Allozymic similarities among species of *Partula* on Moorea

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Variation in allozymes at 23 loci was examined in 62 populations, representing the seven species of land snails of the genus *Partula* inhabiting the island of Moorea in French Polynesia. All but four of the 23 loci are polymorphic in at least one species, and the average heterozygosity per individual is 0.13. In contrast to their high variability within species, the allozymes show relatively little divergence between species. Coefficients of genetic identity between populations from different species range from 0.73 to 0.99, with an average of 0.89. Coefficients of identity between conspecific populations average 0.94, and range from 0.77 to 1.00. Within each of the two "species complexes", the mean coefficient of identity between species that hybridise is the same as that between non-hybridising species, suggesting that allozymic variation and reproductive isolation are independent of each other. The rate of divergence on Moorea is apparently consistent with the rate that has been calculated for the Society Islands as a whole (a change in Nei's D of approximately 0.13 per million years). The high levels of similarity between species appear to be consequences of their recent origins. Some populations of *Partula taeniata* in southern Moorea differ from other populations of their own species to an extent greater than any interspecific differences elsewhere on the island, emphasising the lack of necessary correlation between allozymic change, morphological divergence, and reproductive isolation.

INTRODUCTION

Snails of the genus *Partula* are found only on islands in the Pacific Ocean, and they have undergone a striking radiation in the Society archipelago. Those on the island of Moorea have been studied the most intensively, both in the field and in the laboratory. They are particularly interesting because they show complex patterns in the degree of their reproductive isolation from each other (Murray and Clarke, 1968; 1980). On Moorea there are two "species complexes": the *taeniata* complex, consisting of *Partula taeniata* Mörch and *P. exigua* Crampton, and the *suturalis* complex, consisting of *P. suturalis* Pfeiffer, *P. aurantia* Crampton, *P. tohiviana* Crampton, and *P. mooreana* Hartman. There is no direct exchange of genes between the two complexes, but within them there are frequent cases of local hybridisation and introgression. Furthermore, the two complexes are linked through *Partula mirabilis* Crampton, which hybridises naturally with *P. taeniata* at some localities and is able to cross with *P. aurantia* and *P. tohiviana* in the laboratory. Despite the poten-

tial for gene flow between the Moorean species, they are generally distinct both morphologically (Murray and Clarke, 1980) and ecologically (Murray *et al.*, 1982).

A study of allozymic variation in laboratory stocks of *Partula taeniata*, *P. mirabilis*, *P. suturalis* and *P. tohiviana* (includes *P. olympia* Crampton) indicated a close genetic similarity between them (Johnson *et al.*, 1977). Comparisons of species from different islands in the archipelago have suggested that the Moorean taxa arose from an evolutionary radiation within the island. The comparisons have also allowed us to estimate the average rate of allozymic divergence between groups of species on different islands (Johnson *et al.*, 1986).

In the present study, we extend the electrophoretic analysis to all the Moorean *Partulae* and investigate the extent of differentiation within, as well as between, species. The data allow us to answer four questions that have been raised by earlier studies. First, does the extent of allozymic difference between species reflect their degree of reproductive isolation? Second, does hybridisation

prevent allozymic divergence between species? Third, do the patterns of differences between species resemble the patterns of geographic variation within species? Finally, is the amount of divergence between species consistent with the average rate of allozymic divergence estimated from comparison between islands, and with the known age of the island?

MATERIALS AND METHODS

Samples were collected from 29 sites on Moorea (fig. 1). They included all the species of *Partula* on the island and comprised a total of 62 populations: *P. taeniata* (22 populations), *P. exigua* (2), *P. mirabilis* (6), *P. suturalis* (23), *P. aurantia* (2), *P. tohiviana* (4), *P. mooreana* (3). Most of the samples consisted of approximately 20 adult snails, although the smallest sample was eight. Our samples represent the major portion of the geographic range of each species, and the differences

in the number of samples for different species reflect the relative sizes of their ranges. In order to avoid the local effects of introgression, immediate areas of hybridization were not included. Reproductive relationships among the taxa have been determined by extensive field and laboratory studies, providing a firm basis for the allozymic comparisons (Murray and Clarke, 1980). In accordance with these relationships, *P. suturalis* Pfeiffer is now regarded as including *P. dendroica* Crampton, and *P. tohiviana* Crampton as including *P. olympia* Crampton.

