 | |
| | | | | N1 | 2 | |
| 9 | Faatoai | Lyra (N4) | $C^{N2}B1^FB2^Z/C^{N3}B1^-B2^-$ | Lyra (N2) | 16 | |
| | | | | N3/N2 | 26 | |
| | | | | Lyra (N4) | 1 | (3) |
| | | | | W | 1 | |
| | Faatoai | Y1 | $C^{Y1}B1^-B2^-/C^{W}B1^-B2^-$ | Lyra (N2) | 17 | (4) |
| | | | | N3/N2 | 28 | |
| | | * | | Lyra (N2) | 1 | |
| | | | | N3/N2 | 1 | |
| 62 | Urufara | N2 | $C^{N2}/C^{N1}$ | N2 | 27 | |
| | | | | N1 | 24 | |
| | | | | Y1 | 0 | |
| | Prog. 5 | Y1 | $C^{Y1}/C^{Y1}$ | N2 | 25 | |
| | | | | N1 | 20 | |
| | | | | Y1 | 7 | (8) |
| 64 | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 32 | |
| | | | | Y1 | 30 | |
| | Prog. 2 | Y1 | $C^{Y1}/C^{Y1}$ | N4 | 46 | |
| | | | | Y1 | 44 | |
| 65 | Prog. 7 | Zonata (N2) | $C^{N2}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N2) | 39 | |
| | | | | N1 | 25 | |
| | | | | Y1 | 19 | |
| | Prog. 6 | N1 | $C^{N1}B1^-B2^-/C^{Y1}B1^-B2^-$ | Zonata (N2) | 20 | |
| | | | | N1 | 4 | |
| | | | | Y1 | 6 | |
| | | * | | Zonata (N2) | 1 | |
| | | | | N1 | 1 | |
| | | | | Y1 | 1 | |
| 67 | Prog. 6 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N4) | 20 | |
| | | | | N1 | 5 | |
| | | | | Y1 | 2 | |
| | Prog. 6 | N1 | $C^{N1}B1^-B2^-/C^{Y1}B1^-B2^-$ | Zonata (N4) | 17 | |
| | | | | N1 | 7 | |
| | | | | Y1 | 11 | |
| 68 | Prog. 6 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Lyra (N4) | 9 | |
| | | | | Lyra (N2) | 5 | |
| | | | | Zonata (N4) | 4 | |
| | | | | N4/N3 | 11 | |
| | Prog. 9 | Lyra (N4) | $C^{N2}B1^FB2^Z/C^{N3}B1^-B2^-$ | Lyra (N4) | 14 | (9) |
| | | | | Lyra (N2) | 5 | |
| | | | | Zonata (N4) | 17 | |
| | | | | N4/N3 | 11 | |

(1) Faded parent, should be Y1 (N2 spire).
(2) By self-fertilisation.
(3) By self-fertilisation.
(4) Spire not scored in parent.

(8) By self-fertilisation.
(9) Parent derived by self-fertilisation.

| | | | | | | |
|---|---|---|---|---|---|---|
| 11 | Roroie | N2 | $C^{N2}P^{1}/C^{Y1}P^{-}$ | N2 | 13 | |
| | | | | Y1 (N2 spire) | 5 | |
| | | | | Y1 | 7 | |
| | Faatoai | Y1 | $C^{Y1}P^{-}/C^{Y1}P^{-}$ | N2 | 8 | (5) |
| | | | | Y1 (N2 spire) | 6 | |
| | | | | Y1 | 5 | |
| | | * | | N2 | 1 | |
| 12 | Faatoai | N1 | $C^{N2}S^{-}/C^{Y1}S^{-}$ | N2 | 3 | (6) |
| | | | | N2 (N4 spire) | 7 | |
| | | | | Y1 | 4 | |
| | | | | Y1 (N4 spire) | 1 | |
| | Moorea | Y1 (N4 spire) | $C^{Y1}S^{N4}/C^{Y1}S^{-}$ | N2 | 22 | |
| | | | | N2 (N4 spire) | 14 | |
| | | | | Y1 | 19 | |
| | | | | Y1 (N4 spire) | 14 | |
| | | * | | N2 (N4 spire) | 1 | |
| 15 | Faatoai | N3 | $C^{N3}/C^{N2}$ | N4/N3 | 33 | |
| | | | | N2 | 28 | |
| | Faatoai | W | $C^{Y1}/C^{W}$ | N4/N3 | 4 | (7) |
| | | | | N2 | 8 | |
| 16 | Faatoai | Frenata (N2) | $C^{N2}B1^{F}B2^{-}/C^{N2}B1^{-}B2^{-}$ | Frenata (N2) | 1 | |
| | | | | N2 | 0 | |
| | Faatoai | N1 | $C^{N1}B1^{-}B2^{-}/C^{N1}B1^{-}B2^{-}$ | Frenata (N2) | 5 | |
| | | | | N2 | 5 | |
| 56 | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 16 | |
| | | | | Y1 | 9 | |
| | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 19 | |
| | | | | Y1 | 6 | |
| 57 | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 14 | |
| | | | | Y1 | 8 | |
| | Prog. 2 | Y1 | $C^{Y1}/C^{Y1}$ | N4 | 19 | |
| | | | | Y1 | 18 | |
| | | * | | N4 | 1 | |
| | | | | Y1 | 1 | |
| 60 | Prog. 6 | Zonata (N4) | $C^{N4}B1^{-}B2^{Z}/C^{Y1}B1^{-}B2^{-}$ | Zonata (N4) | 15 | |
| | | | | Y1 | 7 | |
| | Prog. 6 | Zonata (N4) | $C^{N4}B1^{-}B2^{Z}/C^{Y1}B1^{-}B2^{-}$ | Zonata (N4) | 22 | |
| | | | | Y1 | 8 | |
| 61 | Prog. 7 | Zonata (N2) | $C^{N2}B1^{-}B2^{Z}/C^{W}B1^{-}B2^{-}$ | Zonata (N2) | 29 | |
| | | | | W (N2 spire) | 4 | |
| | Prog. 7 | Zonata (N2) | $C^{N2}B1^{-}B2^{Z}/C^{W}B1^{-}B2^{-}$ | Zonata (N2) | 27 | |
| | | | | W (N2 spire) | 12 | |
| | | * | | Zonata (N2) | 2 | |

(5) Spire not scored in parent.
(6) Faded parent, should be N2.
(7) Faded parent, should be Y1.

