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Clines in the Genetic Distance between Two Species of Island Land Snails: How `Molecular Leakage' Can Mislead us about Speciation [and Discussion]

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Clines in the genetic distance between two species of island land snails: how 'molecular leakage' can mislead us about speciation

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SUMMARY

Two species of land snails, *Partula taeniata* and *Partula suturalis*, occur sympatrically on the island of Moorea in French Polynesia. The genetic distance between them varies clinally from north to south. Their extreme difference in the south is attributed to an invasion from the neighbouring island of Tahiti. Their genetic closeness in the north, despite large morphological and ecological differences, is attributed to 'molecular leakage', convergence of the neutral and advantageous genes in the two species through occasional hybridization. Rates of hybridization as low as 1 in 100000 can render two species nearly homogeneous in their gene frequencies over periods of time that are short on an evolutionary scale, and therefore can completely mislead us about the phylogenetic history of the taxa concerned. In such circumstances the only valid phylogenetic information may be contained in genes that are kept distinct by natural selection.

1. INTRODUCTION

It is often supposed that to reconstruct the true phylogeny of organisms we should use characters or sequences that are, as nearly as possible, selectively neutral. Those under selection are not regarded as satisfactory because different lineages can converge when they are exposed to similar environments. Here we report evidence that, in groups of sympatric species, neutral sequences may be very seriously misleading about evolutionary relationships, whereas genes under selection may yet contain valid phylogenetic information.

The primary observations are on allelic frequencies in land snails of the genus *Partula* from the island of Moorea in French Polynesia. Since the pioneering studies of Garrett (1884) and Crampton (1932), the Partulae of Moorea and other Pacific islands have been exceptionally productive of information about the origin, variation and differentiation of species. Studies on the evolution of the group have recently been reviewed (Cowie 1992; Johnson *et al.* 1993*a*).

The Society Islands, to which Moorea belongs, were formed successively as the Pacific plate moved in a northwesterly direction, at approximately 11 cm per year, over a 'hot-spot' in the mantle (Duncan & McDougall 1976). Consequently the islands at the northwest end of the chain (Bora Bora about 3.3. Ma old; Tahaa, about 2.9 Ma old; and Raiatea and Huahine, about 2.5 Ma old) are older than those at the southeast (Moorea, about 1.5 Ma old, and Tahiti, about 1 Ma old). The snails seem to have populated the newer islands from the older ones, carried by birds or blown by typhoons. Until recent extinctions (Murray *et al.* 1988), each island typically harboured several endemic species. Moorea had seven. (The Partulae of Moorea are now extinct on the island, but there are living representatives of most species in the laboratory, and in many zoos, as well as a large array of frozen and preserved populations. To avoid oscillating between the present and past tenses when referring to living material, collections and populations, we will keep to the present tense.) A study of allozymic differences between the species in the Society archipelago showed that, with a few exceptions, the species from one island resemble each other more than they resemble any species from another island (Johnson *et al.* 1986*b*). It was reasonable to conclude that most of the speciation occurred *in situ* on each island, through a series of successive radiations each starting with a single invasion, or with a 'burst' of invasions over a short period of evolutionary time. Subsequent invasions would be less likely to succeed because they would encounter competitors already adapted to the local environment.

Our earlier analysis (Johnson *et al.* 1986*b*) was carried out using pooled samples from each species. This paper uses a larger set of data to show an unexpected cline in the degree of difference between two sympatric taxa, *Partula suturalis* Pfeiffer and *P. taeniata* Mörch. It suggests that secondary invasions have occurred, and that the resemblances between species within islands may have been at least partly due to gene flow, rather than being a necessary consequence of evolution *in situ*. If this is correct, our results exemplify an important general point that neutral genes can be unsatisfactory indicators of phylogenetic relationships among sympatric species.

2. THE MOOREAN SPECIES OF *PARTULA*

Anatomical and reproductive relations between the Moorean species of *Partula* were studied by Murray & Clarke (1980), who recognized two major groups. The first, the *P. suturalis* group, contains four species (*P. suturalis*, *P. aurantia* Crampton *P. tohiveana* Crampton and *P. mooreana* Hartman); the second, the *P. taeniata* group, contains two (*P. taeniata* and *P. exigua* Crampton). Within each of these groups there is clear evidence of natural hybridization, some of it sporadic, some of it more intense but restricted to particular populations. There are natural hybrids of *P. suturalis* with *P. aurantia*, *P. suturalis* with *P. tohiveana*, *P. aurantia* with *P. tohiveana*, and *P. taeniata* with *P. exigua*. The seventh species, *P. mirabilis* Crampton forms a bridge between the two species groups, because it hybridizes naturally with *P. taeniata*, and in the laboratory with *P. aurantia* and *P. tohiveana*. Despite these possibilities for genetic exchange, most species in most places on Moorea are clearly distinct from each other. As many as four can coexist in one place without any loss of anatomical integrity (Murray & Clarke 1980).

The two commonest Moorean species are *Partula taeniata* and *P suturalis*, which both occur throughout the island. *P. taeniata* is found alone in some habitats at low altitudes, but otherwise the two are widely sympatric (Crampton 1932). They differ ecologically, *P. taeniata* favouring shrubs up to about 5 m in height, and *P. suturalis* favouring the trunks of the purau tree, *Hibiscus tiliaceus* L. (Murray *et al.* 1993). Despite these broad preferences, they are often found on the same host plant. There is no direct evidence of natural hybridization between them, and when they are grown together in the laboratory they do not cross (Murray & Clarke 1980). They are anatomically very different, *P. suturalis* being substantially larger. They even differ in the genetics of their shell-colour and banding polymorphisms (Murray & Clarke 1976*a*, *b*).

Both species show north–south clines in the size and shape of the shell. The northern *P. taeniata* tend to be smaller and fatter than those from the south. On the other hand the southern *P. suturalis* tend to be smaller and fatter than those from the north (Crampton 1932; Lundman 1947; Johnson et al. 1993*b*). These opposing clines argue against any simple explanation in terms of climatic or vegetational patterns, although the southern valleys tend to be wetter and lusher than the northern ones. The two clines are not exact mirror images of eachother. The shapes of *P. taeniata* and *P. suturalis* are most alike in the northeastern and midwestern valleys, and most different in the far southern and northwestern ones. Shell sizes are most alike in the eastern and northeastern valleys and most different in the centre and northwest. It is important for the present analysis that the northwestern populations show particularly strong morphological differences between *P. taeniata* and *P. suturalis*.

There is another way in which northern and southern populations differ. The shells of *P. suturalis* from the north of the island are coiled to the left and those from the south are coiled to the right. There is a narrow zone of transition, containing both dextral and sinistral shells, in between. The genetic change of coil from sinistral to dextral coincides with the sympatric presence of other species in the *P. suturalis* group that are themselves sinistral (*P. mooreana* and *P. tohiveana*). Snails of opposite coil are less likely to mate with each other, and the change represents a stage in the evolution of reproductive isolation (Clarke & Murray 1969; Johnson 1982; Johnson *et al.* 1990). *Partula taeniata* is dextral throughout the island, so we would expect the barriers to gene flow between *P. taeniata* and *P. suturalis* to be greater in the north than in the south.

3. MATERIALS AND METHODS

Sixty-one samples, representing seven species of *Partula* (*P. taeniata*, *P. suturalis*, *P. mooreana P. mirabilis*, *P. tohiveana*, *P. aurantia* and *P. exigua*) were collected at 27 localities on the island of Moorea (see figure 1). In addition nine samples, representing seven species (*P. otaheitana* (Bruguière), *P. jackieburchi* Kondo, *P. hyalina* Broderip, *P. filosa* Pfeiffer, *P. nodosa* Pfeiffer, *P. affinis* Pease, and *P. clara* Pease), were collected at three localities on the neighbouring island of Tahiti. Eight pooled samples representing each of three species from the island of Raiatea (*P. faba* Martin, *P. dentifera* Pfeiffer, and *P. hebe* Pfeiffer), three from the island of Huahine (*P. rosea* Broderip, *P. varia* Broderip and *P. arguta* Pease), one from Bora Bora (*P. lutea* Lesson) and one from Rarotonga in the Cook Islands (*P. assimilis* Pease) were used to root the trees of Moorean and Tahitian species. All samples are listed in table 1. Further details about localities and sampling methods are to be found in Johnson *et al.* (1986*a*, *b*, 1993*b*).