Samples were examined at 23 loci by conventional starch-gel electrophoresis. The procedures were those used in earlier studies (Johnson *et al.*, 1977; 1986). Because of the large number of populations and loci, the data are presented in summary form. The full details of each population are available upon request and are deposited in the library of the Royal Society of London. Based on the 23 loci, unbiased estimates of genetic identity, *I*, and their standard errors (Nei, 1978) were calculated

Figure 1 Map showing collecting sites on Moorea. Lines indicate ridges. Numbers are codes for localities.

for all pairs of the 62 populations. This matrix of genetic identities was summarized by UPGMA clustering (Sneath and Sokal, 1973).

RESULTS

All but four (*G6pd*, *Mdh-4*, *6Pgd*, *Sod*) of the 23 loci are polymorphic in at least one of the seven species. Average heterozygosities are high, ranging from 0.07 in *P. exigua* to 0.17 in *P. mooreana*, with an overall mean of 0.13 (table 1). With few exceptions, the genotypic frequencies are close to Hardy-Weinberg expectations, confirming the rarity of self-fertilisation in the field.

Despite the high degree of variability within populations, there is little divergence among species. They generally share the same alleles, usually with rather small differences in allelic frequencies (table 1, fig. 2). No locus distinguishes completely between any pair of species, although the high frequency of *Est-1*^{1,21} in *P. exigua* is in marked contrast to the low frequency of that allele in most species of the *P. suturalis* complex. Alleles that are common in any one species are found in all the others. Of the 53 alleles that occur at a frequency of 0.05 or more in at least one species, only three are unique to a species. These "unique" alleles are found in only a few populations: *Got-2*^{1,00} in *P. tohiveana* from site 5, *Mdh-3*^{4,50} in *P. tohiveana* from sites 4 and 5, and *Pgm-2*^{0,87} in *P. suturalis* from sites 7, 8 and 9.

Based on the 23 loci, the average genetic identity between species ranges from 0.80 for *P. exigua*

and *P. mooreana* to 0.94 for *P. mirabilis* and *P. aurantia* (table 2). The average *I* between species is 0.89, compared with an average of 0.94 between populations within species. *I* is greater than 0.90 for all pairs of species within a species complex. Although the averages differ, the ranges of values within and between species are very similar: 0.73 to 0.99 between species; 0.77 to 1.00 within species. The amount of genetic divergence is not related to the degree of reproductive isolation (table 3). The average identity is the same (0.90) between species that hybridise and between those in the same complex that do not. Only between species complexes is there a clear decrease in *I*.

Despite the fact that the *I* values are generally high, and despite the lack of association between *I* and the degree of reproductive isolation, there are nevertheless patterns in the allozyme variation, as shown by the phenogram of the 62 populations (fig. 3). The clearest pattern is the clustering by species complex, which is complete except for the populations of *P. taeniata* and *P. suturalis* from sites 7 and 8 and *P. taeniata* from site 15 (see below). The allozymes place *P. mirabilis*, which forms a reproductive link between the two complexes, well within the *P. suturalis* group.

The second pattern to be seen in the phenogram is the grouping of conspecific populations, although there are many exceptions. Only *P. exigua* and *P. tohiveana* form inclusive monospecific clusters, whereas *P. aurantia* and *P. mooreana* are scattered within the *P. suturalis* complex. Nevertheless, 19 of the 22 populations of *P. taeniata* form a tight group, and 19 of the 23 populations of *P. suturalis* are grouped, albeit with one *taeniata* and one *mooreana* population included in the group. This clustering of conspecific populations occurs despite the large overlap of values of *I* within and between species and despite an average standard error of 0.04 for individual estimates of *I*. It reflects the fact that the highest genetic identities tend to be those between populations of the same species that are geographically close to each other. Thus, if intraspecific comparisons within *P. taeniata* and *P. suturalis* are grouped by intervals of 1 km, and if the disparate populations from sites 7 and 8 are excluded, the average genetic identity decreases smoothly with increasing geographic distance (fig. 4). As a consequence, the allozymic clusters within these species largely reflect geographic groupings.

