THE INHERITANCE OF POLYMORPHIC
SHELL CHARACTERS IN PARTULA (GASTROPODA)

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THE land snails of the genus Partula display a rich and varied series of poly-
morphisms. The species, about 100 in number, which make up the genus
are distributed on the "high" volcanic islands of the Pacific from the Marianas
in the west to the Marquesas and Austral Islands in the east. Most of the species
are confined to single islands; but within their limited distributions, they have
developed an extraordinary degree of polymorphism.

Present knowledge of the variation within species of Partula is based largely
on the work of PROFESSOR H. E. CRAMPTON. In three large monographs he de-
scribed the composition of populations inhabiting Tahiti (1916), the Marianas
(1925), and Moorea (1932). Almost all of the species include several color forms
and one or more patterns of banding of the shell. In many instances parallel
series of forms are found in different species.

As one of the first scientists in the United States to appreciate the importance
of Mendel's work, PROFESSOR CRAMPTON was interested throughout his life in
the problem of the relative importance of the effects of heredity and environment.
He adduced evidence from his studies on Partula that variation is not produced
directly by environmental influence but is the result of essentially random muta-
tion. Moreover, although he believed in the importance of orthodox Darwinian
selection, CRAMPTON (1928) considered the varieties of shell pattern and color
in Partula to be "indifferent characters", unaffected by selection. To account for
the spread of such characters, he invoked the processes of recurrent mutation and
migration (CRAMPTON 1932). Since the publication of CRAMPTON's data, the
polymorphism in Partula has been discussed as a possible example of random
variation resulting from genetic drift (pro: HUXLEY 1942; con: CAIN and
SHEPPARD 1950; FORD 1964).

CRAMPTON's arguments for a genetic basis for the polymorphism rested largely
on his population data. While it is true that he obtained some information from
the dissection of individuals containing embryonic snails, the scoring of most
characters *in utero* is unreliable. CRAMPTON certainly intended to undertake the
breeding of Partula in the laboratory (CRAMPTON 1929), but the work was not
carried out.

In this paper we are reporting data which confirm the genetic basis of some
of the principal forms of *Partula taeniata* Mörch and *P. suturalis* Pfeiffer. Hence
we consider it appropriate to dedicate our results to the memory of PROFESSOR
H. E. CRAMPTON.

METHODS

Breeding: The foundation stocks for this study were collected in 1962 on the island of Moorea in the Society group. We spent four months (May to August) on the island. In the course of sampling the populations from which CRAMPTON's collections were derived, some of the material was maintained alive and was subsequently transferred to the laboratories at the Universities of Edinburgh and Virginia.

It has proved possible to rear the animals on a simple regime. They are kept in plastic boxes lined at the bottom with moistened toilet paper to provide a humid atmosphere. The animals are fed a diet of lettuce and oatmeal, with a sprinkling of powdered calcium carbonate to provide material for the shell. They also eat some of the paper.

The snails are ovoviviparous hermaphrodites and normally produce young by cross-fertilization (see below). CRAMPTON (1916) has stated that "it is certain that fertilization is not mutual; one acts as the male and the other as a female." Our experience does not support this contention. Mutual fertilization is quite usual in our crosses.

The young are usually born one at a time. When two are produced at once, the second is almost always much smaller. It rarely survives. The time required for individuals to reach maturity varies with the species. The median for animals whose birth and maturity dates are known is 353 days (range: 219 to 373) for *P. suturalis* and 153 days (range: 104 to 289) for *P. taeniata*.

The onset of maturity is marked internally by enlargement of the reproductive organs and externally by the formation of a reflected lip. Fertile matings may take place during lip formation, but the appearance of the first offspring occurs much later. Median values for elapsed time between lip formation and first offspring for typical groups of *P. suturalis* and *P. taeniata* are 192 days (range: 121 to 373) and 145 days (range: 110 to 232) respectively. From the time that
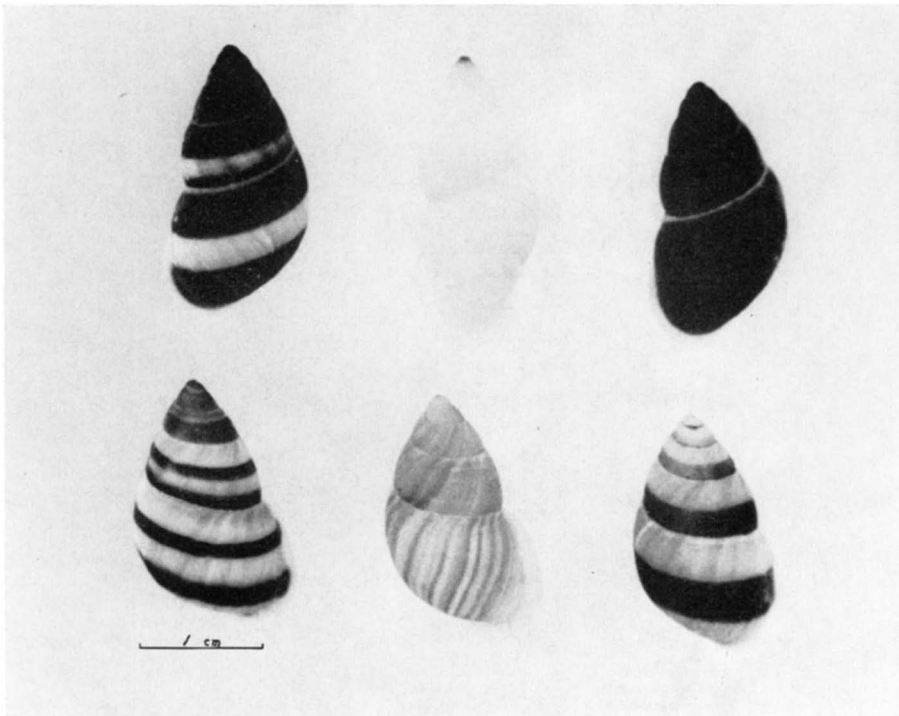