| | | | | | | |
|---|---|---|---|---|---|---|
| 69 | Prog. 8 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{N2}B1^{-}B2^{-}$ | Lyra (N2) | 30 | |
| | | | | N3/N2 | 5 | |
| | Prog. 8 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{N2}B1^{-}B2^{-}$ | Lyra (N2) | 56 | |
| | | | | N3/N2 | 24 | |
| | | * | | Lyra (N2) | 1 | |
| 70 | Prog. 8 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{N2}B1^{-}B2^{-}$ | Lyra (N4/N3) | 25 | |
| | | | | N4/N3 | 16 | |
| | Prog. 8 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{N2}B1^{-}B2^{-}$ | Lyra (N4/N3) | 32 | |
| | | | | N4/N3 | 17 | |
| 72 | Prog. 6 | Zonata (N4) | $C^{N4}B1^{-}B2^{Z}/C^{Y1}B1^{-}B2^{-}$ | Lyra (N4) | 18 | |
| | | | | Zonata (N4) | 24 | |
| | | | | Frenata (N2) | 22 | |
| | | | | N1 | 15 | |
| | Prog. 16 | Frenata (N2) | $C^{N2}B1^{F}B2^{-}/C^{N1}B1^{-}B2^{-}$ | Lyra (N4) | 3 | |
| | | | | Zonata (N4) | 0 | |
| | | | | Frenata (N2) | 4 | |
| | | | | N1 | 6 | |
| | | * | | Zonata (N4) | 1 | |
| | | | | N1 | 1 | |
| 73 | Prog. 12 | N2 (N4 spire) | $C^{N2}S^{-}/C^{Y1}S^{N4}$ | N2 (N4 spire) | 10 | |
| | | | | N2 | 3 | |
| | | | | Y1 (N4 spire) | 12 | |
| | | | | Y1 | 0 | |
| | Prog. 12 | Y1 (N4 spire) | $C^{Y1}S^{N4}/C^{Y1}S^{-}$ | N2 (N4 spire) | 8 | |
| | | | | N2 | 10 | |
| | | | | Y1 (N4 spire) | 9 | |
| | | | | Y1 | 0 | |
| 74 | Prog. 10 | N2 | $C^{N2}P^{1}/C^{Y1}P^{-}$ | N4/N3 | 14 | (10) |
| | | | | N2 | 21 | |
| | | | | Y1 (N2 spire) | 6 | (11) |
| | Prog. 10 | N2 | $C^{N2}P^{1}/C^{Y1}P^{-}$ | N4/N3 | 6 | |
| | | | | N2 | 20 | |
| | | | | Y1 (N2 spire) | 9 | |
| 75 | Prog. 13 | Y1 | $C^{Y1}/C^{Y1}$ | Y1 | 61 | |
| | Prog. 13 | Y1 | $C^{Y1}/C^{Y1}$ | Y1 | 49 | |
| 77 | Prog. 11 | Y1 (N2 spire) | $C^{Y1}/C^{Y1}$ | Y1 (N2 spire) | 27 | |
| | | | | Y1 | 33 | |
| | Prog. 11 | Y1 | $C^{Y1}/C^{Y1}$ | Y1 (N2 spire) | 26 | |
| | | | | Y1 | 27 | |
| | | * | | Y1 | 1 | |
| 78 | Prog. 18 | Lyra (N3) | $C^{N3}B1^{F}B2^{Z}/C^{N1}B1^{-}B2^{-}$ | Lyra (N4/N2) | 56 | |
| | | | | N1 | 23 | |
| | Prog. 18 | Lyra (N3) | $C^{N3}B1^{F}B2^{Z}/C^{N1}B1^{-}B2^{-}$ | Lyra (N4/N2) | 38 | |
| | | | | N1 | 19 | |

(10) Segregation difficult.
(11) Spire not scored in 1966.

| Mating No. | Provenance | Parents: Phenotype | Parents: Inferred genotype | Progeny: Phenotype | No. | Notes |
|---|---|---|---|---|---|---|
| 109 | Urufara | O2 (Orange lip) | | O2 (Orange lip) | 2 | |
| | | | | Y1 | 0 | |
| | Prog. 57 | Y1 | | O2 (Orange lip) | 0 | |
| | | | | Y1 | 1 | |
| | | * | | Y1 | 1 | |
| 111 | Prog. 6 | N1 | $C^{N1}/C^{Y1}$ | N1 | 0 | |
| | | | | Y1 | 0 | |
| | Prog. 62 | Y1 | $C^{Y1}/C^{Y1}$ | N1 | 4 | |
| | | | | Y1 | 4 | |
| 113 | Prog. 4 | N4 | $C^{N4}/C^{Y1}$ | N4 | 16 | |
| | | | | Y1 | 17 | |
| | Prog. 4 | Y1 | $C^{Y1}/C^{Y1}$ | N4 | 9 | |
| | | | | Y1 | 11 | |
| 116 | Roroie | P2 (Pink lip) | $C^{Y1}p^{2}L^{P}/C^{Y1}p^{2}L^{W}$ | P2 (Pink lip) | 20 | |
| | | | | P2 | 23 | |
| | Prog. 58 | Y1 | $C^{Y1}p^{-}L^{W}/C^{Y1}p^{-}L^{W}$ | P2 (Pink lip) | 4 | |
| | | | | P2 | 2 | |
| | | * | | P2 (Pink lip) | 3 | |
| | | | | P2 | 1 | |
| 121 | Prog. 74 | N4 | $C^{N2}p^{1}/C^{N2}p^{1}$ | N3/N2 | 14 | |
| | Prog. 74 | N3 | $C^{N2}p^{1}/C^{N2}p^{1}$ | N3/N2 | 12 | |
| | | * | | N3/N2 | 1 | |
| 123 | Prog. 74 | N2 | $C^{N2}p^{1}/C^{Y1}p^{-}$ | N3 | 8 | |
| | | | | N2 | 10 | |
| | | | | Y1 | 4 | |
| | Prog. 74 | N2 | $C^{N2}p^{1}/C^{Y1}p^{-}$ | N3 | 3 | |
| | | | | N2 | 8 | |
| | | | | Y1 | 3 | |
| | | * | | Y1 | 1 | |
| 126 | Prog. 62 | N1 | $C^{N1}/C^{Y1}$ | N1 | 6 | |
| | | | | Y1 | 5 | |
| | Prog. 62 | Y1 | $C^{Y1}/C^{Y1}$ | N1 | 5 | |
| | | | | Y1 | 4 | |
| 128 | Prog. 62 | N2 | $C^{N2}/C^{Y1}$ | N2 | 14 | |
| | | | | N1 | 6 | |
| | | | | Y1 | 6 | |
| | Prog. 62 | N1 | $C^{N1}/C^{Y1}$ | N2 | 15 | |
| | | | | N1 | 6 | |
| | | | | Y1 | 7 | |