Although clear patterns are evident in the phenogram, there are several anomalies. The most striking are produced by the populations from sites 7 and 8, on the slopes of Mount Ahutau, the

Figure 2 The frequency distribution of loci with respect to genetic identity in comparisons among species of *Partula* from Moorea.

Table 1 Allelic frequencies and proportions of heterozygotes at nineteen variable loci in species of *Partula* from Moorea

Locus	Allele	<i>taeniata</i>	<i>exigua</i>	<i>mirabilis</i>	<i>suturalis</i>	<i>aurantia</i>	<i>tohivaeana</i>	<i>mooreana</i>
N, Individuals (Populations)		380 (21)	305 (12)	133 (6)	501 (23)	38 (2)	86 (4)	70 (3)
<i>Alph</i>	1.07	0.03	—	—	0.01	—	—	—
	1.02	0.04	—	0.17	0.14	0.08	—	0.26
	0.95	0.91	0.95	0.80	0.79	0.84	0.92	0.74
	0.87	0.01	0.05	0.01	0.03	0.08	0.01	—
	0.61	0.01	—	0.02	0.03	—	0.07	—
Heterozygosity		0.11	0.10	0.20	0.27	0.24	0.14	0.14
<i>Est-1</i>	1.26	0.02	—	—	0.01	—	—	—
	1.21	0.23	0.95	0.04	0.13	0.03	0.05	0.03
	1.15	0.75	0.05	0.90	0.81	0.93	0.95	0.86
	1.09	—	—	0.04	0.05	0.02	—	0.10
	1.05	—	—	0.02	—	0.02	—	0.01
Heterozygosity		0.28	0.10	0.14	0.24	0.14	0.10	0.26
<i>Est-2</i>	1.09	—	—	—	0.01	—	—	—
	1.05	0.02	—	0.01	0.03	—	—	0.04
	1.00	0.94	1.00	0.99	0.95	0.99	1.00	0.96
	0.95	0.04	—	—	0.01	0.01	—	—
		0.11	0	0.02	0.07	0.03	0.01	0.08
<i>Got-1</i>	1.70	0.02	—	0.01	—	0.01	—	—
	1.50	0.81	0.98	0.80	0.47	0.59	0.84	0.85
	1.00	0.16	0.02	0.19	0.51	0.40	0.16	0.15
	0.71	0.01	—	—	0.02	—	—	—
		0.13	0.05	0.27	0.44	0.58	0.23	0.21
<i>Got-2</i>	—1.00*	—	—	—	—	—	0.06	—
	—1.10	1.00	1.00	1.00	1.00	1.00	0.94	1.00
	Heterozygosity	0	0	0	0	0	0.02	0
<i>Idh-1</i>	1.16	0.09	0.02	0.31	0.32	0.25	0.58	0.35
	1.06	0.03	—	—	—	—	0.01	—
	1.00	0.79	0.96	0.61	0.62	0.72	0.40	0.39
	0.89	0.09	0.02	0.08	0.06	0.03	0.01	0.26
		0.23	0.10	0.48	0.38	0.24	0.44	0.61
<i>Idh-2</i>	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00
	0.50	—	—	—	0.01	—	—	—
	Heterozygosity	0	0	0	0.01	0.03	0	0
<i>Ldh</i>	1.10	0.13	0.10	0.40	0.15	0.80	0.09	0.48
	1.00	0.86	0.90	0.60	0.84	0.20	0.87	0.52
	0.90	0.01	—	—	0.01	—	0.04	—
		0.16	0.20	0.33	0.26	0.34	0.20	0.35
<i>Mdh-1</i>	1.26	0.64	0.84	—	—	—	—	0.01
	1.11	—	—	0.01	0.03	—	0.13	0.10
	1.00	0.36	0.16	0.80	0.93	0.99	0.85	0.88
	0.81	—	—	0.19	0.03	—	—	0.01
	0.70	—	—	—	0.01	0.01	0.02	—
		0.32	0.18	0.27	0.11	0.03	0.20	0.08
<i>Mdh-2</i>	1.50	0.03	0.14	—	0.04	0.01	—	0.11
	1.00	0.95	0.86	1.00	0.95	0.99	1.00	0.89
	0.70	0.02	—	—	0.01	—	—	—
		0.05	0.26	0	0.09	0.03	0	0.19
<i>Mdh-3</i>	4.50	—	—	—	—	—	0.14	—
	1.00	0.96	1.00	0.97	1.00	1.00	0.86	1.00
	—2.50*	0.04	—	0.03	—	—	—	—
		0.07	0	0.04	0	0	0.16	0.01
<i>Mpi</i>	1.07	0.01	—	—	0.04	—	0.03	—
	1.00	0.86	1.00	0.92	0.81	0.89	0.58	0.69
	0.95	—	—	0.03	—	—	0.01	—
	0.92	0.13	—	0.04	0.14	0.08	0.34	0.31
	0.88	—	—	0.01	0.01	0.03	0.04	—