Tissues of individual snails from each sample were

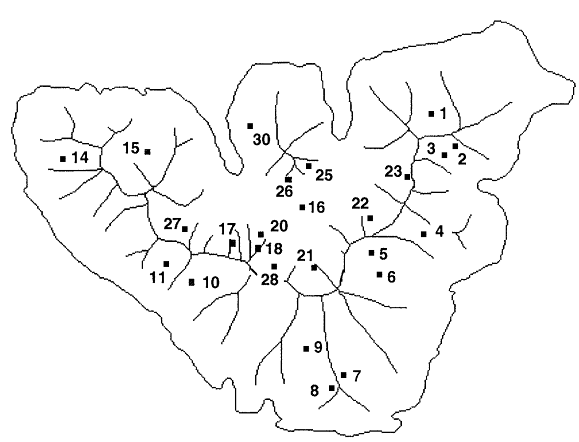

Figure 1. A map of the island of Moorea, showing the locations at which samples of *Partula* were collected. The two samples whose locations are not shown (565 and 566) were collected near sample 3. Details about the species found in each sample are given by table 1. The maximum diameter of the island is approximately 15 km.

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Table 1. *Localities and species sampled*

(Sample number refers to table 2 (see appendix). For Moorea localities, see figure 1; for other islands, see text. The sample sizes are averaged over the numbers used for each of the 19 enzymes, and the figures in brackets represent the extremes. Where there are no bracketed numbers, the samples for all enzymes were identical in size. Note the small size of sample 54 with 4 individuals (8 chromosomes), and of samples 59, 65 and 67 with 3 individuals (6 chromosomes) each.)

island	sample number	locality	*species*	mean size	sample (range)
Moorea	1	21	*P. taeniata*	21.7	(11–23)
	2	21	*P. suturalis*	20	
	3	27	*P. taeniata*	19.9	(16–22)
	4	27	*P. suturalis*	22	
	5	23	*P. suturalis*	12	
	6	23	*P. taeniata*	14.6	(13–20)
	7	5	*P. suturalis*	14.6	(13–19)
	8	4	*P. taeniata*	23	
	9	4	*P. suturalis*	11	
	10	28	*P. taeniata*	21.9	(20–22)
	11	28	*P. suturalis*	71	
	12	30	*P. suturalis*	14.9	(3–16)
	13	1	*P. taeniata*	6	
	14	1	*P. suturalis*	20	
	15	2	*P. taeniata*	19	
	16	6	*P. taeniata*	19.9	(19–20)
	17	6	*P. suturalis*	20	
	18	7	*P. taeniata*	9	
	19	7	*P. suturalis*	20	
	20	8	*P. taeniata*	21	
	21	8	*P. suturalis*	20	
	22	9	*P. taeniata*	21	
	23	9	*P. suturalis*	19	
	24	10	*P. taeniata*	20	
	25	10	*P. suturalis*	19.9	(19–20)
	26	11	*P. taeniata*	20	
	27	11	*P. suturalis*	22	
	28	14	*P. taeniata*	19.7	(15–20)
	29	14	*P. suturalis*	20	
	30	15	*P. taeniata*	19.7	(17–20)
	31	15	*P. suturalis*	22	
	32	16	*P. taeniata*	17.3	(17–20)
	33	17	*P. taeniata*	2	
	34	17	*P. suturalis*	20	
	35	18	*P. taeniata*	20	
	36	18	*P. suturalis*	20	
	37	20	*P. taeniata*	20.3	(20–23)
	38	20	*P. suturalis*	19.9	(19–20)
	39	22	*P. taeniata*	11.3	(11–14)
	40	22	*P. suturalis*	19.2	(19–20)
	41	25	*P. taeniata*	19.9	(19–20)
	42	25	*P. suturalis*	19.8	(17–20)
	43	26	*P. taeniata*	16.2	(11–20)
	44	21	*P. mirabilis*	8	
	45	21	*P. tohiveana*	21	
	46	23	*P. aurantia*	18	
	47	565	*P. exigua*	20	
	48	566	*P. exigua*	10	
	49	5	*P. tohiveana*	11	
	50	4	*P. tohiveana*	23	
	51	28	*P. mirabilis*	57	
	52	28	*P. mooreana*	34	
	53	3	*P. aurantia*	20	
	54	3	*P. exigua*	4	
	55	9	*P. mooreana*	14	
	56	10	*P. mooreana*	22	
	57	16	*P. mirabilis*	20	
	58	18	*P. mirabilis*	15	
	59	20	*P. mirabilis*	3	
	60	22	*P. tohiveana*	20	
	61	26	*P. mirabilis*	20	

Table 1 (*cont.*)

island	sample number	locality	*species*	mean size	sample (range)
Tahiti	62	577	*P. otaheitana*	12	
	63	578	*P. otaheitana*	19	
	64	742	*P. jackieburchi*	24	
	65	742	*P. affinis*	3	
	66	577	*P. hyalina*	16	
	67	742	*P. hyalina*	3	
	68	577	*P. filosa*	21	
	69	578	*P. nodosa*	22	
	70	578	*P. clara*	16	
Raiatea	71		*P. faba*	48	
	72		*P. dentifera*	64	
	73		*P. hebe*	115	
Huahine	74		*P. rosea*	54	
	75		*P. varia*	113	
	76		*P. arguta*	30	
Bora Bora	77		*P. lutea*	40	
Rarotonga	78		*P. assimilis*	20	

homogenized, electrophoresed and stained using the techniques described by Johnson *et al.* (1977, 1986*a*). For this analysis we took data on 19 variable enzyme loci, ignoring loci that were invariant across all 78 samples. The variable loci were *Alph*, *Est-1*, *Est-2*, *Got-1*, *Got-2*, *Idh-1*, *Idh-2*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Mpi*, *Np*, *Pep-2*, *Pep-4*, *Pep-6*, *6pgd*, *Pgi*, *Pgm-1* and *Pgm-2*. Further details about these loci are given by Johnson *et al.* (1977, 1986*a*).

The gene-frequencies at the 19 loci allowed us to compare all samples with all others, using Nei's 'unbiased' coefficients of genetic distance (Nei 1978). The matrix of distances, shown on table 2 (see appendix), was used to generate UPGMA, Fitch-Margoliash, and neighbour-joining trees with the PHYLIP suite of programs (Felsenstein 1993).

4. RESULTS AND DISCUSSION

Figure 2 is a map of the genetic distances between sympatric populations of *P. taeniata* and *P. suturalis*. It is remarkable in three ways. In the first place it shows a clear, if irregular, cline from larger differences in the south to smaller differences in the north. Second, by the standards of *Partula* the differences in the south are very large, as great as some of those between species on Moorea and Raiatea (about 270 km apart), or even on Raiatea and Saipan (about 7500 km apart). Third, by the same standards the differences in the north are very small, those in localities 1 and 15 being less than the median value of distances within Moorean species (0.041). We are therefore faced with trying to answer two, possibly separate, questions. Why are the differences in the south so large? Why are the differences in the north so small?