FIGURE 1.—Phenotypes of *Partula suturalis* Pfeiffer. Top row, left to right, *bisecta, apex,* and *atra.* Bottom row, left to right, *frenata, strigata,* and *cestata.*

the production of young commences, offspring are born at fairly regular intervals as long as the maternal animal retains viable sperm. The interval between births is approximately 22 days for *P. suturalis* and 19 days for *P. taeniata*. During the first few weeks of life the tiny snails are very delicate, at least under laboratory conditions. Once the initial stages of growth are past, however, the mortality becomes very low.

Since it is of interest in this study to know from which individual each offspring is derived, the parents are kept in separate boxes. Virgin and/or immature individuals are placed together and remain in the same box until both of them have been mature for three months. They are then separated. If a fertile mating has taken place, one or both parents begin to produce young. Six to 18 months later, the production of young begins to decline. It is then necessary to remate the pair for continued reproduction.

The rather long interval between birth and maturity, the protracted period of reproduction, the high mortality of young snails, and the labor of caring for animals all combine to limit the numbers of young that can be produced for study.

Scoring: In scoring the polymorphic forms, we have followed CRAMPTON's example except where compelling reasons have forced us to reform the classification. (a) *Partula suturalis: Partula suturalis* has presented few difficulties in scoring. Our matings include six forms recognized by CRAMPTON. Three of them are banded (*frenata*, *bisecta*, and *cestata*), and three are more or less uniformly colored (*atra*, *apex*, and *strigata*). The patterns of these forms are shown in Figure 1.

(b) *Partula taeniata:* Among the banded varieties of *Partula taeniata*, the categories used by CRAMPTON have been found to be satisfactory. These are *frenata*, *zonata*, and *lyra*, whose patterns are shown in Figure 2. Difficulties have arisen, however, in the scoring of shell color. CRAMPTON recognized only four categories in one progression from white (*pallida*) to brownish purple (*phaea-purpurea*). He realized that it was possible to construct a graded series over the whole range, but that not all shells could be fitted into the linear arrangement so formed.

In our work with *P. taeniata* we have resorted to a two-dimensional classification of color. The hue is designated by a letter, and the saturation and intensity are indicated by a numerical suffix.
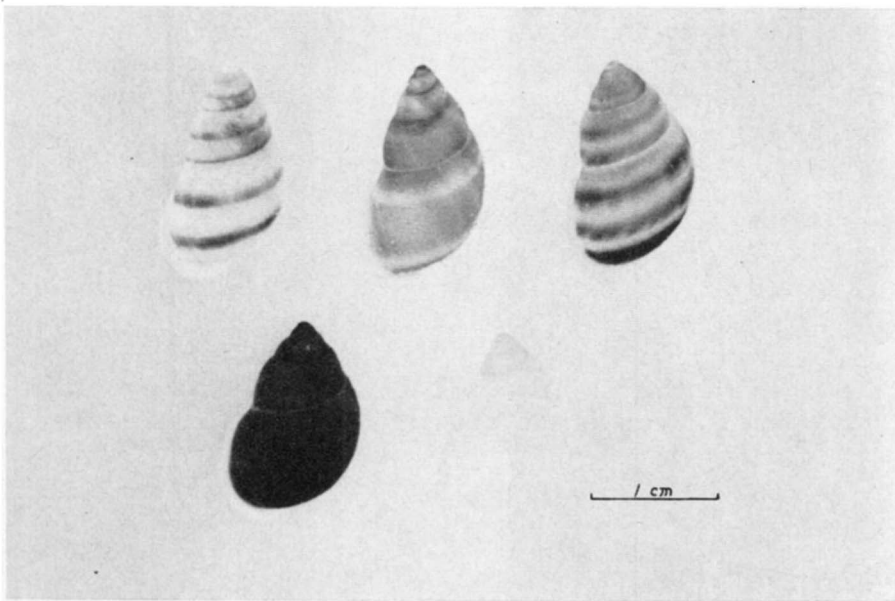

FIGURE 2.—Phenotypes of *Partula taeniata* Mörch. Top row, left to right, *frenata*, *zonata*, and *lyra*. Bottom row, left to right, N4 and W. These are the extreme types of the N series.

We recognize the following categories and have defined their limits by the use of standard shells.

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 (no matings involving the pink series are reported here).