Table 1—continued

Locus	Allele	<i>taeniata</i>	<i>exigua</i>	<i>mirabilis</i>	<i>suturalis</i>	<i>aurantia</i>	<i>tohiviana</i>	<i>mooreana</i>
Heterozygosity		0.23	0	0.12	0.27	0.20	0.38	0.44
<i>Np</i>	1.12	0.42	0.04	—	—	—	—	—
	1.00	0.20	—	0.02	0.12	0.18	0.21	0.29
	0.84	0.34	0.96	0.97	0.74	0.76	0.79	0.71
	0.73	0.03	—	0.01	0.13	0.06	—	—
	0.65	—	—	—	0.01	—	—	—
Heterozygosity		0.44	0.08	0.04	0.35	0.28	0.18	0.44
<i>Pep-2</i>	1.05	0.02	—	0.01	0.01	—	0.01	—
	1.00	0.97	1.00	0.84	0.95	0.96	0.98	1.00
	0.95	0.01	—	0.15	0.04	0.04	0.01	—
Heterozygosity		0.05	0	0.24	0.06	0.08	0.04	0
<i>Pep-4</i>	1.03	—	—	—	0.02	0.01	—	—
	1.00	0.90	1.00	1.00	0.95	0.99	1.00	1.00
	0.97	0.10	—	—	0.03	—	—	—
Heterozygosity		0.04	0	0.01	0.04	0.03	0.01	0
<i>Pep-6</i>	1.11	—	0.05	0.02	0.01	—	0.03	—
	1.00	0.74	0.95	0.25	0.48	0.44	0.80	0.27
	0.85	0.21	—	0.73	0.51	0.54	0.17	0.73
	0.71	0.05	—	—	—	0.02	—	—
Heterozygosity		0.36	0.10	0.43	0.40	0.44	0.20	0.27
<i>Pgi</i>	1.38	—	0.02	0.02	—	—	—	0.01
	1.00	0.86	0.93	0.92	0.86	0.89	1.00	0.66
	0.75	—	—	—	0.02	0.04	—	—
	0.50	0.14	0.05	0.06	0.12	0.07	—	0.33
Heterozygosity		0.21	0.05	0.12	0.20	0.16	0	0.30
<i>Pgm-1</i>	1.08	0.24	0.56	0.01	0.03	—	—	0.01
	1.05	—	—	—	—	0.09	—	0.10
	1.02	0.66	0.44	0.28	0.73	0.29	0.04	0.40
	0.98	—	—	0.09	—	—	—	—
	0.95	0.10	—	0.62	0.24	0.62	0.96	0.49
Heterozygosity		0.35	0.38	0.29	0.36	0.52	0.07	0.44
<i>Pgm-2</i>	1.12	—	—	—	0.01	—	—	—
	1.09	—	—	0.01	0.05	0.02	—	—
	1.04	0.97	1.00	0.96	0.82	0.98	1.00	0.90
	1.00	0.02	—	—	0.01	—	—	0.10
	0.95	0.01	—	0.03	0.02	—	—	—
	0.87	—	—	—	0.09	—	—	—
	0.04	0.04	0	0.08	0.14	0.03	0	0.10
Average Heterozygosity (23 loci)		0.139	0.070	0.134	0.160	0.148	0.103	0.170

* Cathodally migrating enzyme.