| Mating No. | Provenance | Parents: Phenotype | Parents: Inferred genotype | Progeny: Phenotype | No. | Note |
|---|---|---|---|---|---|---|
| 137 | Prog. 8 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{N2}B1^{-}B2^{-}$ | Lyra (N2) | 19 | |
| | | | | N2/N1 | 9 | |
| | Prog. 8 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{N1}B1^{-}B2^{-}$ | Lyra (N2) | 1 | |
| | | | | N2/N1 | 0 | |
| 138 | Prog. 18 | Lyra (N3) | $C^{N3}B1^{F}B2^{Z}/C^{N1}B1^{-}B2^{-}$ | Lyra (N3/N2) | 16 | |
| | | | | N1 | 8 | |
| | Prog. 18 | Lyra (N3) | $C^{N3}B1^{F}B2^{Z}/C^{Y1}B1^{-}B2^{-}$ | Lyra (N3/N2) | 10 | |
| | | | | N1 | 3 | |
| 139 | Prog. 67 | Zonata (N4) | $C^{N4}B1^{-}B2^{Z}/C^{N1}B1^{-}B2^{-}$ | Zonata (N4) | 10 | |
| | | | | N1 | 5 | |
| | Prog. 67 | Zonata (N4) | $C^{N4}B1^{-}B2^{Z}/C^{N1}B1^{-}B2^{-}$ | Zonata (N4) | 7 | |
| | | | | N1 | 3 | |
| 140 | Prog. 73 | N2( N4 spire) | $C^{N2}S^{-}/C^{Y1}S^{N4}$ | | | |
| | Prog. 73 | Y1 (N4 spire) | $C^{Y1}S^{N4}/C^{Y1}S?$ | | | |
| | | * | | Y1 (N4 spire) | 1 | |
| 141 | Prog. 77 | Y1 | $C^{Y1}/C^{Y1}$ | Y1 | 20 | |
| | Prog. 77 | Y1 | $C^{Y1}/C^{Y1}$ | Y1 | 19 | |
| 142 | Prog. 77 | Y1 (N2 spire) | $C^{Y1}/C^{Y1}$ | Y1 (N2 spire) | 10 | |
| | | | | Y1 | 1 | |
| | Prog. 77 | Y1 (N2 spire) | $C^{Y1}/C^{Y1}$ | Y1 (N2 spire) | 6 | |
| | | | | Y1 | 2 | |
| | | * | | Y1 (N2 spire) | 1 | |
| 143 | Prog. 77 | Y1 (N2 spire) | $C^{Y1}/C^{Y1}$ | Y1 (N2 spire) | 1 | |
| | | | | Y1 | 3 | |
| | Prog. 77 | Y1 | $C^{Y1}/C^{Y1}$ | Y1 (N2 spire) | 7 | |
| | | | | Y1 | 0 | |
| | | * | | Y1 | 1 | |
| 144 | Prog. 9 | Lyra (N2) | $C^{N2}B1^{F}B2^{Z}/C^{Y1}B1^{-}B2^{-}$ | Lyra (N3) | 0 | |
| | | | | Lyra (N2) | 2 | |
| | | | | N3 | 1 | |
| | | | | Y1 (N2 spire) | 5 | |
| | Prog. 9 | N3 | $C^{N3}B1^{-}B2^{-}/C^{Y1}B1^{-}B2^{-}$ | Lyra (N3) | 1 | |
| | | | | Lyra (N2) | 1 | |
| | | | | N3 | 1 | |
| | | | | Y1 (N2 spire) | 2 | |
| | | * | | Lyra (N2) | 1 | |
| | | | | Y1 (N2 spire) | 1 | |
| 145 | Prog. 116 | P2 (Pink lip) | $C^{Y1}p^{2}L^{P}/C^{Y1}p^{-}L^{W}$ | P2 (Pink lip) | 1 | |
| | | | | Y1 | 1 | |
| | Prog. 116 | P2 (Pink lip) | $C^{Y1}p^{2}L^{P}/C^{Y1}p^{-}L^{W}$ | P2 (Pink lip) | 10 | |
| | | | | Y1 | 3 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| 129 | Prog. 74 | N3 | $C^{N2}p^1/C^{N2}p^1$ | N3/N2 | 7 | (12) |
| | | | | N2/N1 | 10 | |
| | Prog. 74 | N2 | $C^{N2}p^1/C^{Y1}p^-$ | N3/N2 | 6 | |
| | | | | N2/N1 | 2 | |
| 130 | Prog. 74 | Y1 (N2 spire) | $C^{Y1}p^-/C^{Y1}p^-$ | Y1 (N2 spire) | 17 | |
| | | | | Y1 | 3 | |
| | Prog. 74 | Y1 (N2 spire) | $C^{Y1}p^-/C^{Y1}p^-$ | Y1 (N2 spire) | 9 | |
| | | | | Y1 | 3 | |
| 131 | Prog. 15 | N3 | $C^{N3}/C^{Y1}$ | N3 | 1 | (13) |
| | | | | N2 | 0 | |
| | | | | Y1 | 1 | |
| | Prog. 15 | N2 | $C^{N2}/C^{Y1}$ | N3 | 11 | |
| | | | | N2 | 5 | |
| | | | | Y1 | 6 | |
| | | * | | Y1 | 1 | |
| 132 | Prog. 2 | N4 | $C^{N4}/C?$ | N4 | 22 | (14) |
| | Prog. 4 | N4 | $C^{N4}/C?$ | N4 | 28 | |
| | | * | | N4 | 1 | |
| 133 | Prog. 6 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N4) | 8 | |
| | | | | Y1 | 3 | |
| | Prog. 6 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N4) | 0 | |
| | | | | Y1 | 0 | |
| 134 | Prog. 6 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N4) | 6 | |
| | | | | Y1 | 0 | |
| | Prog. 6 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N4) | 18 | |
| | | | | Y1 | 3 | |
| | | * | | Zonata (N4) | 1 | |
| | | | | Y1 | 1 | |
| 135 | Prog. 7 | Zonata (N2) | $C^{N2}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N2) | 51 | |
| | | | | Y1 (N2 spire) | 15 | |
| | Prog. 7 | Zonata (N2) | $C^{N2}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Zonata (N2) | 42 | |
| | | | | Y1 (N2 spire) | 17 | |
| 136 | Prog. 9 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 3 | |
| | | | | Zonata (N2) | 3 | |
| | | | | Y1 (N2 spire) | 1 | |
| | Prog. 7 | Zonata (N2) | $C^{N2}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 0 | |
| | | | | Zonata (N2) | 1 | |
| | | | | Y1 (N2 spire) | 0 | |
| | | * | | Lyra (N2) | 1 | |
| 146 | Prog. 123 | N2 | $C^{N2}p^1/C^{Y1}p^-$ | N2 | 13 | |
| | | | | Y1 | 7 | |
| | Prog. 123 | Y1 | $C^{Y1}p^-/C^{Y1}p^-$ | N2 | 2 | |
| | | | | Y1 | 1 | |
| 147 | Prog. 123 | N2 | $C^{N2}p^1/C^{Y1}p^-$ | N2 | 1 | |
| | | | | Y1 | 2 | |
| | Prog. 123 | Y1 | $C^{Y1}p^-/C^{Y1}p^-$ | N2 | 4 | |
| | | | | Y1 | 3 | |
| 165 | Prog. 9 | N3 | $C^{N3}/C^{Y1}$ | N4 | 4 | |
| | | | | N3 | 8 | |
| | | | | Y1 (N2 spire) | 7 | |
| | Prog. 9 | N3 | $C^{N3}/C^{Y1}$ | N4 | 6 | |
| | | | | N3 | 17 | |
| | | | | Y1 (N2 spire) | 8 | |
| 166 | Prog. 72 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N1}B1^-B2^-$ | Zonata (N4) | 32 | |
| | | | | N1 | 10 | |
| | Prog. 72 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N1}B1^-B2^-$ | Zonata (N4) | 25 | |
| | | | | N1 | 13 | |
| | | * | | Zonata (N4) | 1 | |
| 167 | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 24 | |
| | | | | Y1 | 9 | |
| | Prog. 113 | N4 | $C^{N4}/C^{Y1}$ | N4 | 9 | |
| | | | | Y1 | 3 | |
| 168 | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 53 | |
| | | | | Y1 | 16 | |
| | Prog. 2 | N4 | $C^{N4}/C^{Y1}$ | N4 | 4 | |
| | | | | Y1 | 0 | |
| | | * | | N4 | 2 | |
| 178 | Prog. 116 | P2 (Pink lip) | $C^{Y1}P^2L^P/C^{Y1}P^-L^W$ | P2 (Pink lip) | 21 | |
| | | | | Y1 | 6 | |
| | Prog. 116 | P2 (Pink lip) | $C^{Y1}P^2L^P/C^{Y1}P^-L^W$ | P2 (Pink lip) | 4 | |
| | | | | Y1 | 4 | |
| 179 | Prog. 116 | P2 (Pink lip) | $C^{Y1}P^2L^P/C^{Y1}P^-L^W$ | P2 (Pink lip) | 5 | |
| | | | | Y1 | 1 | |
| | Prog. 116 | P2 (Pink lip) | $C^{Y1}P^2L^P/C^{Y1}P^-L^W$ | P2 (Pink lip) | 7 | |
| | | | | Y1 | 5 | |
| 180 | Prog. 116 | P2 (Pink lip) | $C^{Y1}P^2L^P/C^{Y1}P^-L^W$ | P2 (Pink lip) | 16 | |
| | | | | Y1 | 4 | |
| | Prog. 116 | P2 (Pink lip) | $C^{Y1}P^2L^P/C^{Y1}P^-L^W$ | P2 (Pink lip) | 13 | |
| | | | | Y1 | 7 | |
| 181 | Prog. 9 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 29 | |
| | | | | Y1 (N2 spire) | 6 | |
| | Prog. 9 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 10 | |
| | | | | Y1 (N2 spire) | 5 | |
| | | * | | Y1 (N2 spire) | 1 | |