The N series corresponds most closely with CRAMPTON's categories. N1 is, approximately, his *fusca*; N2, *fulva*; and N3 and N4, *phaea-purpurea*. When CRAMPTON took notice of other colors he recorded them as variants (e.g., "pinkish variant" of *fusca*).

It can be seen that the yellow and pink shells do not reach the extreme intensity of the brownish-purples.

There are other problems involved in the color scoring of *P. taeniata*. Some of them are discussed below in connection with specific matings. At this point, however, we should mention the difficulty produced by "weathering." Shells show a tendency to become lighter with age, and this is particularly true of living animals. For example, yellow parents almost invariably become white before their offspring have reached a scorable size. This fading is arrested if the animal is killed as soon as it reaches maturity.

<div align="center">RESULTS</div>

Tables 1 and 2 record the results of 66 matings with two species of Partula from Moorea. They give information on the inheritance of color, banding (occurrence and type) and direction of shell coiling.

1. *P. taeniata: Color.* The *taeniata* matings involve the N series, Y1 and W. In many instances they demonstrate segregation and dominance.

A large number of matings (1, 2, 3, 5, 56, 57, 58, 63, 64, and 113) show, by means of both backcrosses and F$_2$'s, that N4 and Y1 segregate. Matings 4, 56, and 58 demonstrate the complete dominance of N4. Number 59, a mating of two recessive homozygotes, does not segregate (the appearance of a single N1 offspring is discussed below). Mating 4 also suggests that N4 is dominant to N1, although the evidence is less satisfactory since the light animals segregating from mating 113 (the F$_1$ cross) are all Y1.

Segregation of N2 and Y1 can be observed in matings 10, 14, 12, and 73, although in the last two cases the relationship is complicated by the presence of the N4 spire. Mating 81 suggests that N2 is dominant to W. N1 and Y1 segregate in the progeny of matings 11, 65, 66, and 67. Mating 6 suggests that N1 may be dominant to Y1.

Not all of the matings involving color of the shell show clear-cut segregations, nor are all the results compatible with a scheme of dominance relationships in which the darker colors are always dominant to the lighter ones. For example, matings 10 and 74 are difficult to interpret in these terms. In mating 10 the parental types segregate as in a normal backcross; but in mating 74 (the F$_1$ cross), which might be expected to produce an ordinary F$_2$, the offspring display a wide variety of phenotypes from N4 to Y1. The N4 progeny are much darker than any of the parents or grandparents. Hence mating 74 apparently shows recombination in a polygenic system. Mating 15 shows a similar effect.

The mode of inheritance of a dark tip to the spire of the shell introduces a further complication. Two matings (12 and 73) show segregation for an N4

TABLE 1

Partula taeniata: *a list of matings and their progeny*

Names of localities are taken from CRAMPTON (1932). "Prog. 2" indicates that the parents of that mating are progeny of mating 2. Phenotypes are explained under "Scoring" and in Figure 2. The asterisk (*) indicates those offspring which may have been produced by either of the two parents.

Mating No.	Provenance	Parents	Progeny	Number obtained	Remarks
1	Faatoai	N4	N4	0	
			Y1	1	
	Pafatu	Y1	N4	1	
			Y1	3	
			N4	1*	
			Y1	1*	
2	Faatoai	N4	N4	12	
			Y1	12	
	Faatoai	Y1	N4	17	
			Y1	17	
			N4	1*	
			Y1	1*	
3	Faatoai	N4	N4	3	
			Y1	2	
	Faatoai	Y1	N4	17	
			Y1	11	
4	Faatoai	N4	N4	24	
			Y1	0	
	Faatoai	N1	N4	26	
			Y1	1	
			N4	1*	
5	Faatoai	N4	N4	1	
			Y1	7	
	Faatoai	Y1	N4	5	
			Y1	5	
			Y1	1*	
6	Faatoai	Zonata(N4)	Zonata(N4)	23	
			N1	15	
	Faatoai	Y1	Zonata(N4)	16	
			N1	14	
7	Fareaito	Zonata(N2)	Zonata(N2)	10	
	Faatoai	W	Zonata(N2)	18	
			Zonata(N2)	1*	
8	Faatoai	Lyra(N2)	Lyra(N2)	20	
			N2/N1	16	
	Faatoai	N2	Lyra(N2)	5	
			N2/N1	5	
9	Faatoai	Lyra(N4)	Lyra(N2)	6	
			N3/N2	9	
			Lyra(N4)	1	
			W	1	
	Faatoai	Y1	Lyra(N2)	5	
			N3/N2	10	
			Lyra(N2)	1*	