Table 2 Average coefficients of genetic identity, based on 23 loci, among populations of seven species of *Partula*. The diagonal set of figures represents comparisons between populations within species

	<i>taeniata</i>	<i>exigua</i>	<i>mirabilis</i>	<i>suturalis</i>	<i>aurantia</i>	<i>tohiviana</i>	<i>mooreana</i>
<i>P. taeniata</i>	0.919	0.901	0.876	0.895	0.852	0.836	0.810
<i>P. exigua</i>		0.980	0.851	0.851	0.815	0.835	0.796
<i>P. mirabilis</i>			0.963	0.934	0.936	0.935	0.925
<i>P. suturalis</i>				0.925	0.915	0.913	0.907
<i>P. aurantia</i>					0.920	0.904	0.925
<i>P. tohiviana</i>						0.968	0.897
<i>P. mooreana</i>							0.910

Table 3. Average coefficients of genetic identity among species of *Partula* representing different stages of divergence

Stage of divergence	$\bar{I} \pm \text{S.E.}$
Conspecific populations	0.941 $\pm$ 0.011
Some gene exchange between species	0.902 $\pm$ 0.007
No hybridization, within species group	0.902 $\pm$ 0.007
Different species groups	0.836 $\pm$ 0.011

southernmost peak of the island. These populations form separate clusters distinct from all other populations, regardless of species. For *P. taeniata* the value of I between the Ahutau populations and populations from other sites is only 0.83, well below the average value obtained from comparisons between species. Although it is not as extreme, the I of 0.90 between *P. suturalis* from Ahutau and from other sites is at least as low as the value for any pair of species within the *P. suturalis* complex.

The *P. taeniata* from Ahutau are particularly aberrant for the *Got-1*, *Idh-1*, and *Pep-4* loci. The frequency of *Got-1*^{1.00} is 0.74, compared with an average of 0.10 (range, 0 to 0.29) elsewhere. *Idh-1*^{1.16} has a frequency of 0.80, compared with 0.02 (range, 0 to 0.07) further north. *Pep-4*^{0.97} reaches a frequency of 0.90, compared with an average of 0.02 (range, 0 to 0.08) in other populations. To clarify the relationships of the Ahutau populations,

additional samples were taken in the southern part of the island, and the frequencies of alleles at these three loci were examined. The average of the frequencies of *Got-1*^{1.00}, *Idh-1*^{1.16}, and *Pep-4*^{0.97} was taken as an index of similarity to the samples from Ahutau. These additional samples show that the divergence of the Ahutau populations is clinal, rather than discontinuous (fig. 5). No linkage disequilibrium was found within the intermediate populations, strengthening the view that there is no present interruption in gene flow.

A similar study of *P. suturalis* also indicates genetic continuity. In this species, the Ahutau populations have peculiar allelic frequencies at several loci, but variation at only one locus approaches a qualitative difference. The *Pgm-2*^{0.87} allele is nearly fixed ($p = 0.94$) on Ahutau, declines in adjacent populations, and is absent outside of the southern part of the island (fig. 6).

DISCUSSION

The allozymic variation of the Moorean Partulae is unusual in three respects. First, the similarities between species are high, often as high as those found between conspecific populations. Second, they are apparently independent of the degree of reproductive isolation. Third, despite the great similarities between species, divergence within

Figure 3 The phenogram (UPGMA clustering) of genetic identities among 62 populations, representing seven species of *Partula*. Locality codes as in fig. 1.

Figure 4 The relation between the value of I , for conspecific populations, and the geographical distance between populations, grouping the comparisons by intervals of 1 km. Open circles = *P. suturalis*, solid = *P. taeniata*. The regression coefficient is significantly negative ($P < 0.01$) and $r^2 = 0.8$ for each species. Populations from Ahutau are excluded.

species can be large, as shown by the populations of *P. taeniata* and *P. suturalis* from Mount Ahutau. These findings stand in sharp contrast to the general finding in other organisms that genetic identities of 0.8 or lower represent differences between species and values of 0.9 or higher indicate differences within species (Thorpe, 1982). Two problems arise in interpreting the general pattern, however. First, for many organisms the current taxonomy is based on indirect evidence, so that we cannot equate "species" with "reproductively isolated taxa". Second, the genetic differences between species may include those accrued after the establishment of reproductive isolation. These difficulties do not apply to *Partula* on Moorea, because their reproductive relationships have been determined from extensive field and laboratory studies (Murray and Clarke, 1980) and because they include several "borderline" species.