(*a*) *The South*

The large differences between *P. taeniata* and *P. suturalis* in the south are due to both species having diverged from their northern conspecifics, as well as from each other, at many loci (Johnson *et al.* 1986*b*, 1993*a*). *P. taeniata* seems to have diverged more than *P. suturalis*, and indeed the southern *P. taeniata* populations differ as much from other *P. taeniata* as they do from *P. suturalis*. The maximum genetic distance within *P. taeniata* is 0.267, between localities 8 and 22. The maximum distance within *P. suturalis* is 0.148, between localities 8 and 30. It should be emphasized at this point that the southern *P. taeniata* are indeed good *P. taeniata*, as they intergrade continuously into the northern ones both morphologically and allozymically. They occupy the appropriate ecological niche, and the southern snails interbreed with northern ones in the laboratory. The same principles apply to the southern *P. suturalis*. They also are good members of their species, despite containing high frequencies of an enzyme allele ($Pgm\text{-}2^{0.87}$) not found elsewhere on Moorea (Johnson *et al.* 1986*a*). Because there are no obvious ecological, physical, or geological reasons why

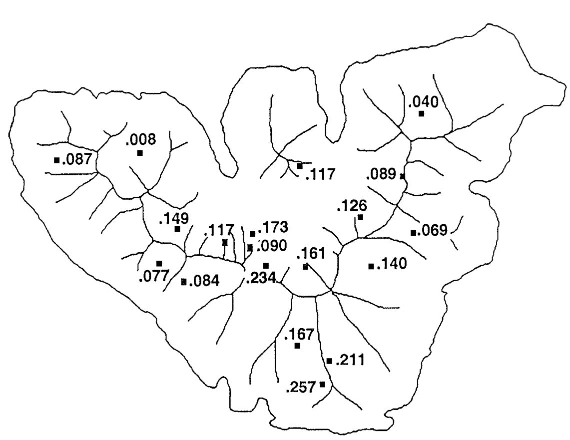

Figure 2. A map of Moorea showing, for each locality at which *Partula taeniata* and *P. suturalis* were found sympatrically, Nei's coefficient of genetic distance between them. There is an obvious, if irregular, gradient from north to south.

the southern snails should be so different from other members of their own species and from each other, we must seek clues about their history.

It is possible that the populations in the south have been changed by an invasion from another island. Because both species are aberrant, there would have to be two sets of invaders, one that hybridized with *P. taeniata* and one that hybridized with *P. suturalis*. It is not unlikely that an event such as a typhoon could move more than one species. The most probable source of invaders is Tahiti, about 20 km away. The next nearest island inhabited by *Partula* is Huahine, more than 200 km away.

There is a second reason to favour Tahiti as a source. It was probably populated from Moorea, which is 0.5 Ma older, and before that time the ancestors of *P. taeniata* and *P. suturalis* might well have begun to differentiate. Thus the Tahitian descendants of proto-suturalis and proto-taeniata, when re-invasion happened, could each be reproductively compatible with its closest Moorean relatives, but not with members of the other species. This would explain why there was not a general mêlée of hybridization, and a resulting in convergence between the taxa.

We tested the hypothesis of an invasion by reconstructing evolutionary trees of populations in Moorea and Tahiti, using the matrix of Nei's distances. All our trees agree, regardless of the method of their construction or the taxa used for rooting them, in showing that the extreme southern *P. taeniata* are more closely related to Tahitian species than to any other taxon in Moorea (see figure 3). They also agree in placing the southern *P. suturalis* firmly with the other Moorean *P. suturalis*. Thus the hypothesis of an invasion is supported by the data from *P. taeniata*, but not by the data from *P. suturalis*. The conflict between the two sets of data can be resolved if we suppose that because *P. suturalis* is a larger and more mobile species its higher level of gene flow has obscured the traces of a Tahitian ancestry. This supposition is consistent with an earlier analysis, in which a Wagner tree, based on pooled samples, indicated that the southern *suturalis* rather than the southern *taeniata*, were closest to the Tahitian taxa (Johnson *et al.* 1986*b*). It is also consistent with observations on restriction sites in the mitochondrial DNA (Murray *et al.* 1991). The southern *P. suturalis* show mitochondrial haplotypes that are as near to a Tahitian species (*P. nodosa*) as to any other Moorean taxon. The southern *P. taeniata* show a single haplotype that is common to both islands. Immigration from Tahiti seems to be the only explanation that accounts for all the facts.

(*b*) *The North*

The extremely short genetic distance (0.008) between *P. taeniata* and *P. suturalis* at locality 15 may be a quirk of sampling, but it resembles the values at other northern localities in being more appropriate to differences within species than to differences between them. The most obvious explanation for such low values is that the species have recently diverged (as has been argued for the African cichlids discussed at this symposium by Meyer *et al.*, this volume). However there are difficulties with this explanation in the present case. As pointed out above, the large differences in the south have apparently been due to invasions from Tahitian populations that originated after the two Moorean species had diverged. Our reconstructed trees suggest the same order of events. Whereas an accelerated rate of divergence might have happened because of special selective factors in the Tahitian environment, this seems unlikely and there is no independent evidence of it. On Moorea the anatomical and ecological differences between *P. suturalis* and *P. taeniata* are very striking. The snails belong to different species groups, and even differ in the genetics of their shell characters. Paradoxically, their anatomical divergence seems to be greatest where they are most alike at the molecular level.

The lack of concordance between morphological and molecular characters extends to other pairs of species. *P. taeniata* and *P. exigua* are very similar in morphology, hybridize in nature, and freely cross in the laboratory (Murray & Clarke 1968; Johnson *et al.* 1977), yet the genetic distance between them in sympatry (about 0.200) is much greater than that between northern *P. taeniata* and *P. suturalis*. *P. mirabilis* is morphologically intermediate between *P. taeniata* and *P. suturalis*. It hybridizes with *P. taeniata*, but genetically it seems always to be nearer *P. suturalis* (at six localities where populations of *P. mirabilis* and *P. taeniata* are sympatric, the genetic distances between them range from 0.110 to 0.185; at four of these localities we also have distances between *P. mirabilis* and *P. suturalis*, which range from 0.029 to 0.093).

How are we to resolve these paradoxes? There is one possible solution that emerges naturally from the fact that we are observing speciation in progress. When newly arisen species are sympatric, or come into sympatry, it is quite possible that their degree of reproductive isolation is enough to ensure their distinctness, but is not yet perfectly complete. It has not been generally appreciated, perhaps, that even a small amount of gene flow can have a very large effect over time. Let us consider the simplest possible case, a single locus with two neutral alleles. If two large populations of equal size differ in the frequencies of the alleles, and if they hybridize at a rate h (defined as the number of successful hybrid matings as a proportion of all matings, calculated in numbers of fertile offspring), the difference in allelic frequencies between the populations will decline at a rate of $2h$ per generation. Thus, if h is small, after $1/h$ generations the difference between the populations will have fallen to about 13.5% of its starting value, and after $2/h$ generations to about 2%.

This simple calculation shows that a level of hybridization undetectable in the field or laboratory can have profound evolutionary consequences. As an extreme example, if the proportion of successful hybrid matings is 1 in 100000, the difference between two large populations will decline to 14% of its starting value in 100000 generations. This, for *Partula*, is about 200000 years, or less than one sixth of its probable span