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TABLE 1—Continued

Mating No.	Provenance	Parents	Progeny	Number obtained	Remarks
10	Roroie	N2	N2	10	
			Y1	9	
	Faatoai	Y1	N2	6	
			Y1	6	
			N2	1*	
11	Faatoai	N1	N1	1	
			Y1	3	
			Y1 (N2 spire)	1	
	Fareaito	Y1	N1	1	
			Y1	1	
			Y1 (N2 spire)	1	
			Zonata (N3)	1	
			N1	1*	
12	Faatoai	N1	N2	0	
			N2 (N4 spire)	2	
			Y1	0	
			Y1 (N4 spire)	1	
	Moorea	Y1 (N4 spire)	N2	9	
			N2 (N4 spire)	3	
			Y1	8	
			Y1 (N4 spire)	4	
13	Faatoai	N2	Y1	3	
	Faatoai	Y1	. .	0	
14	Faatoai	N2	N2	6	
			Y1	8	
	Faatoai	Y1	. .	0	
			N2	2*	
15	Faatoai	N3	N4/N2	26	
	Faatoai	W	N4/N2	12	
16	Faatoai	Frenata (N2)	Frenata (N2)	1	
			N2	0	
	Faatoai	N1	Frenata (N2)	5	
			N2	5	
17	Faatoai	Frenata (N2)	Frenata (N2)	1	
			N1	2	
	Faatoai	N1	Frenata (N2)	8	
			N1	5	
18	Faatoai	Lyra (N4)	Lyra (N4/N2)	11	Background color of offspring is N1
			N4	3	
			Y1	0	
	Faatoai	N1	Lyra (N4/N2)	9	Background color of offspring is N1
			N4	11	
			Y1	2	

56	Prog. 2	N4	N4	9
			Y1	7
	Prog. 2	N4	N4	18
			Y1	5
57	Prog. 2	N4	N4	8
			Y1	8
	Prog. 2	Y1	N4	16
			Y1	9
			Y1	1*
58	Prog. 5	N4	N4	8
			Y1	2
	Prog. 5	N4	N4	11
			Y1	4
			Y1	1*
59	Prog. 5	Y1	Y1	3
	Prog. 5	Y1	Y1	13
			N1	1
60	Prog. 6	Zonata(N4)	Zonata(N4)	8
			Y1	7
	Prog. 6	Zonata(N4)	Zonata(N4)	12
			Y1	4
61	Prog. 7	Zonata(N2)	Zonata(N2)	8
			W(N2 spire)	2
	Prog. 7	Zonata(N2)	Zonata(N2)	10
			W(N2 spire)	4
			Zonata(N2)	2*
62	Urufara	N2	N2/N1	16
	Prog. 5	Y1	N2/N1	2
			Y1	6
63	Prog. 5	N4	N4	3
			Y1	4
	Prog. 5	Y1	N4	3
			Y1	4
64	Prog. 2	N4	N4	6
			Y1	3
	Prog. 2	Y1	N4	5
			Y1	5
65	Prog. 7	Zonata(N2)	Zonata(N2)	6
			N1	4
			Y1	1
	Prog. 6	N1	Zonata(N2)	2
			N1	0
			Y1	2
			Y1	1*
66	Prog. 6	Zonata(N4)	Zonata(N4)	6
			N1	2
			Y1	3
	Prog. 6	N1	Zonata(N4)	3
			N1	1
			Y1	7

TABLE 1—Continued

Mating No.	Provenance	Parents	Progeny	Number obtained	Remarks
67	Prog. 6	Zonata (N4)	Zonata (N4)	11	
			N1	1	
			Y1	1	
	Prog. 6	N1	Zonata (N4)	6	
			N1	2	
			Y1	6	
68	Prog. 6	Zonata (N4)	Zonata (N4)	4	Extremely dark
			Lyra (N4)	3	
			Lyra (N2)	0	
			N4	3	
	Prog. 9	Lyra (N4)	Zonata (N4)	4	Extremely dark
			Lyra (N4)	3	
			Lyra (N2)	2	
			N4	1	
69	Prog. 8	Lyra (N2)	Lyra (N2)	4	
			N3/N2	5	
	Prog. 8	Lyra (N2)	Lyra (N2)	11	
			N3/N2	3	
70	Prog. 8	Lyra (N2)	Lyra (N4/N3)	7	
			N4/N3	8	
	Prog. 8	Lyra (N2)	Lyra (N4/N3)	10	
			N4/N3	9	
71	Prog. 16	Frenata (N2)	Frenata (N2)	3	
			N1	5	
	Prog. 17	Frenata (N2)	Frenata (N2)	11	
			N1	3	
72	Prog. 6	Zonata (N4)	Lyra (N4)	1	
			Zonata (N4)	3	
			Frenata (N2)	1	
			N1	1	
	Prog. 16	Frenata (N2)	Lyra (N4)	3	
			Zonata (N4)	0	
			Frenata (N2)	3	
			N1	5	
73	Prog. 12	N2 (N4 spire)	N2 (N4 spire)	1	
			N2	1	
			Y1 (N4 spire)	2	
			Y1	0	
	Prog. 12	Y1 (N4 spire)	N2 (N4 spire)	2	
			N2	4	
			Y1 (N4 spire)	1	
			Y1	0	
74	Prog. 10	N2	N4	2	
			N3	6	
			N2	8	

			Y1	1
	Prog. 10	N2	N4	0
			N3	2
			N2	8
			Y1	1
75	Prog. 13	Y1	Y1	6
	Prog. 13	Y1	Y1	14
77	Prog. 11	Y1 (N2 spire)	Y1 (N2 spire)	14
			Y1	16
	Prog. 11	Y1	Y1 (N2 spire)	11
			Y1	3
78	Prog. 18	Lyra (N3)	Lyra (N4/N2)	17
			N1	6
	Prog. 18	Lyra (N3)	Lyra (N4/N2)	7
			N1	4
81	Prog. 15	N2	W	1
		Self		
113	Prog. 4	N4	N4	4
			Y1	2
	Prog. 4	Y1	N4	3
			Y1	2

TABLE 2

Partula suturalis: *a list of matings and their progeny*

Names of localities are taken from CRAMPTON (1932). "Prog. 20" indicates that the parents of that mating are progeny of mating 20. Phenotypes are explained under "Scoring" and in Figure 1. Additional sinistral (S) and dextral (D) offspring which cannot be scored for pattern are added under remarks. The asterisk (*) indicates those offspring which may have been produced by either of the two parents. The dagger (†) marks offspring in which the type of banding cannot yet be scored with confidence.