(12) Segregation difficult.
(13) Possible segregation in N3 of 4 dark and 8 light.
(14) One parent derived by self-fertilisation.

| Mating No. | Provenance | Parents: Phenotype | Parents: Inferred genotype | Progeny: Phenotype | Progeny: No. | Notes |
|---|---|---|---|---|---|---|
| 182 | Prog. 68 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N3}B1^-B2^-$ | Zonata (N4) | 12 | |
| | | | | Zonata (N4 extreme) | 18 | |
| | | | | N4 | 14 | |
| | Prog. 68 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N3}B1^-B2^-$ | Zonata (N4) | 3 | |
| | | | | Zonata (N4 extreme) | 18 | |
| | | | | N4 | 5 | |
| | | * | | Zonata (N4) | 1 | |
| | | | | N4 | 2 | |
| 183 | Prog. 68 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 47 | |
| | | | | Y1 | 13 | |
| | Prog. 68 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 38 | |
| | | | | Y1 | 7 | |
| | | * | | Lyra (N2) | 2 | |
| 184 | Prog. 68 | Lyra (N4) | $C^{N2}B1^FB2^Z/C^{N4}B1^-B2^Z$ | Lyra (N2) | 8 | |
| | | | | Lyra (N4) | 22 | |
| | | | | Zonata (N4) | 11 | |
| | Prog. 68 | Lyra (N4) | $C^{N2}B1^FB2^Z/C^{N4}B1^-B2^Z$ | Lyra (N2) | 15 | |
| | | | | Lyra (N4) | 36 | |
| | | | | Zonata (N4) | 6 | |
| | | * | | Lyra (N4) | 1 | |
| 185 | Prog. 72 | Frenata (N2) | $C^{N2}B1^FB2^-/C^{Y1}B1^-B2^-$ | Frenata (N2) | 21 | |
| | | | | Y1 | 5 | |
| | Prog. 72 | Frenata (N2) | $C^{N2}B1^FB2^-/C^{Y1}B1^-B2^-$ | Frenata (N2) | 21 | |
| | | | | Y1 | 4 | |
| 186 | Prog. 72 | Lyra (N4) | $C^{N4}B1^-B2^Z/C^{N2}B1^FB2^-$ | Zonata (N4) | 14 | |
| | | | | Lyra (N4) | 22 | |
| | | | | Frenata (N2) | 12 | |
| | Prog. 72 | Lyra (N4) | $C^{N4}B1^-B2^Z/C^{N2}B1^FB2^-$ | Zonata (N4) | 3 | |
| | | | | Lyra (N4) | 13 | |
| | | | | Frenata (N2) | 7 | |
| | | * | | Lyra (N4) | 1 | |
| 187 | Prog. 72 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N1}B1^-B2^-$ | Zonata (N4) | 15 | |
| | | | | N1 | 6 | |
| | Prog. 72 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{N1}B1^-B2^-$ | Zonata (N4) | 31 | |
| | | | | N1 | 12 | |
| | | * | | Zonata (N4) | 1 | |
| 188 | Prog. 74 | N2 | $C^{N2}P^1/C^{Y1}P^1$ | N3/N2 | 28 | |
| | | | | P1 | 13 | |
| | Prog. 74 | N2 | $C^{N2}P^1/C^{Y1}P^-$ | N3/N2 | 13 | |
| | | | | P1 | 2 | |
| | | * | | N3/N2 | 2 | |
| | | | | P1 | 1 | |
| 189 | Prog. 74 | N3 | $C^{N2}P^1/C^{N2}P^1$ | N3/N2 | 7 | |
| | Prog. 74 | N3 | $C^{N2}P^1/C^{N2}P^1$ | N3/N2 | 6 | |
| 208 | Prog. 73 | N2 (N4 spire) | $C^{N2}S^-/C^{Y1}S^{N4}$ | N2 | 1 | |
| | Prog. 73 | N2 (N4 spire) | $C^{N2}S^-/C^{Y1}S^{N4}$ | | | |
| 209 | Prog. 73 | N2 (N4 spire) | $C^{N2}S^-/C^{Y1}S^{N4}$ | N2 | 3 | |
| | | | | N2 (N4 spire) | 5 | |
| | | | | Y1 (N4 spire) | 5 | |
| | | | | Y1 | 0 | |
| | Prog. 73 | N2 (N4 spire) | $C^{N2}S^-/C^{Y1}S^{N4}$ | N2 | 2 | |
| | | | | N2 (N4 spire) | 7 | |
| | | | | Y1 (N4 spire) | 3 | |
| | | | | Y1 | 0 | |
| | | * | | N2 (N4 spire) | 1 | |
| 227 | Prog. 68 | Lyra (N4) | $C^{N2}B1^FB2^Z/C^{N4}B1^-B2^Z$ | Lyra (N2) | 5 | |
| | | | | Lyra (N4) | 6 | |
| | | | | Zonata (N4) | 5 | |
| | Prog. 68 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 7 | |
| | | | | Lyra (N4) | 7 | |
| | | | | Zonata (N4) | 8 | |
| | | * | | Zonata (N4) | 2 | |
| 237 | Parent 68 | Lyra (N4) | $C^{N2}B1^FB2^Z/C^{N3}B1^-B2^-$ | Lyra (N2) | 2 | |
| | | | | N4/N3 | 0 | |
| | Parent 59 | Y1 | $C^{Y1}B1^-B2^-/C^{Y1}B1^-B2^-$ | Lyra (N2) | 0 | |
| | | | | N4/N3 | 2 | |
| | | * | | N4/N3 | 1 | |
| 238 | Parent 70 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{N2}B1^-B2^-$ | Lyra (N4) | 0 | |
| | | | | Lyra (N2) | 0 | |
| | | | | Zonata (N4) | 1 | |
| | | | | N2 | 0 | |