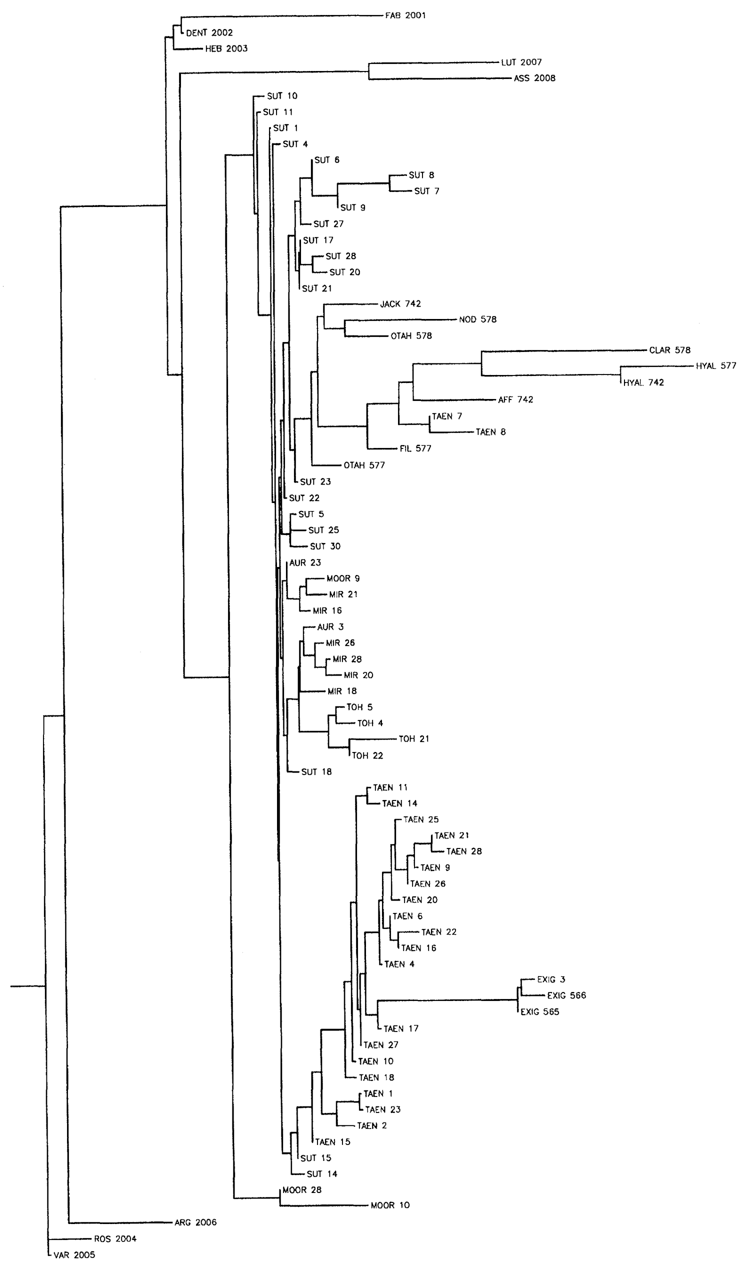

Figure 3. A neighbour-joining tree of all the samples. The tree for Tahiti and Moorea is rooted by the inclusion of species from the older islands of Raiatea (species abbreviated as fab, dent and heb), Huahine (those abbreviated as ros, var and arg), Bora Bora (that abbreviated as lut) and Rarotonga (that abbreviated as ass). Note that populations of *P. taeniata* from the extreme south of Moorea (taen 7 and taen 8) group with the species from Tahiti (abbreviated as otah, jack, aff, hyal, fil and nod). Equivalent populations of *P. suturalis* from the extreme south (sut 7 and sut 8), however, group with their Moorean conspecifics. The association of southern *P. taeniata* with the Tahitian species has been found consistently in all the trees studied, including those produced by UPGMA and the Fitch-Margoliash method. Bootstrapping by loci shows the association in 65 out of 100 trials.

of life on Moorea. Convergence will be opposed by random drift, but with little effect if the population sizes are more than twice the reciprocal of the hybridization rate.

It is now easy to see how discrepancies can arise between anatomical and molecular characters. Suppose that a new species originates on another island and then invades Moorea. Initially it will show both anatomical and molecular differences from the local species. If its reproductive isolation is less than absolutely perfect, however, any differences in the frequencies of genes that are selectively neutral or unequivocally advantageous will gradually or quickly be lost. The longer any two species exist together, the more alike they will become, except only in those characters that are important to the ecological, reproductive or behavioural distinctions between them. These exceptions must be a small proportion of the genome. During a long coexistence the two species will probably evolve characters that reduce their probability of hybridizing, either through changes directly related to mating, like the reversal of coil in *P. suturalis*,

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or through ecological displacements. Thus as they grow more alike at the molecular level, they will become progressively less able to mate with each other. The relative speed at which complete isolation evolves will no doubt vary from case to case, but the process can in principle lead to a negative relationship between the extent of hybridization and the similarity of gene frequencies .

This scenario of 'molecular leakage' fits *Partula* very well. It accommodates the known facts of interspecific hybridization. It not only explains the lack of concordance between morphology, molecules and reproductive isolation, but also the exceptionally high levels of allozymic heterozygosity (Johnson *et al.* 1986*a*) and the widespread sharing of mitochondrial haplotypes between species on different islands (Murray *et al.* 1991). Thus evolutionary trees based upon neutral alleles may be misleading when they suggest that speciation on each island has occurred *in situ*.

5. GENERAL CONCLUSIONS

If trees based upon neutral (or indeed generally advantageous) genetic differences in *Partula* can seriously mislead us about its evolutionary history, we have to ask whether this reflects a general problem. Of course, 'molecular leakage' is restricted to taxa in sympatry. It might be argued that the matter is only serious when the taxa have diverged very recently, because otherwise they would have evolved complete isolation. The available evidence suggests that this is not the case. Prager & Wilson (Prager *et al.* 1974; Prager & Wilson 1975), using 'immunological distances' between albumins, estimated that the mean time to the common ancestors of bird species known to be capable of hybridizing was about 21 Ma. The figure in frogs was similar, but in mammals it was 2 Ma. For our purposes these estimates have several pitfalls. 'Immunological clocks' may be set wrongly because of uncertainties in the fossil record, and they may not run to time. The viability of hybrids is not enough to produce introgression, which requires them to be fertile. These considerations suggest that Prager & Wilson's times may be too long. On the other hand, taxa with very low rates of hybridization (10^{-4} or less) would not have been included in the survey, and from this viewpoint the times may be too short. In either case it seems unlikely that the 3 or 4 Ma available for the evolution of *Partula* in the Society Islands will have exhausted the possibilities of introgression. We know that on Moorea there is the potential for gene flow between any species and any other (Johnson *et al.* 1993*a*). The paper by Grant & Grant, this volume, make a similar point with respect to the finches in the Galapagos and the honeycreepers in the Hawaiian Islands.

Rieseberg & Soltis (1991), reviewing the evidence for 'reticulate evolution' in plants, have argued that the introgression of nuclear genes and cytoplasmic organelles may bias phylogenetic reconstruction at all taxonomic levels, and a similar case has been made by Dowling & DeMarais (1993) for cyprinid fishes. Avise (1994) reviews other examples of introgression. Perhaps we need to re-examine cases of unusual genetic homogeneity between sympatric species of animals (such as the African and other cichlid fishes; see, for example, Meyer *et al.* 1990; Schliewen *et al.* 1994), and ask if they too are not due, at least in part, to 'molecular leakage'.

How can we escape being misled? It will not be enough to look at a larger number of genes or other stretches of DNA, because if some genes have been rendered homogeneous the greatest part of the genome will probably have suffered the same fate. If we examine the sequences of individual alleles, some will reflect one ancestry and some the other, but once allelic frequencies have been made roughly equal we will not know which ancestry belongs to which species, and may erroneously conclude that the polymorphism is older than the speciation. Only when events have been relatively recent, like the invasion of southern Moorea from Tahiti, will we be able to detect them.

For events in the longer term, possible sources of information are the genes that evolved in allopatry to determine the adaptive distinctions between the species, and in genes closely linked to them. The neutral parts of such sequences should preserve true records of their phylogenetic history. We may need to distinguish them from genes producing later adaptations, such as reinforcement or ecological displacement, by mutation from introgressed alleles. However, it may be good enough to separate out the selected loci, and show that most of them are consistent in their phylogenies.

The only other hope is that the general progress towards uniformity might be retarded by linkage to selected loci. However, we are not aware of any quantitative models that tell us how much of the genome can be preserved from introgressive convergence by linkage, or for how long. Intuition, and the general shortage of linkage disequilibrium, suggests that the amount may be small and the time short. If so, we are left with the challenge to detect and sequence 'adaptive' genes, so that we can reveal the true patterns of speciation.

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Discussion

G. Hewitt (*UEA, Norwich, U.K.*). Do we have information on the geological age of different parts of Moorea? The southern location which has such marked divergence between the species may have been (or now is) where two forms have diverged into species and then spread north onto younger land, hybridizing more. This does not need a Tahitian colonization. Perhaps this region of Moorea was the source of Tahiti's *Partula*?

B. C. Clarke. Potassium/ Argon dates have been obtained from various locations on Moorea (Duncan & McDougall). They vary somewhat from place to place, but not in a pattern that suggests anything special about the southern end of the island. Supposing that this region was the source of the Tahitian *Partula* leaves us without an explanation of the north-south cline (see figure 2), and is at variance with the tree (figure 3), which suggests the reverse.

G. M. Wragg (*Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.*). Polynesian people have been voyaging among the islands of central Polynesia for approximately 2 millennia. When land snails are transported to new islands as a result of man's activities – as evidenced by dated archaeological sites etc – the possibility of measuring genetic and morphological change over a known amount of time arises. A comparison of this relatively short-term divergence (<2000 years) to the genetic and morphological divergence found between naturally occurring taxa may be of value in elucidating relationships between indigenous populations. Is there any evidence of man-transported taxa among the *Partula* land snails of Moorea?