Mating No.	Provenance	Parents	Progeny	Number obtained	Remarks
20	Opunohu	Frenata S	Frenata S	12	& 8S
			Bisecta S	5	
	Opunohu	Bisecta D	Frenata D	16	& 15D
			Bisecta D	5	
					& 1S* & 1D*
21	Moorea	Frenata S	Frenata S	16	& 8S
	Moorea	Bisecta S	Frenata S	4	& 1S
22	Moorea	Frenata D	Frenata S	3	& 21S
			Atra S	2	
	Moorea	Bisecta D	Frenata S	12	& 10S
			Atra S	3	
					& 1S*
23	Roroie	Frenata D	Frenata D	2	& 29D
			Cestata D	1	
	Faatoai	Cestata S	Frenata S	1	& 9S
			Cestata S	0	
			Frenata D	1*	& 1D*

TABLE 2—Continued

Mating No.	Provenance	Parents	Progeny	Number obtained	Remarks
24	Faamaariri	Frenata S	Frenata S	7	& 6S
	Faamaariri	Cestata D	Frenata D	3	& 3D
25	Faatoai	Frenata S	Frenata S	6	& 5S
	Maramu	Bisecta D	Frenata D	15	& 12D
26	Faamaariri	Bisecta D	Bisecta D	4	& 16D
			Atra D	4	
	Faamaariri	Atra S	Bisecta S	4	& 15S
			Atra S	1	
27	Faamaariri	Apex S	Apex S	6	
			Frenata S	3	
			Atra S	3	
	Faamaariri	Bisecta D	Apex D	6	& 8D
			Frenata D	2	
			Atra D	0	
28	Fareaito	Atra D	Atra D	30	& 15D
			Atra S	1	
	Faatoai	Cestata S	Atra S	6	
29	Opunohu	Strigata D			
	Opunohu	Atra D	Strigata D	5	& 20D
			Atra D	8	
			Strigata D	1*	
83	Prog. 20	Frenata S	Frenata S	6	& 16S
			Bisecta S	3	
	Prog 20	Frenata S	Frenata D	7	& 11D
			Frenata S	1	
			Bisecta D	7	
84	Prog. 20	Frenata D	Frenata S	11	& 11S
			Bisecta S	1	
	Prog. 20	Frenata D	Frenata S	3	& 3S
			Bisecta S	1	
85	Prog. 25	Frenata S	Frenata S	6	& 9S
			Bisecta S	0	
	Prog. 25	Frenata S	Frenata S	0	& 8S
			Bisecta S	1	
86	Prog. 20	Frenata D	Frenata S	3	& 14S
			Bisecta S	3	
	Prog. 20	Bisecta S	Frenata D	2	
			Bisecta D	4	
87	Prog. 24	Frenata S	Frenata S	3	& 9S
			Cestata S	2	
			Strigata S	0	
	Prog. 24	Frenata S	Frenata S	4	& 14S
			Cestata S	1	
			Strigata S	1	

88	Prog. 26	Bisecta D	Bisecta S	3	& 11S
			Atra S	4	
	Prog. 26	Atra S	Bisecta S	4	& 12S
			Atra S	2	
89	Prog. 27	Apex S	Apex S	9	& 2S
			Apex D	1	
			Bisecta S	6	
	Prog. 27	Apex S	Apex S	8	& 5S
			Bisecta S	6	
91	Prog. 29	Atra D	Atra D	4	& 13D
	Prog. 28	Atra D			
108	Prog. 27	Frenata S	Frenata S	1	& 2S
			Apex S	3	
	Prog. 27	Frenata S	Frenata S	4	& 11S
			Apex S	0	
114	Prog. 28	Atra S	Atra S	10	
			†Banded S	3	
	Prog. 28	Atra S	Atra S	4	
			†Banded S	3	
			Atra S	1*	
115	Prog. 28	Atra S	Atra S	1	
			†Banded S	2	
	Prog. 28	Atra S	Atra S	6	
			†Banded S	0	
117	Prog. 28	Atra D	Atra S	5	
	Prog. 28	Atra D			
			Atra S	1*	
118	Prog. 28	Atra D	Atra S	1	
			†Banded S	1	
	Prog. 28	Atra D	Atra S	6	
			†Banded S	2	
			Atra S	1*	
			†Banded S	1*	
119	Prog. 25	Frenata D	S	1	
	Prog. 25	Frenata D			

spire, and two (11 and 77) show segregation for an N2 spire. In mating 73 the N4 spire behaves as a dominant. The N2 spire of mating 11 seems to be a recessive, since neither of the parents showed the character. In all the cases the dark spire segregates as if it were unlinked to general shell color, but it may not be entirely independent of the color of the rest of the shell. In mating 12 neither parent gives any hint of over-all purple shell color, although the spire of the Y1 is an intense dark purple. The N2 progeny of this mating and of number 73 all show a pale violet tinge, whether or not they bear the N4 spire.