| | Parent 134 | Zonata (N4) | $C^{N4}B1^-B2^Z/C^{Y1}B1^-B2^-$ | Lyra (N4) | 3 | |
| | | | | Lyra (N2) | 5 | |
| | | | | Zonata (N4) | 2 | |
| | | | | N2 | 1 | |
| | | | | Y1 | 1 | (15) |
| | | * | | Lyra (N2) | 1 | |
| 239 | Parent 138 | Lyra (N3) | $C^{N3}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N3) | 8 | |
| | | | | Zonata (N2) | 3 | |
| | | | | Y1 (N2 spire) | 3 | |
| | Parent 61 | Zonata (N2) | $C^{N2}B1^-B2^Z/C^{W}B1^-B2^-$ | Lyra (N3) | 8 | |
| | | | | Zonata (N2) | 2 | |
| | | | | Y1 (N2 spire) | 9 | |
| | | * | | Zonata (N2) | 3 | |
| | | | | Y1 (N2 spire) | 2 | |
| 240 | Parent 136 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{Y1}B1^-B2^-$ | Lyra (N2) | 0 | |
| | | | | N2 | 0 | |
| | Parent 137 | Lyra (N2) | $C^{N2}B1^FB2^Z/C^{N2}B1^-B2^-$ | Lyra (N2) | 1 | |
| | | | | N2 | 1 | |
| 241 | Parent 74 | N2 | $C^{N2}P^1/C^{Y1}P^-$ | N2 | 0 | |
| | | | | Y1 (N2 spire) | 2 | |
| | Parent 10 | Y1 | $C^{Y1}P^-/C^{Y1}P^-$ | N2 | 4 | |
| | | | | Y1 (N2 spire) | 5 | |
| | | * | | Y1 (N2 spire) | 1 | |

(15) By self-fertilisation.

TABLE 2

*Loci and alleles identified in matings of* Partula taeniata

| | Locus | Alleles | |
|---|---|---|---|
| Linked | *C* Ground colour of shell | $C^{N4}$, $C^{N3}$, $C^{N2}$, $C^{N1}$ | Neutral brown with decreasing intensity of a purplish hue |
| | | $C^{Y1}$ | Pale yellow |
| | | $C^{W}$ | White |
| | *P* Pink shell colour | $P^2$, $P^1$ | Pink of decreasing intensity |
| | | $P^-$ | Unmodified |
| | *L* Pigmentation of lip | $L^P$ | Pink |
| | | $L^W$ | White |
| | *S* Pigmentation of spire | $S^{N4}$ | Dark spire |
| | | $S^-$ | Unmodified |
| | *B1* Banding of shell | $B1^F$ | Frenata |
| | | $B1^-$ | Unbanded |
| | *B2* Banding of shell | $B2^Z$ | Zonata |
| | | $B2^-$ | Unbanded |

Unassigned segregations: Orange *vs.* yellow shell; Orange *vs.* white lip; N2 *vs.* unmodified spire colour.

offspring, except for mating 62, where the Y1 young are almost certainly the products of selfing. And finally, there is evidence of linkage between the banding loci (see below) and the locus determining the segregation of related pairs of colour alleles ($C^{N4}/C^{N2}$, mating 186; $C^{N4}/C^{N1}$, mating 6; $C^{N4}/C^{Y1}$, mating 66; $C^{N3}/C^{N1}$, mating 138; $C^{N2}/C^{N1}$, mating 71; $C^{N2}/C^{Y1}$, mating 185; $C^{N2}/C^{W}$, mating 61) indicating that, at the very least, these colour segregations are controlled by closely linked loci.

### (ii) *Locus* P*: pink shell colour*

It is likely that pink colour is determined by a separate locus, *P*. Mating 145, 178, 179 and 180 (all derived from 116) show regular $F_2$ segregations of medium pink (P2) and pale yellow (Y1), suggesting control by a single locus, with pink dominant to yellow. However, pink offspring appear unexpectedly in the offspring of mating 188 of the lineage of mating 10. One might suspect an error in mating 188 except that pink is an uncommon phenotype in *P. taeniata* and that one parent of mating 10 is from the same locality as is the pink parent of mating 116. The simplest hypothesis to account for this result is that the gene for pink colouration ($P^1$) has been transmitted from the N2 parent of mating 10, its expression masked by the $C^{N2}$ allele at the principal colour locus. By crossing over, one parent of mating 188 now carries $P^1$ in association with $C^{Y1}$, allowing the expression of pink in the $C^{Y1}C^{Y1}$ homozygote. Although there is no direct proof of the allelism of $P^1$ and $P^2$ of the lineage of 116, similarity of phenotype and origin argue for this interpretation.