B. C. Clarke. I am sure that people carried *Partula* around on vegetation. Unfortunately, though, I know of no reports associating *Partula* shells with dated archaeological sites. It seems very unlikely indeed that the invasion from Tahiti mentioned in out paper was anything to do with human activity. The earliest known occurrence of people on Moorea is around 600 A.D. (D. Lepovski, personal communication). Perhaps they might have been there as early as the beginning of the millenium. This is not nearly enough time, I believe, top establish the north-south clines of shell-characters and allozymes in both *P. suturalis* and *P. taeniata*, when the annual average movement of the snails is only a few metres (Murray & Clarke 1984). It would be delightfully upsetting to a lot of conventional theories if the radiation of *Partula* in the Society Islands were found to have happened since the arrival of man.

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APPENDIX

Table 2. *Nei's Coefficients of genetic distance between all pairs of samples*[a]

(The species and localities corresponding to the sample numbers are given in table 1.)

sample nos.	1	2	3	4	5	6	7	8	9	10
1	.0000	.1698	.0476	.1467	.1615	.0726	.1727	.0144	.1208	.0090
2	.1698	.0000	.0900	.0164	.0085	.0995	.0229	.1185	.0350	.1831
3	.0476	.0900	.0000	.0776	.0908	.0456	.0861	.0262	.0667	.0615
4	.1467	.0164	.0776	.0000	.0363	.0836	.0586	.1021	.0421	.1643
5	.1615	.0085	.0908	.0363	.0000	.0887	.0178	.1056	.0218	.1763
6	.0726	.0995	.0456	.0836	.0887	.0000	.0895	.0413	.0673	.1222
7	.1727	.0229	.0861	.0586	.0178	.0895	.0000	.1168	.0229	.1761
8	.0144	.1185	.0262	.1021	.1056	.0413	.1168	.0000	.0688	.0319
9	.1208	.0350	.0667	.0421	.0218	.0673	.0229	.0688	.0000	.1257
10	.0090	.1831	.0615	.1643	.1763	.1222	.1761	.0319	.1257	.0000
11	.2137	.0208	.1330	.0376	.0364	.1156	.0472	.1508	.0600	.2342
12	.1848	.0198	.0996	.0482	.0217	.0809	.0185	.1318	.0424	.2089
13	.0809	.1000	.0598	.0792	.0945	.0040	.1010	.0470	.0618	.1219
14	.1208	.0312	.0641	.0401	.0242	.0480	.0224	.0681	.0069	.1358
15	.1465	.0897	.0760	.0808	.0869	.0457	.0702	.0942	.0525	.1725
16	.0138	.1336	.0332	.1088	.1179	.0377	.1250	.0119	.0785	.0289
17	.1670	.0181	.0955	.0155	.0436	.0978	.0459	.1188	.0433	.1779
18	.1552	.1220	.1171	.1288	.1292	.1913	.1546	.1377	.1409	.1513
19	.2646	.0823	.1915	.0778	.1127	.1928	.1335	.2207	.1300	.2892
20	.2394	.1235	.1542	.1537	.1233	.2237	.1639	.1980	.1680	.2513
21	.2575	.1065	.1701	.1069	.1366	.1960	.1262	.1960	.1315	.2620
22	.0212	.1606	.0282	.1356	.1450	.0920	.1516	.0270	.1028	.0222
23	.1783	.0310	.1068	.0316	.0485	.1111	.0408	.1234	.0429	.1836
24	.0461	.1018	.0107	.0787	.0983	.0463	.0880	.0268	.0613	.0490
25	.1505	.0336	.0950	.0128	.0428	.0904	.0550	.1056	.0370	.1628
26	.0497	.1029	.0087	.0867	.1045	.0609	.1094	.0216	.0745	.0645
27	.1209	.0279	.0704	.0131	.0364	.0489	.0456	.0741	.0236	.1410
28	.0798	.1099	.0285	.0766	.1227	.0904	.1226	.0488	.0860	.0858
29	.1361	.0303	.0670	.0260	.0342	.0632	.0331	.0880	.0314	.1502
30	.0948	.0408	.0205	.0292	.0406	.0342	.0421	.0470	.0277	.1156
31	.1061	.0330	.0439	.0209	.0284	.0428	.0364	.0545	.0109	.1195
32	.0108	.1334	.0362	.1114	.1253	.0524	.1304	.0110	.0855	.0257
33	.0526	.1091	.0092	.1121	.1058	.0680	.1014	.0327	.0800	.0614
34	.1703	.0000	.0996	.0099	.0114	.1078	.0366	.1208	.0346	.1811
35	.0488	.0921	.0094	.0888	.0780	.0359	.0706	.0243	.0491	.0670
36	.1633	.0144	.0907	.0282	.0292	.1134	.0285	.1152	.0236	.1615
37	.0197	.1324	.0363	.1007	.1254	.0717	.1372	.0299	.0903	.0283
38	.2270	.0157	.1401	.0458	.0264	.1548	.0295	.1748	.0578	.2303
39	.0260	.1539	.0699	.1267	.1380	.0333	.1542	.0182	.0989	.0649
40	.1348	.0134	.0628	.0277	.0147	.0740	.0136	.0918	.0153	.1426
41	.0303	.1278	.0160	.1090	.1180	.0774	.1333	.0230	.0910	.0409
42	.1531	.0357	.0754	.0607	.0299	.0655	.0170	.0911	.0194	.1714
43	.0129	.1447	.0256	.1297	.1302	.0774	.1273	.0159	.0850	.0113
44	.1854	.0575	.1142	.0811	.0469	.1178	.0304	.1201	.0351	.1779
45	.2568	.0982	.1603	.1589	.0807	.1879	.0495	.2134	.0918	.2426
46	.1413	.0213	.0811	.0366	.0101	.0780	.0141	.0912	.0094	.1445
47	.1456	.2309	.1169	.2249	.2067	.1037	.2278	.1240	.1930	.1886
48	.1681	.2688	.1583	.2641	.2406	.1432	.2601	.1667	.2294	.1933
49	.1441	.1014	.0935	.0967	.0767	.1044	.0554	.1083	.0363	.1339
50	.2009	.1090	.1326	.1176	.0951	.1409	.0511	.1520	.0498	.1800
51	.1953	.0723	.1305	.0775	.0897	.1376	.0471	.1498	.0593	.1777
52	.2100	.0984	.1335	.1135	.0931	.1363	.0588	.1471	.0776	.2096
53	.1694	.0543	.1046	.0441	.0725	.1331	.0517	.1297	.0420	.1529
54	.1558	.2575	.1274	.2470	.2351	.1114	.2593	.1325	.2203	.2087
55	.1636	.0562	.1005	.0570	.0681	.1097	.0543	.1182	.0495	.1589
56	.2868	.1808	.2518	.1765	.1972	.2531	.1404	.2654	.1583	.2639
57	.1470	.0486	.0793	.0547	.0477	.0790	.0390	.0911	.0312	.1507
58	.2173	.0395	.1418	.0646	.0460	.1766	.0502	.1719	.0578	.1999
59	.1807	.0827	.1395	.0993	.0973	.1666	.0612	.1569	.0684	.1524
60	.1812	.0901	.1178	.1247	.0574	.1278	.0359	.1351	.0372	.1693
61	.1613	.0810	.1036	.0833	.0757	.1083	.0540	.1131	.0376	.1532
62	.1699	.0259	.0963	.0333	.0296	.0868	.0781	.1234	.0720	.2064
63	.1529	.1005	.0952	.0936	.1086	.0805	.1224	.1217	.1068	.1911
64	.1655	.0765	.1263	.0749	.0720	.0909	.1141	.1406	.0867	.2041
65	.2556	.1468	.2098	.1440	.1508	.1976	.2159	.2402	.1826	.2981
66	.3058	.3447	.3195	.3375	.3537	.3989	.4057	.3017	.3660	.3092
67	.2165	.2670	.2308	.2596	.2722	.3011	.3186	.2122	.2740	.2202
68	.1689	.1203	.1019	.1181	.1024	.0968	.1275	.1172	.0990	.2039
69	.2083	.1579	.1293	.1640	.1587	.1424	.1594	.1603	.1479	.2344
70	.3372	.2932	.2499	.3105	.2888	.3543	.3358	.3102	.3379	.3650
71	.3384	.2751	.2528	.2259	.2731	.2340	.2755	.2851	.2645	.3889
72	.1306	.1431	.1058	.0960	.1259	.0968	.1342	.1034	.0946	.1420
73	.1628	.1153	.1291	.0802	.1202	.1596	.1370	.1468	.1244	.1590
74	.2227	.2889	.2306	.2334	.2611	.1983	.2645	.2146	.2319	.2240
75	.1963	.2517	.1954	.1901	.2274	.1844	.2364	.1859	.1875	.2030
76	.2787	.2779	.2832	.2032	.2748	.2185	.3143	.2708	.2568	.3266
77	.4177	.4052	.3921	.3319	.4119	.3749	.3609	.3853	.3451	.4162
78	.3121	.4250	.3815	.4135	.3987	.2928	.3703	.3060	.3601	.3544