Banding: A large number of matings show segregation of the banded and un-banded conditions (6, 8, 9, 16, 17, 18, etc.). These segregations involve banding patterns of three types. In each case the banded condition is dominant. This can be seen for *zonata* in matings 7, 60, and 61 (the anomalous appearance of *zonata* in mating 11 is discussed below), for *lyra* in matings 69, 70, and 78; for *frenata* in mating 71; and for combinations of these patterns in 68 and 72. These last two matings provide some information on the relationships of the three patterns. They suggest that the *lyra* pattern may arise in two different ways. In mating 68, *lyra* and *zonata* segregate as if they were allelic, whereas in mating 72, *lyra* appears to be produced by the presence together of *zonata* and *frenata* in the same individual. Mating 72 may also be explained by assuming that *zonata*, *frenata*, and *lyra* are alleles at one locus, while another locus determines the presence or absence of all types of banding.

2. *P. suturalis: Pattern.* All six of the shell patterns which have been tested in *P. suturalis* show clear-cut segregations, but the interactions among them are not simple. We have the most information about the *frenata* pattern. It shows segregation with *bisecta* (20, 83, 84, 85, and 86), with *atra* (22 and 27), with *cestata* (23 and 87), with *apex* (27 and 108), and less certainly with *strigata* (87). *Frenata* is dominant to *bisecta* (21, 25, 83, 84, and 85), to *cestata* (24 and 87), to *apex* (108, but see below), and probably to *atra* (22).

We suggest that the results of these matings are best explained by the hypothesis that *frenata* is determined by the epistatic effects of dominant genes at two loci. Four of the matings lend support to this hypothesis. Mating 20, an apparent backcross, differs significantly (P < 0.01) from a 1:1 ratio but is compatible with a 3:1 ratio expected from a mating of type *AABb* × *aaBb*. Except for the complication of the appearance of *atra* in place of *bisecta*, mating 22 is another apparent backcross which shows a 3:1 ratio. Mating 86, a backcross derived from mating 20, conforms to the 3:5 ratio expected from a mating of type *AaBb* × *Aabb*. Among the apparent F_2's from mating 20, mating 83 shows a ratio of 14:10 which is only just compatible with a 3:1 ratio ($\chi^2 = 3.56$; P ~ 0.05). It is however, a good fit (0.9 > P > 0.8) with the 9:7 ratio resulting from the cross of two double heterozygotes.

Atra shows segregation with *bisecta* (26 and 88), with *strigata* (29), and with a banded pattern which is almost certainly *cestata* (114, 115, 118), as well as with *frenata*. *Atra* is dominant to *cestata* (28) and breeds true in matings 91 and 117. The simplest explanation of the results of mating 22 is that *bisecta* and *atra* are determined by alleles at one of the two loci postulated for *frenata*, but the distinction could as easily depend on another locus.

The most extraordinary interactions are those which are found in the series of matings 27, 89, and 108. From the initial mating of *apex* × *bisecta* which produced *apex*, *frenata*, and *atra*; a second generation mating of *apex* × *apex* produced *apex* and *bisecta* while *frenata* × *frenata* produced *frenata* and *apex*. If the two-locus hypothesis for *frenata* be accepted, a further two loci for *apex* are necessary to explain these results. Thus mating 89 becomes a 9:7 segregation for *apex* and non-*apex* (*bisecta*) and mating 108, a 9:7 segregation for *frenata*

and non-*frenata*. The non-*frenata* offspring of 108 should be 3 *apex* to 1 *bisecta*. The latter type has not appeared among the offspring, as indeed it did not in mating 27 where the expectations on the four-locus hypothesis are 9 *apex* : 4 *frenata* : 2 *atra* : 1 *bisecta*. Clearly more data are needed before a final decision can be reached.

Coiling: Partula suturalis is unusual among gastropods in that dextrally and sinistrally coiled individuals occur in a single species. Some populations are entirely dextral or sinistral, but others show mixtures of the two types in various proportions.

CRAMPTON (1916) found by means of his dissections of uterine contents that individuals may bear offspring of similar or of opposite coil and that usually all of the offspring within one individual are of the same type, whether the same as or different from the parent. In very rare cases he found offspring of both types within one individual. CRAMPTON was familiar with the work of BOYCOTT and DIVER (1923) and BOYCOTT, DIVER, GARSTANG, and TURNER (1930) on *Limnaea peregra* and suggested that in Partula, the maternal genotype might also determine the direction of coil in the offspring. Instances of mixed broods he interpreted as genuine mutations.