### (iii) *Orange shell colour*

In mating 109, orange shell colour has been shown to segregate with yellow (Y1). However, in the absence of further crosses, nothing can be said about its allelic relationships.

### (iv) *Locus* L*: the colour of the lip*

In most populations of *P. taeniata*, the majority of individuals have shells with white peristomes, regardless of the colour of the remainder of the shell. However, other colours of lip such as pink, orange and purple are occasionally found. Usually the coloured lips are associated with shells of a similar colour.

Mating 116, a backcross, and the four $F_2$ segregations (145, 178, 179 and 180) derived from it indicate that pink lip colour is determined by a single locus, with pink ($L^P$) dominant to white ($L^W$). This locus is different from that for pink shell colour ($P$) but is linked to it (see below).

A single rather unsuccessful mating gives some information about orange lip. Since the orange lip is an unusual phenotype, mating 109 is probably a backcross of a heterozygote for orange lip to a white lipped homozygote. If so, then the meagre results suggest that the orange lip, like pink lip, is dominant to white, but there is no evidence that orange and pink are allelic.

### (v) *Locus* S*: the colour of the spire*

It is usual in *P. taeniata* for the shell to be coloured uniformly from just behind the peristome to the apex. In some populations, however, a significant proportion of the individuals show a darkening of the spire. The earliest whorls may be markedly darker than the rest of the shell, even by as much as three steps on the scale of intensity.

The lineage from mating 12 establishes the mode of inheritance of the darkest spire colour (N4). A single locus is involved, and dark spire ($S^{N4}$) is dominant to light spire ($S^-$). After the initial backcross, matings 73 and 209 are successive $F_2$ segregations.

The less intense (N2) spire colour, which in some shell colours is still distinguishably darker than the remainder of the shell, is rather more problematical, for several reasons. First, the contrast is less clear, and scoring is therefore more difficult. Second, some of the later matings suggest that in the early stages of the breeding programme we may not have noted all instances of N2 spires. Third, fading, particularly in living specimens, prevents an accurate rescoring of some of our initial parents. The fading problem is discussed more fully below, but it suffices to say that we believe the paler parents of matings, 7, 9, 10 and 11 to have originally had darker (N2) spires.

Making this assumption, the inheritance of the N2 spire becomes intelligible. In the lineage from mating 11, for example, mating 77 segregates as a backcross. From these offspring, the plain yellows of mating 141 do not segregate, while 142 is an $F_2$ and 143 is a backcross. The N2 spire behaves as a dominant at a single locus, just as the N4 spire discussed above, but there is no information on allelism. Lineages from 7, 8 and 10 are consistent with this interpretation.

(vi) *Locus* B1 *and locus* B2: *bands on the shell*

The lineages beginning with matings 6, 7, 8, 9, 16, 17 and 18 demonstrate segregations of the three common forms of banding, zonata, frenata and lyra, with the unbanded condition. Considering only the segregation of banded and unbanded, the data are consistent with control by a single locus with banded dominant to unbanded. Further analysis of the relationships of the three types of banding suggests, however, that at least two loci are involved.

This conclusion is based on the observation that the lyra phenotype can be produced in two different ways. On the one hand it shows segregation with zonata and with unbanded as if all three types were determined by alleles at a single locus, with zonata dominant to unbanded and lyra dominant to both. This pattern of inheritance is shown by mating 68 and matings derived from it. One parent in 68 carries zonata from mating 6 in the heterozygous condition with unbanded. The other carries lyra from mating 9, also heterozygous with unbanded. Its colour alleles show it to have originated by self-fertilisation. Four types of offspring are produced in 68, unbanded homozygotes and three classes of bandeds. There are zonatas with dark (N4) bands, shown by 182 to be heterozygotes between zonata and unbanded (with the colour allele $C^{N3}$). There are lyras with light (N2) bands, shown by 183 to be heterozygotes between lyra and unbanded (with the colour allele $C^{Y1}$). Finally there are lyras with dark (N4) bands, heterozygotes of lyra and zonata, which in 184 produce homozygous light lyras, homozygous dark zonatas, and heterozygotes like themselves. Mating 227, with light and dark lyras as parents, yields light lyras (presumably both homozygotes and heterozygotes, but in deficient numbers), dark lyra heterozygotes, and dark zonatas which are heterozygotes with unbanded. This consistent behaviour of the lyra " allele " is repeated in the lineages from matings 8 and 18.

On the other hand, the lyra phenotype may also be produced by the conjunction of zonata and frenata in the same individual. This configuration is illustrated in mating 72 and its derivatives. As in 68, the zonata parent comes from mating 6 and is heterozygous for unbanded. The frenata parent is from mating 16 and is also heterozygous for unbanded. Again there is an unbanded class and three classes of banded young. The zonatas are shown by matings 166 and 187 to be heterozygotes with unbanded (of $C^{N1}$ colour type). The frenatas, in mating 185, appear to be heterozygotes with unbanded (of $C^{Y1}$ colour type). But mating 186 shows the lyras to be heterozygotes of zonata and frenata, producing all three banding types in a 1 : 2 : 1 ratio.

A simple genetic hypothesis will accommodate all these results. We suggest that two loci ($B1$ and $B2$), separate but tightly linked, control the expression of banding. Unbandeds are recessive at both loci. A dominant allele at one locus ($B1^F$) produces frenata; a dominant at the other ($B2^Z$), zonata. Linked in repulsion ($B1^F B2^- / B1^- B2^Z$) the two dominants together behave as a heterozygote and produce lyra. Linked in coupling ($B1^F B2^Z$) they behave as an allele of zonata, frenata and unbanded. The dominance of the lyra " allele " over zonata alone is consistent with this interpretation. Random samples from natural populations are also compatible with this hypothesis since the number of individuals of lyra pattern is usually in excess of the expected number of frenata/zonata heterozygotes.

## 4. Problems of interpretation

Some of our matings have given rise to problems that have been difficult to resolve. These include the fading of shell colours, other problems in scoring, and some apparent inconsistencies between matings.