sample nos.	11	12	13	14	15	16	17	18	19	20
1	.2137	.1848	.0809	.1208	.1465	.0138	.1670	.1552	.2646	.2394
2	.0208	.0198	.1000	.0312	.0897	.1336	.0181	.1220	.0823	.1235
3	.1330	.0996	.0598	.0641	.0760	.0332	.0955	.1171	.1915	.1542
4	.0376	.0482	.0792	.0401	.0808	.1088	.0155	.1288	.0778	.1537
5	.0364	.0217	.0945	.0242	.0869	.1179	.0436	.1292	.1127	.1233
6	.1156	.0809	.0040	.0480	.0457	.0377	.0978	.1913	.1928	.2237
7	.0472	.0185	.1010	.0224	.0702	.1250	.0459	.1546	.1335	.1639
8	.1508	.1318	.0470	.0681	.0942	.0119	.1188	.1377	.2207	.1980
9	.0600	.0424	.0618	.0069	.0525	.0785	.0433	.1409	.1300	.1680
10	.2342	.2089	.1219	.1358	.1725	.0289	.1779	.1513	.2892	.2513
11	.0000	.0330	.0974	.0484	.0982	.1743	.0264	.1277	.0855	.1144
12	.0330	.0000	.0853	.0263	.0922	.1297	.0531	.1144	.1321	.1062
13	.0974	.0853	.0000	.0407	.0253	.0354	.0956	.1810	.1952	.2117
14	.0484	.0263	.0407	.0000	.0570	.0704	.0435	.1436	.1400	.1632
15	.0982	.0922	.0253	.0570	.0000	.0982	.0782	.2063	.1730	.2472
16	.1743	.1297	.0354	.0704	.0982	.0000	.1397	.1582	.2537	.2191
17	.0264	.0531	.0956	.0435	.0782	.1397	.0000	.1265	.0599	.1605
18	.1277	.1144	.1810	.1436	.2063	.1582	.1265	.0000	.2108	.0345
19	.0855	.1321	.1952	.1400	.1730	.2537	.0599	.2108	.0000	.2354
20	.1144	.1062	.2117	.1632	.2472	.2191	.1605	.0345	.2354	.0000
21	.1044	.1482	.1927	.1287	.1687	.2378	.0740	.2129	.0317	.2573
22	.2093	.1767	.0941	.1075	.1442	.0188	.1683	.1370	.2830	.1936
23	.0260	.0547	.1018	.0409	.0928	.1436	.0150	.1396	.0450	.1647
24	.1301	.1069	.0483	.0544	.0769	.0250	.0898	.1160	.1983	.1759
25	.0325	.0546	.0674	.0383	.0688	.1072	.0331	.1358	.1043	.1590
26	.1298	.1311	.0654	.0744	.0910	.0421	.0931	.1131	.1845	.1477
27	.0417	.0349	.0380	.0101	.0658	.0712	.0271	.1435	.1084	.1694
28	.1277	.1521	.0841	.0830	.1075	.0634	.0873	.1308	.1815	.1794
29	.0621	.0335	.0715	.0205	.0780	.0860	.0371	.1588	.1220	.1880
30	.0731	.0538	.0460	.0241	.0462	.0574	.0432	.1377	.1287	.1673
31	.0573	.0427	.0414	.0104	.0468	.0608	.0340	.1300	.1203	.1632
32	.1807	.1297	.0606	.0760	.1211	.0062	.1414	.1584	.2528	.2271
33	.1450	.1297	.0822	.0822	.0978	.0483	.1069	.1268	.2025	.1577
34	.0196	.0313	.1035	.0360	.0947	.1359	.0123	.1175	.0717	.1251
35	.1428	.1052	.0592	.0550	.0613	.0364	.0955	.1540	.1899	.2000
36	.0440	.0313	.1096	.0266	.0924	.1258	.0199	.1150	.0953	.1415
37	.1834	.1546	.0730	.0948	.1142	.0169	.1380	.1411	.2293	.2265
38	.0199	.0337	.1408	.0638	.1069	.1886	.0430	.1363	.0948	.1260
39	.1850	.1421	.0415	.0869	.1182	.0174	.1593	.2035	.2543	.2668
40	.0508	.0274	.0872	.0185	.0675	.0991	.0241	.1344	.0992	.1520
41	.1890	.1556	.0908	.0976	.1236	.0268	.1428	.1430	.2384	.1946
42	.0521	.0270	.0601	.0127	.0486	.1070	.0618	.1668	.1450	.1777
43	.2075	.1550	.0902	.0909	.1290	.0116	.1511	.1510	.2645	.2248
44	.0485	.0679	.1084	.0395	.0870	.1440	.0530	.1426	.1477	.1647
45	.1429	.0641	.1938	.0945	.1493	.1926	.1604	.2236	.2673	.2039
46	.0392	.0295	.0774	.0133	.0683	.0967	.0286	.1253	.1122	.1408
47	.2483	.1970	.1188	.1553	.2117	.1142	.2403	.2634	.3481	.2628
48	.2872	.2202	.1576	.1884	.2644	.1383	.2771	.2819	.3923	.2963
49	.1541	.0790	.1071	.0442	.1022	.0782	.1208	.2063	.2416	.2468
50	.1283	.0838	.1312	.0558	.1074	.1325	.1092	.2130	.2352	.2448
51	.0835	.0746	.1304	.0484	.1190	.1434	.0462	.1831	.1543	.2370
52	.1084	.1035	.1360	.0659	.1056	.1596	.1014	.2069	.2092	.2560
53	.0898	.0646	.1285	.0407	.1178	.1195	.0449	.1702	.1378	.2225
54	.2718	.2208	.1296	.1794	.2346	.1256	.2671	.2864	.3750	.2709
55	.0404	.0786	.0849	.0436	.0699	.1325	.0303	.1298	.1130	.1638
56	.1754	.1827	.2245	.1487	.1895	.2428	.1519	.2909	.2489	.3643
57	.0515	.0546	.0730	.0219	.0759	.1011	.0371	.1402	.1291	.1626
58	.0743	.0481	.1720	.0577	.1598	.1658	.0602	.1563	.1404	.1575
59	.1016	.0993	.1462	.0675	.1338	.1396	.0631	.1729	.1596	.2207
60	.1183	.0610	.1286	.0460	.1099	.1211	.1209	.1836	.2370	.1846
61	.0999	.0795	.1084	.0357	.1053	.1124	.0610	.1807	.1646	.2239
62	.0726	.0462	.1052	.0645	.1159	.1342	.0566	.1609	.1051	.1620
63	.1176	.1185	.0946	.0911	.1085	.1314	.0859	.1927	.1603	.2180
64	.1043	.1045	.0892	.0969	.0872	.1399	.0830	.1985	.1339	.2134
65	.1786	.1526	.1908	.1967	.1854	.2420	.1498	.1157	.1934	.1549
66	.4457	.3430	.4255	.3787	.4721	.3203	.3876	.2519	.4798	.3371
67	.3592	.2634	.3231	.2840	.3670	.2276	.3029	.1747	.3975	.2622
68	.1592	.1007	.1185	.0987	.1338	.1337	.1205	.0994	.1880	.1492
69	.1952	.1833	.1579	.1439	.1515	.1803	.1630	.2603	.2491	.2825
70	.3533	.2924	.3800	.3490	.4005	.3396	.3266	.2002	.3240	.2084
71	.3051	.2565	.2530	.2559	.2554	.2835	.2936	.4519	.3201	.4785
72	.1821	.1446	.0949	.0914	.1269	.0830	.1475	.2327	.2214	.3159
73	.1686	.1408	.1599	.1201	.1807	.1270	.1309	.1996	.1913	.2863
74	.3312	.2649	.1962	.2106	.2673	.1668	.2954	.3431	.4254	.4675
75	.2955	.2597	.1845	.1912	.2184	.1573	.2457	.3298	.3066	.4469
76	.3013	.3056	.2066	.2614	.2441	.2387	.2656	.3885	.3345	.4679
77	.4084	.3344	.3520	.3035	.4031	.3358	.3562	.3450	.4032	.4886
78	.4609	.3074	.3127	.3194	.4186	.2732	.4349	.3690	.4330	.4978

[a] This table is symmetrical in the sense that the upper right and lower left sections are identical.