Despite the local exchange of genes within each species complex, and the potential for exchange between complexes, hybridisation is apparently

unimportant in maintaining the resemblances between species. Within a complex, species that hybridise are no more similar than those that do not. Furthermore, comparisons between species near areas of hybridisation do not show unusually high degrees of similarity. For example, in the northeast near sites 2, 3 and 23, hybridisation occurs between *P. taeniata* and *P. exigua* and between *P. suturalis* and *P. aurantia* (Murray and Clarke, 1968). Nevertheless, the *P. exigua* of the northeast most closely resemble the *P. taeniata* from site 6, well south of the range of *P. exigua*, and *P. aurantia* is most similar to *P. suturalis* from sites 14 and 15, in the northwest. The apparent ineffectiveness of hybridisation in bringing about biochemical resemblance is consistent with the fact that distinct morphologies and ecologies are also maintained by the species that can hybridise (Murray and Clarke, 1980; Murray *et al.*, 1982).

Despite the great similarities between species and the absence of species-specific alleles, the average genetic identities observed between

Figure 5 The geographic variation of allozymes characteristic of the populations from Ahutau among populations of *P. taeniata* from southern Moorea. The "Ahutau Index" is the average of the frequencies of *Got-1*^{1.00}, *Idh-1*^{1.16}, and *Pep-4*^{0.97}, and is indicated by the blackened sectors.

species generally lie outside those observed within species (excluding the Ahutau populations). The average genetic identities decrease with geographical distance in both *P. taeniata* and *P. suturalis*, but even at the largest distances, the average identities are above 0.90, which is the average value between species within either species complex. Thus in general there is a consistent compressed scale of genetic divergence.

This compressed scale is consistent with the recent radiation of *Partula* on Moorea. Comparisons of species from different islands show an average rate of allozymic divergence (measured as Nei's $D = -\ln I$) of about $0.13D$ per million years (Johnson *et al.*, 1986). At that rate, the maximum genetic distance on Moorea, which is about 1.5 million years old (Duncan and McDougall, 1976), should be 0.20. This corresponds to a genetic identity of 0.82, remarkably close to the lowest average value actually observed. Thus, the overall amount of allozymic divergence on Moorea is not anomalous, and recentness of speciation is the most probable reason for the high similarities between species.

This is not the complete story, however, because there are anomalous patterns within Moorea. In particular, the average divergence distinguishing the populations of *P. taeniata* on Mount Ahutau from the rest of the species is larger than the average divergence between species. Morphologically, these populations lie within the pattern of geographic variation of *P. taeniata* as a whole. The smooth genetic transition between the Ahutau populations and their northern counterparts indicates continuing gene flow and the absence of reproductive isolation. Thus, the Ahutau populations provide, on a smaller scale, a situation similar to that of *Cepaea nemoralis*, in which reproductive isolation has failed to develop despite large amounts of genetic divergence (Johnson *et al.*, 1984). That this occurs on Moorea in *Partula*, which is characterised by speciation with little allozymic change, implies one of two things. The populations on Mount Ahutau may have become isolated before speciation occurred within the *P. taeniata* and *P. suturalis* groups. This would be consistent with the estimates of evolutionary rates discussed above. Alternatively,

Figure 6 The geographic variation in the frequency of $Pgm-2^{0.87}$ among populations of *P. suturalis* from southern Moorea.

the Ahutau populations may have had a more recent origin, in which case the rates of evolution have been very variable. A finer probe of phylogenetic relationships will be necessary to discriminate between these alternatives. In either case, the Ahutau populations emphasise the heterogeneity of patterns of divergence that can occur within a group as apparently cohesive as *Partula* on Moorea and demonstrate that biochemical, morphological and reproductive divergence are not necessarily correlated, even within and between closely-related taxa.

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