Fading can be seen in the parents of some of our matings. This is particularly true of the shells of living animals; the fading is minimised if the snails are killed shortly after reaching maturity. The lighter colours are most susceptible to change. Old Y1 individuals become chalky white and N2 spires lose their distinctive contrast. These changes have caused problems in two ways. First, in our initial matings we did not score the parents for the dusky (N2) spire in matings 7, 9, 10 and 11; and it is now too late to do so with any certainty. From the breeding results, however, it is highly probable that the lighter parent in each of these matings bore a dusky spire. Second, there are three cases in which we believe that fading has led us to mis-score the general shell colour of parents in our initial crosses. Our results suggest that the lighter parents in 7 and 15 should have been scored as Y1 instead of W and that the darker parent of 12 should have been N2 instead of N1. Again we cannot now rescore these individuals with any accuracy.

Another factor affecting the intensity of shell colour is the rate of growth of individual snails. Although it is difficult to quantify the extent of the effect, it appears that rapid growth leads to a slight dilution of the shell pigmentation. This phenomenon may be responsible for the variability of some broods (74, 129), for the blurring of segregations in others (78, 121, 131, 138), and for the differences between broods in still others (69 and 70).

Lastly there are two clearly anomalous results. In mating 182 we have a segregation of homozygous $C^{N4}$ zonatas, homozygous $C^{N3}$ (N4 phenotype) unbandeds, and heterozygotes ($C^{N4}/C^{N3}$). The heterozygotes are more extreme than the parents, which should be of the same genotype. Another anomaly is the single white offspring of mating 9. Further breeding has thrown no new light on its origin, although mutation cannot be excluded.

## 5. Self-fertilisation and differential viability

In an earlier paper (Murray and Clarke, 1966) we presented evidence that *Partula taeniata* is capable of self-fertilisation, but that production of young by snails isolated from birth averaged only about 2 per cent of the normal output of animals allowed to cross. At that time we were unable to say anything about the frequency of self-fertilisation in snails which are permitted to cross, although some young produced by selfing could be identified. We can now examine the effects of self-fertilisation within matings in which cross-fertilisation is also taking place.

In backcross matings, the occurrence of self-fertilisation will cause a disturbance of the Mendelian ratios, each animal producing an excess of offspring of its own phenotype. Since all of the offspring of the recessive by selfing are homozygous recessive, then the number of excess young of that type affords a direct estimate of self-fertilisation. In the case of the heterozygote, the 3 : 1 segregation produced by selfing should yield only half as great a deviation. Eleven of our matings produce information of this sort; five are segregating for N4 and Y1, and six for banded and unbanded. Since we had considered the possibility of changes in the frequency of self-fertilisation over time, the data from successive matings of each pair of animals were recorded separately. In the event, it appears that the amount of selfing following the first mating is much greater than after subsequent matings.

The data are presented in summary form in table 3. Unfortunately the numbers of offspring from individual matings are too few to carry out a meaningful test of heterogeneity between matings. Indeed, although the expected deviation from a 1:1 ratio should be twice as large among the

TABLE 3

*Combined offspring of matings segregating as backcrosses of banded vs. unbanded (matings 6, 9, 18, 65, 67, and 144) and N4 vs. Y1 (matings 2, 3, 57, 64, and 113). Offspring of the first matings in each case are shown separately from those of second and later matings*

| | 1st matings | | 2nd and later matings | |
|---|---|---|---|---|
| | Like parent | Unlike parent | Like parent | Unlike parent |
| Banded matings | | | | |
| Offspring of dominant | 30 | 18 | 109 | 110 |
| Offspring of recessive | 39 | 26 | 84 | 102 |
| N4 matings | | | | |
| Offspring of dominant | 18 | 14 | 77 | 74 |
| Offspring of recessive | 25 | 24 | 134 | 142 |

offspring of the recessive as among the offspring of the dominant, heterogeneity cannot be demonstrated among the four combined progenies from the first matings ($\chi^2_{(3)} = 1{\cdot}51$; $0{\cdot}7 > P > 0{\cdot}5$) nor those from the second and later matings ($\chi^2_{(3)} = 0{\cdot}34$; $P > 0{\cdot}95$). On the other hand, there is a significant excess of phenotypes like the parent among offspring of the first matings ($\chi^2_{(1)} = 4{\cdot}64$; $P < 0{\cdot}05$) and a significant difference between first matings and the rest ($\chi^2_{(1)} = 4{\cdot}94$; $P < 0{\cdot}05$).

In order to estimate the amount of self-fertilisation taking place in matings such as these, the simplest method is to assume that the deviations afford a direct measure of the phenomenon. Thus we have the proportion of selfed young, $S$, equal to the number of excess young like the parent among the offspring of the recessive plus twice the number among the offspring of the dominant, divided by the total number of progeny. For the first matings of both banded and N4 matings:

$$S = \frac{2(12)+13+2(4)+1}{48+65+32+49} = 23{\cdot}7\%$$

There is no evidence for self-fertilisation among broods from the second and later matings, but there is some interest in calculating an average frequency of self-fertilisation over the whole of the reproductive life of these individuals. In this case:

$$S = \frac{2(11)-5+2(7)-7}{1026} = 2{\cdot}3\%$$

These estimates can be slightly refined since we have two independent estimates of the deviation in each mating. Because these deviations are in opposite directions we can obtain joint estimates of self-fertilisation and of the viability of one of the homozygotes. It can be shown that if selection is considered to act against the dominant homozygote and that if the recessive homozygote is equal in viability to the heterozygote, then the proportion of selfing ($S$) and the viability ($V$) of the dominant homozygote are given by the following expressions:

From the offspring of the dominant:

$$S = \frac{2(D_1 - R_1)}{VR_1 + D_1} \quad \text{or} \quad V = \frac{2(D_1 - R_1) - D_1 S}{R_1 S}.$$

And from the offspring of the recessive:

$$S = \frac{R_2 - D_2}{R_2 + D_2} \quad \text{and} \quad V \text{ cannot be estimated,}$$

where the $D$'s are the numbers of dominant offspring and the $R$'s, the numbers of recessives in each case. If selection is operating against the recessive homozygote, then $S$ and $V$ (viability of the recessive homozygotes) are given by:

From the offspring of the dominant:

$$S = \frac{2(VD_3 + R_3)}{VD_3 + R_3} \quad \text{or} \quad V = \frac{2R_3 + R_3 S}{2D_3 - D_3 S}.$$

And from the offspring of the recessive:

$$S = \frac{R_4 - VD_4}{R_4 + VD_4} \quad \text{or} \quad V = \frac{R_4 - R_4 S}{D_4 + D_4 S}$$

Taking complementary expressions for each side of the mating, values for $S$ and $V$ can be derived. In the present case the expressions based on the calculation of the viability of the dominant homozygotes lead to unrealistic results, largely because of the small numbers of dominant homozygotes expected in these matings. To account for the overall deficiency of recessive offspring in terms of differential viability of the dominant homozygote requires unrealistically high selective values. On the other hand, the expressions based on the relative viability of the recessive homozygote provide reasonable estimates, not very different from the preliminary ones derived above. Table 4 lists these estimates.