Table 2 (*cont.*)

sample nos.	21	22	23	24	25	26	27	28	29	30
1	.2575	.0212	.1783	.0461	.1505	.0497	.1209	.0798	.1361	.0948
2	.1065	.1606	.0310	.1018	.0336	.1029	.0279	.1099	.0303	.0408
3	.1701	.0282	.1068	.0107	.0950	.0087	.0704	.0285	.0670	.0205
4	.1069	.1356	.0316	.0787	.0128	.0867	.0131	.0766	.0260	.0292
5	.1366	.1450	.0485	.0983	.0428	.1045	.0364	.1227	.0342	.0406
6	.1960	.0920	.1111	.0463	.0904	.0609	.0489	.0904	.0632	.0342
7	.1262	.1516	.0408	.0880	.0550	.1094	.0456	.1226	.0331	.0421
8	.1960	.0270	.1234	.0268	.1056	.0216	.0741	.0488	.0880	.0470
9	.1315	.1028	.0429	.0613	.0370	.0745	.0236	.0860	.0314	.0277
10	.2620	.0222	.1836	.0490	.1628	.0645	.1410	.0858	.1502	.1156
11	.1044	.2093	.0260	.1301	.0325	.1298	.0417	.1277	.0621	.0731
12	.1482	.1767	.0547	.1069	.0546	.1311	.0349	.1521	.0335	.0538
13	.1927	.0941	.1018	.0483	.0674	.0654	.0380	.0841	.0715	.0460
14	.1287	.1075	.0409	.0544	.0383	.0744	.0101	.0830	.0205	.0241
15	.1687	.1442	.0928	.0769	.0688	.0910	.0658	.1075	.0780	.0462
16	.2378	.0188	.1436	.0250	.1072	.0421	.0712	.0634	.0860	.0574
17	.0740	.1683	.0150	.0898	.0331	.0931	.0271	.0873	.0371	.0432
18	.2129	.1370	.1396	.1160	.1358	.1131	.1435	.1308	.1588	.1377
19	.0317	.2830	.0450	.1983	.1043	.1845	.1084	.1815	.1220	.1287
20	.2573	.1936	.1647	.1759	.1590	.1477	.1694	.1794	.1880	.1673
21	.0000	.2542	.0378	.1592	.1254	.1574	.1120	.1447	.1171	.1202
22	.2542	.0000	.1669	.0262	.1333	.0323	.1150	.0458	.1232	.0765
23	.0378	.1669	.0000	.0917	.0319	.1009	.0291	.0835	.0431	.0540
24	.1592	.0262	.0917	.0000	.0837	.0226	.0565	.0288	.0594	.0284
25	.1254	.1333	.0319	.0837	.0000	.0984	.0167	.0799	.0392	.0451
26	.1574	.0323	.1009	.0226	.0984	.0000	.0767	.0130	.0878	.0330
27	.1120	.1150	.0291	.0565	.0167	.0767	.0000	.0714	.0149	.0239
28	.1447	.0458	.0835	.0288	.0799	.0130	.0714	.0000	.0866	.0430
29	.1171	.1232	.0431	.0594	.0392	.0878	.0149	.0866	.0000	.0217
30	.1202	.0765	.0540	.0284	.0451	.0330	.0239	.0430	.0217	.0000
31	.1113	.0893	.0377	.0355	.0295	.0532	.0090	.0578	.0118	.0081
32	.2340	.0259	.1484	.0356	.1222	.0488	.0808	.0750	.0855	.0628
33	.1705	.0357	.1175	.0266	.1279	.0074	.0989	.0339	.0926	.0410
34	.1042	.1620	.0269	.1054	.0252	.1051	.0256	.1067	.0340	.0447
35	.1763	.0413	.1097	.0233	.1050	.0217	.0749	.0538	.0659	.0219
36	.0973	.1474	.0299	.0904	.0463	.1003	.0294	.1040	.0356	.0457
37	.2283	.0169	.1479	.0340	.0954	.0488	.0879	.0594	.0998	.0618
38	.1237	.2080	.0407	.1493	.0341	.1543	.0636	.1536	.0676	.0844
39	.2536	.0655	.1634	.0677	.1292	.0731	.0836	.1072	.1072	.0797
40	.1143	.1234	.0382	.0711	.0456	.0813	.0284	.0989	.0199	.0244
41	.2225	.0157	.1509	.0327	.1209	.0217	.0999	.0392	.1007	.0508
42	.1358	.1419	.0568	.0805	.0469	.0941	.0366	.1128	.0393	.0338
43	.2345	.0100	.1577	.0254	.1404	.0372	.1040	.0633	.1025	.0649
44	.1191	.1595	.0398	.0917	.0629	.1089	.0626	.1071	.0617	.0694
45	.2649	.2164	.1590	.1799	.1520	.2137	.1434	.2530	.1189	.1306
46	.1169	.1245	.0321	.0718	.0379	.0883	.0249	.0993	.0248	.0346
47	.3176	.1445	.2481	.1168	.2401	.1244	.1706	.1606	.1289	.1396
48	.3610	.1723	.2866	.1348	.2793	.1845	.2021	.2235	.1543	.1874
49	.2233	.1054	.1128	.0810	.0921	.1266	.0649	.1343	.0577	.0652
50	.2006	.1594	.0959	.1119	.1055	.1555	.0845	.1552	.0828	.0956
51	.1214	.1764	.0439	.1003	.0822	.1359	.0524	.1185	.0497	.0815
52	.1781	.1829	.0964	.1198	.0911	.1452	.0948	.1385	.0905	.0854
53	.1277	.1436	.0484	.0892	.0616	.1219	.0362	.1064	.0376	.0592
54	.3455	.1566	.2756	.1364	.2613	.1290	.1894	.1695	.1522	.1553
55	.1026	.1498	.0337	.0804	.0460	.0923	.0518	.0872	.0697	.0648
56	.2434	.2770	.1522	.2187	.1293	.2629	.1561	.2408	.1695	.1944
57	.1015	.1279	.0330	.0649	.0608	.0748	.0349	.0778	.0413	.0409
58	.1487	.1885	.0669	.1414	.0871	.1581	.0657	.1641	.0440	.0910
59	.1308	.1596	.0602	.1133	.0944	.1356	.0761	.1285	.0831	.1073
60	.2187	.1417	.1079	.1129	.1097	.1429	.0910	.1693	.0821	.0889
61	.1314	.1400	.0591	.0810	.0930	.1055	.0532	.1064	.0379	.0632
62	.1528	.1782	.0875	.1183	.0751	.1216	.0488	.1479	.0479	.0481
63	.1716	.1599	.1024	.1060	.1165	.1026	.0883	.1125	.0991	.0763
64	.2051	.1889	.1164	.1418	.0851	.1385	.0834	.1663	.1024	.0855
65	.2946	.2832	.2138	.2369	.1646	.2196	.1766	.2682	.1980	.1830
66	.5014	.3282	.4307	.3476	.4044	.3401	.3625	.3878	.3621	.3493
67	.4075	.2364	.3376	.2517	.3141	.2490	.2746	.2944	.2736	.2596
68	.1811	.1646	.1301	.1061	.1476	.1079	.1021	.1397	.1063	.0834
69	.2209	.1920	.1776	.1452	.1886	.1370	.1579	.1588	.1599	.1197
70	.3437	.3138	.3416	.3020	.3688	.2506	.3383	.2988	.3330	.2856
71	.3143	.3250	.2690	.2637	.2242	.2932	.2217	.2862	.2278	.1891
72	.2039	.1116	.1292	.0698	.0849	.1353	.0720	.1170	.0788	.0792
73	.1866	.1391	.1235	.0993	.0826	.1658	.0846	.1351	.0814	.0999
74	.3957	.2124	.2901	.1646	.2184	.2798	.1885	.2585	.1965	.2112
75	.2979	.1847	.2333	.1525	.1725	.2267	.1692	.2054	.1812	.1747
76	.4185	.2935	.2983	.2681	.1752	.2960	.2054	.2805	.2484	.2333
77	.3501	.3853	.3027	.3193	.3094	.4032	.2841	.3520	.2946	.3334
78	.3830	.3745	.3770	.3435	.4029	.4095	.3189	.4498	.3344	.3667