The breeding data confirm, by means of much larger series than can be found *in utero*, that almost without exception all the offspring from any individual are of one type. Among 718 offspring where the parent is known, only three individuals show the opposite coil from the rest of the brood. In mating 28, one parent gave 45 dextrals and 1 sinistral; in 83, one gave 25 dextrals and 1 sinistral; and in 89, one gave 17 sinistrals and 1 dextral. These three matings are not related genetically or in geographical origin. The frequency with which these anomalous individuals appear argues for an ontogenetic origin for them. They are too rare to suggest genetic segregation, but are probably too common to be mutations.

Dextral and sinistral animals can give rise to broods of either type. The most instructive matings are those in which the parents are derived from populations which are entirely dextral or sinistral. Matings 25 and 28, with one dextral and one sinistral parent, are of this type. All four parents have produced offspring which are of the same coil as themselves. Six matings from the progeny (from 25: 85 and 119; from 28: 114, 115, 117, and 118) involving both sinistral and dextral individuals (S: 85, 114, and 115; D: 117, 118, and 119) have produced only sinistral offspring. (One parent in 117 and one in 119 have no young). These matings demonstrate the regularity of the inheritance of coiling and show that sinistrality is dominant. In the latter respect Partula differs from Limnaea, where dextrality is dominant (BOYCOTT, DIVER, GARSTANG, and TURNER 1930). It resembles Limnaea, however, in the determination of the individual phenotype by the genotype of the maternal parent.

DISCUSSION

Self-fertilization: Since the snails of the genus Partula are hermaphroditic, it is important to determine whether or not self-fertilization takes place, and if so,

TABLE 3

Young produced by self-fertilization: the numbers of isolated individuals and their progeny

Species	Number	Number producing young	Number of young	Number producing infertile eggs	Number of infertile eggs
P. taeniata Mörch	30	8	11	21	143
P. suturalis Pfeiffer	10	1	6	2	3
P. mooreana Hartman	4	0	0	0	0
P. olympia Crampton	5	1	1	3	19
P. aurantia Crampton	5	1	2	1	1
P. mirabilis Crampton	1	1	1	0	0
P. tohiveana Crampton	5	0	0	2	4

to what extent. To this end, a series of animals has been maintained in isolation. All were separated from all other snails well before maturity, many within the first week after birth. Of 65 animals initially isolated in 1963 and 1964, all are still living. Sixty have been mature for at least a year; 28, mostly *taeniata*, have been mature for more than two years.

Table 3 shows the composition of the group according to species and fertility. It is apparent that at least five of the species are capable of self-fertilization. On the other hand it is also apparent that self-fertilization is a rare event. A comparison can be made in the case of *P. taeniata* where eight of the 30 isolated individuals produced a total of 11 young. The mean length of time since these 30 animals reached maturity is 25 months. In a comparable period, a group of 30 individuals mated in pairs produced 549 young. Thus the progeny production by self-fertilization is only 2% of the normal output under these conditions.

The number of infertile eggs (shown in Table 3) is another index of the reduction of reproductive capacity. Partula species are ovoviviparous, the shell undergoing resorption in the uterus. The production of shelled eggs, which never develop, is an indication of the failure of fertilization and in our breeding program it is used as a signal for remating. Hence the large number of infertile eggs produced by isolated snails indicates an interference with reproduction.

The question of whether individuals or species differ in their capacity for self-fertilization cannot be satisfactorily answered. In *P. taeniata* the numbers of individuals producing 0, 1, 2, and 3 young agree closely with the Poisson expectations, but the numbers are very small. If the results for all species are lumped, a procedure of doubtful validity, the resulting distribution is significantly different from a Poisson series ($P < 0.05$). This is largely because of the single case in *P. suturalis* in which one animal produced six young. The other nine *suturalis* have produced no young at all. Hence it appears that exceptional individuals may well be capable of frequent self-fertilization, while in general the process is quite rare.

Another problem of interest is whether mating would increase or decrease the frequency of self-fertilization. With known genetic markers, this problem can be solved when more material becomes available.

There is evidence for some self-fertilization among the matings, although it is

difficult to exclude all other possibilities. Perhaps the most likely case is in mating 4 (*P. taeniata*) in which a single Y1 young appeared with 51 N4 young. Mating 18 (*P. taeniata*) with two Y1s in a brood of 36, is similar. Another probable case is in mating 62, (*P. taeniata*). When first mated, the Y1 parent produced six Y1 young. After a second mating the same animal produced two N2 offspring, similar to the 16 young from the other parent. It is only the large number of Y1 young that calls into question the hypothesis of self-fertilization.

Heterogeneity and deviation from expectation: Where a number of matings of the same type are available for study, we have tested the homogeneity of the data. A convenient method of combining the results of F_2 and back-cross matings has been described by MATHER (1951).

a. *P. taeniata.* There are eight backcross and two F_2 matings in which the consistency of the results of the N4/Y1 segregation can be tested. Although there is considerable variation in the individual results, as might be expected from the small numbers, the overall fit is almost perfect ($P \sim 0.98$) and the heterogeneity is not significant ($0.5 > P > 0.3$). In four backcrosses N2 and Y1 show little deviation from expectation ($0.7 > P > 0.5$) and no significant heterogeneity ($0.2 > P > 0.1$). The N1/Y1 segregations, which are all complicated either by spire color inheritance (11) or by joint segregation of banding (65, 66, and 67) are homogeneous ($0.7 > P > 0.5$) but show a significant excess of Y1 ($\chi^2_{(1)} = 4.90$; $P < 0.05$).