TABLE 4

*Estimates of viability of the recessive homozygotes ($V$) and of the proportion of self-fertilisation ($S$) in backcross matings of* P. taeniata

| | $S$ | $V$ |
|---|---|---|
| 1st matings | | |
| Banded | 0·3 | 0·81 |
| N4 | 0·1 | 0·86 |
| Combined | 0·21 | 0·83 |
| 2nd and later matings | | |
| Banded | 0 | 0·92 |
| N4 | 0 | 0·95 |
| Combined | 0 | 0·93 |
| All matings combined | 0·025 | 0·95 |

It appears, therefore, that there is a tendency for *P. taeniata* to reproduce by self-fertilisation during the earlier part of the reproductive period, approximately 20 per cent of the young arising by this method. The frequency of self-fertilisation then declines to an undetectable level so that the overall proportion for the entire reproductive life is about 2·5 per cent. This value accords well with our previous independent estimate of 2 per cent based on the reproduction of isolated virgins (Murray and Clarke, 1966). It suggests that the level of self-fertilisation is much the same whether or not cross-fertilisation takes place.

There is also in these matings a suggestion of relative inviability of the recessive homozygotes, although in neither the N4 nor the banded matings do the lumped segregations show a significant deficiency. The comparison in viability here is primarily with the heterozygotes, since very few dominant homozygotes (about 8 in all matings) are expected among the offspring.

Viability differences may also be examined among the offspring of $F_2$ matings. In an earlier paper (Murray and Clarke, 1966) we reported a significant deficiency of banded offspring from crosses of heterozygotes for banded and unbanded. Taking all matings of this type together, there is still an overall deficiency of bandeds, but the deviation is no longer significant ($0{\cdot}2 > P > 0{\cdot}1$) nor is there any heterogeneity detectable among the matings ($0{\cdot}5 > P > 0{\cdot}3$).

Before dismissing differences in viability, however, we must consider the possibility of compensating differences between the two homozygotes. In the case of heterozygous advantage, when the coefficient of selection against the dominant homozygote is three times that against the recessive homozygote, then no disturbance of the expected Mendelian ratio will be observed. We have reason to suspect, from the backcross results, that there is some degree of inviability of the recessive homozygotes. There is therefore a consistent, though non-significant, indication of heterozygote advantage over both homozygotes in these matings.

## 6. Linkage, allelism and the supergene

The results of the matings have been presented as if the principal elements of the genetic polymorphism of *P. taeniata* were controlled by multiple alleles at six or more separate loci. It is apparent, however, that these loci are not independent of each other. In fact, the linkage among them is so strong that the appearance of a recombinant is a very rare event.

The evidence for linkage between the locus for pink shell colour ($P$) and that for lip colour ($L$) is provided by the offspring of mating 116. The pink parent in 116 is homozygous for pink shell but heterozygous for pink lip colour. Four matings, 145, 178, 179 and 180, have produced a total of 108 $F_2$ offspring without the appearance of a single recombinant individual. These matings clearly show that, while pink lip is not invariably associated with pink shell, the two loci concerned are closely linked. Linkage between the two colour loci $P$ and $C$ has already been invoked to account for the results of mating 188.

Clear evidence for linkage of the loci for shell colour ($C$) and spire colour ($S$) is found in the lineage from mating 12. The allele for dark spire ($S^{N4}$) is carried in heterozygous condition by a parent that is homozygous for the allele determining yellow shell colour ($C^{Y1}$). Mating 73 is therefore an

$F_2$ segregation with respect to the dark spire; but since the locus for dark spire is closely linked to that for Y1 colour, none of the yellows in this generation bears a plain spire. In the succeeding matings, 209 repeats this pattern, with all plain-spired individuals belonging to the N2 class. The two offspring of 140 and 208 are also consistent with the hypothesis of linkage since one is a plain-spired N2 and the other is a dark-spired Y1.

The hypothesis that banding is controlled by two linked loci has been discussed above. If there are indeed two loci then they must certainly be linked. Otherwise the lyras of lineage 68 would be expected to segregate for all three banding types.

It is also of importance to establish the linkage of the banding loci (*B*1 and *B*2) to that for shell colour (*C*). If we assume that the banding loci determine pattern only and that the hue and intensity of the colour are controlled by the locus for shell colour, then the evidence is overwhelming. For example, in mating 6 all the banded offspring are very dark (N4) while the unbandeds are light (N1). This pattern of inheritance continues throughout the lineage. The unequivocal demonstration of linkage, however, requires proof that the determinants of banding are not simply alleles at the colour locus. In the absence of undoubted recombinants, this alternative cannot be excluded.

This dilemma merely serves to emphasise our general thesis. None of the elements of the polymorphism for shell colour and pattern has been shown to segregate independently of the rest. All our data are consistent with the interpretation of the polymorphism as the expression of a single compound locus or supergene with a large number of possible combinations of elements segregating as alleles. In this respect the polymorphism of *P. taeniata* illustrates a principle which is becoming more and more familiar as more examples of complex polymorphisms are being analysed. Where many elements are involved in the production of a polymorphism and where not all possible combinations of the elements are selectively advantageous, then linkage provides a method for maintaining the appropriate combinations. This is essentially the evolutionary hypothesis of linkage disequilibrium developed by Fisher (1930) in *The Genetical Theory of Natural Selection*.

Since that time a number of polymorphisms have been analysed to show that genetic control is accomplished by means of one or more complex loci or supergenes. Some classic examples are colour patterns in fish (Winge, 1927), in poppies (Philp, 1934), in grouse locusts (Nabours, 1929; Nabours *et al.*, 1933), in helicid snails (Cain *et al.*, 1960, 1968) and in butterflies (Sheppard, 1959; Clarke and Sheppard, 1972). Complex loci are also responsible for the inheritance of the elements of the heterostyle condition in primroses (Mather, 1950; Dowrick, 1956) and of the Rhesus blood groups in man (Fisher, 1953). The comparative genetics of colour and pattern of five species of isopod in the genus *Sphaeroma* (Lejuez, 1966) provides a particularly instructive example, since the linkage relationships of homologous loci vary widely within the group.

The genetics of *Partula taeniata* may therefore be seen as an example of a general phenomenon characteristic of complex polymorphisms. The analogy with *Cepaea nemoralis* is particularly striking. Many similar elements may be recognised in the two species. Colour of the shell, colour of the lip and presence or absence of banding of the shell are under simple genetic control in each, and linkage plays a significant role. Since the species are so distantly related and so different in the expression of these characters it seems highly unlikely that the similarities are the result of genetic homology. On the contrary, we can conclude that the two systems are independently derived and that the species have converged in response to similar environmental problems.

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