The segregation for banded and unbanded can be tested for consistency in eight F_2 and nine backcross matings. In this case, however, a joint test cannot be employed as there is evidence that the results of the two groups of matings are not compatible with each other. The backcrosses are in good agreement with the expected 1:1 ratio ($0.5 > P > 0.3$) and are homogeneous ($0.7 > P > 0.5$). On the other hand there is an overall deficiency of banded offspring among the F_2 matings. The deficiency is significant when tested either by χ^2 or by χ, which takes into account the direction of the deviations (P in each case < 0.01). Despite the fact that this result is heavily influenced by mating 70, a putative F_2 which produced 17 banded and 17 unbanded offspring, the F_2 matings are homogeneous ($0.3 > P > 0.2$).

The agreement of these backcross and F_2 data can be tested by using the F distribution to compare $(\Sigma x)^2/n$ for each group of matings. The difference between the groups is highly significant ($P << 0.01$). The overall ratio of banded to unbanded offspring among the F_2 matings (137:70) approximates a 2:1 rather than a 3:1 ratio. This result suggests that the homozygous banded individuals are subvital or lethal. This hypothesis is being investigated with additional matings.

b. *P. suturalis.* The segregations which are of most interest in *P. suturalis* are those between *frenata* and *bisecta* or *atra* (20, 22, 86; 83, 84, 85). These show a significant departure from expectation on the hypothesis of a single segregating locus ($\chi^2_{(1)} = 3.87$; $P < 0.05$). There is also significant heterogeneity ($\chi^2_{(5)} = 15.31$; $P < 0.01$). In order to explain these results an alternative hypothesis of two segregating loci has been proposed (see above).

Relatively little information can be gained from combining the results of mat-

ings of other types. Suffice it to say that with the *bisecta/atra* and *atra/*banded segregations no significant deviation or heterogeneity is detectable.

Anomalies: There are a number of irregularities among the data which require some comment. These fall into three groups. First, there are a few instances which appear to be cases of self-fertilization. The three probable occurrences in matings 4, 18, and 62 are discussed above. Second, there are two cases which appear to be technical errors. These are the N1 offspring in mating 59 and the *zonata* in mating 11. The N1 is a long, thin, brown individual among a brood of short, broad, yellows. The *zonata*, a type which behaves elsewhere as a simple dominant, appears here in an entirely unbanded brood. While some unusual genetic event cannot be ruled out as an explanation, the best course would seem to be to treat these as errors, pending further investigation.

Finally, there are a few matings in which the general pattern of segregation, with the darker types dominant to the lighter types, seems to break down. Matings 10 and 74, where a generation of segregation is followed by continuous variation, have been discussed above. Mating 15 also produces progeny continuously varying from N4 to N2. Among the matings with bandeds, the F_2 progeny of mating 8 (matings 69 and 70) show a gradual darkening. The genetic basis of this variation must be investigated further.

Allelism and linkage: A problem on which the present matings shed very little light is that of allelism. In *P. suturalis* for example, although we have some evidence that *frenata* and *apex* appear to be controlled by two loci each, we do not know whether *bisecta, atra, cestata,* and *strigata* are determined at one or more of these loci.

In *P. taeniata* it is not clear whether the color and banding patterns are controlled at the same locus. Matings 65, 66, and 67 would seem to indicate either that the banding patterns are allelic with color, or that they are closely linked to it. Matings 9 and 68 also suggest such an interpretation. There are, however, some difficulties. In mating 9 it appears that banding and N4 are linked in repulsion, but if such is the case then that parent in 68 which came from mating 9 must be a crossover. As such, the unbanded offspring of 68 should be Y1 unless the parent derived from mating 6 was also a crossover. However, in that event, light *zonata* offspring would be expected. More study of this condition is obviously required.

SUMMARY

Polymorphic land snails of the genus Partula are cross-fertilizing hermaphrodites, but self-fertilization occurs at a low frequency in at least five species from

Moorea, French Polynesia.—In *P. taeniata*, segregation has been shown for a series of color forms ranging from deep brownish-purple through white to yellow. In general, darker forms are dominant to the lighter forms. In some crosses, however, clear segregations do not occur, and the basis of inheritance appears to be recombination in a polygenic system. Three different banding types (*frenata*, *zonata*, and *lyra*) segregate with the unbanded condition. All three are dominant to unbanded, and they show segregation among themselves. The *lyra* pattern may perhaps also be formed by the joint presence of *zonata* and *frenata* in the same individual. There is some evidence that homozygous banded individuals are subvital or lethal.—In *P. suturalis*, the *frenata* pattern seems to be determined by the epistatic effects of dominant genes at two loci. *Frenata* segregates with *bisecta*, *atra*, *cestata*, *apex* and *strigata*. *Atra* is dominant to *cestata*. One hypothesis compatible with the data is that *bisecta*, *atra*, and *cestata* are multiple alleles at one of the two *frenata* loci, and that *apex* is determined by a further two loci. Direction of coiling of the shell in *P. suturalis* is determined by the genotype of the maternal parent. Sinistrality is dominant to dextrality.

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