sample nos.	31	32	33	34	35	36	37	38	39	40
1	.1061	.0108	.0526	.1703	.0488	.1633	.0197	.2270	.0260	.1348
2	.0330	.1334	.1091	.0000	.0921	.0144	.1324	.0157	.1539	.0134
3	.0439	.0362	.0092	.0996	.0094	.0907	.0363	.1401	.0699	.0628
4	.0209	.1114	.1121	.0099	.0888	.0282	.1007	.0458	.1267	.0277
5	.0284	.1253	.1058	.0114	.0780	.0292	.1254	.0264	.1380	.0147
6	.0428	.0524	.0680	.1078	.0359	.1134	.0717	.1548	.0333	.0740
7	.0364	.1304	.1014	.0366	.0706	.0285	.1372	.0295	.1542	.0136
8	.0545	.0110	.0327	.1208	.0243	.1152	.0299	.1748	.0182	.0918
9	.0109	.0855	.0800	.0346	.0491	.0236	.0903	.0578	.0989	.0153
10	.1195	.0257	.0614	.1811	.0670	.1615	.0283	.2303	.0649	.1426
11	.0573	.1807	.1450	.0196	.1428	.0440	.1834	.0199	.1850	.0508
12	.0427	.1297	.1297	.0313	.1052	.0313	.1546	.0337	.1421	.0274
13	.0414	.0606	.0822	.1035	.0592	.1096	.0730	.1408	.0415	.0872
14	.0104	.0760	.0822	.0360	.0550	.0266	.0948	.0638	.0869	.0185
15	.0468	.1211	.0978	.0947	.0613	.0924	.1142	.1069	.1182	.0675
16	.0608	.0062	.0483	.1359	.0364	.1258	.0169	.1886	.0174	.0991
17	.0340	.1414	.1069	.0123	.0955	.0199	.1380	.0430	.1593	.0241
18	.1300	.1584	.1268	.1175	.1540	.1150	.1411	.1363	.2035	.1344
19	.1203	.2528	.2025	.0717	.1899	.0953	.2293	.0948	.2543	.0992
20	.1632	.2271	.1577	.1251	.2000	.1415	.2265	.1260	.2668	.1520
21	.1113	.2340	.1705	.1042	.1763	.0973	.2283	.1237	.2536	.1143
22	.0893	.0259	.0357	.1620	.0413	.1474	.0169	.2080	.0655	.1234
23	.0377	.1484	.1175	.0269	.1097	.0299	.1479	.0407	.1634	.0382
24	.0355	.0356	.0266	.1054	.0233	.0904	.0340	.1493	.0677	.0711
25	.0295	.1222	.1279	.0252	.1050	.0463	.0954	.0341	.1292	.0456
26	.0532	.0488	.0074	.1051	.0217	.1003	.0488	.1543	.0731	.0813
27	.0090	.0808	.0989	.0256	.0749	.0294	.0879	.0636	.0836	.0284
28	.0578	.0750	.0339	.1067	.0538	.1040	.0594	.1536	.1072	.0989
29	.0118	.0855	.0926	.0340	.0659	.0356	.0998	.0676	.1072	.0199
30	.0081	.0628	.0410	.0447	.0219	.0457	.0618	.0844	.0797	.0244
31	.0000	.0682	.0656	.0317	.0399	.0308	.0750	.0705	.0809	.0184
32	.0682	.0000	.0541	.1375	.0383	.1214	.0261	.1946	.0151	.0997
33	.0656	.0541	.0000	.1172	.0183	.1051	.0551	.1590	.0897	.0780
34	.0317	.1375	.1172	.0000	.1014	.0157	.1318	.0197	.1567	.0162
35	.0399	.0383	.0183	.1014	.0000	.0899	.0439	.1452	.0598	.0493
36	.0308	.1214	.1051	.0157	.0899	.0000	.1280	.0385	.1539	.0137
37	.0750	.0261	.0551	.1318	.0439	.1280	.0000	.1728	.0502	.1033
38	.0705	.1946	.1590	.0197	.1452	.0385	.1728	.0000	.2176	.0428
39	.0809	.0151	.0897	.1567	.0598	.1539	.0502	.2176	.0000	.1264
40	.0184	.0997	.0780	.0162	.0493	.0137	.1033	.0428	.1264	.0000
41	.0727	.0311	.0268	.1324	.0271	.1272	.0196	.1838	.0616	.0990
42	.0316	.1122	.0968	.0489	.0643	.0439	.1176	.0503	.1194	.0298
43	.0758	.0094	.0337	.1486	.0265	.1241	.0200	.2028	.0454	.0970
44	.0463	.1564	.1094	.0578	.0993	.0543	.1606	.0592	.1778	.0498
45	.1231	.1959	.1808	.1182	.1488	.0946	.2065	.0895	.2481	.0706
46	.0156	.1073	.0884	.0189	.0655	.0189	.1106	.0394	.1257	.0077
47	.1473	.1230	.1084	.2416	.1258	.2485	.1622	.3136	.1351	.1907
48	.1821	.1489	.1527	.2765	.1710	.2792	.1858	.3504	.1766	.2174
49	.0471	.0900	.1230	.1025	.0787	.0689	.0997	.1270	.1235	.0506
50	.0708	.1431	.1480	.1091	.1187	.0684	.1646	.1160	.1838	.0655
51	.0594	.1454	.1383	.0707	.1260	.0420	.1691	.0957	.1871	.0518
52	.0839	.1739	.1518	.1073	.1216	.0968	.1535	.1031	.1964	.0841
53	.0414	.1137	.1314	.0493	.1080	.0242	.1279	.0858	.1609	.0343
54	.1706	.1346	.1177	.2689	.1406	.2800	.1776	.3468	.1393	.2176
55	.0479	.1469	.1026	.0490	.0990	.0492	.1354	.0606	.1714	.0449
56	.1788	.2629	.2722	.1724	.2443	.1530	.2180	.1556	.2978	.1509
57	.0233	.1102	.0800	.0460	.0717	.0356	.1317	.0806	.1321	.0312
58	.0636	.1564	.1505	.0374	.1414	.0291	.1813	.0592	.2119	.0320
59	.0756	.1544	.1312	.0803	.1300	.0483	.1543	.0928	.2019	.0566
60	.0667	.1337	.1239	.0961	.0958	.0672	.1495	.0935	.1669	.0461
61	.0373	.1136	.1013	.0762	.0856	.0483	.1446	.1187	.1485	.0402
62	.0493	.1329	.1280	.0275	.0976	.0570	.1372	.0771	.1386	.0385
63	.0812	.1424	.1035	.1003	.0929	.1117	.1398	.1500	.1451	.0722
64	.0779	.1628	.1410	.0696	.1065	.1035	.1321	.1061	.1491	.0654
65	.1702	.2642	.2351	.1346	.2080	.1662	.2201	.1704	.2542	.1459
66	.3378	.2837	.3614	.3457	.3424	.3346	.3239	.4233	.3198	.3451
67	.2498	.1962	.2685	.2697	.2487	.2519	.2327	.3403	.2306	.2595
68	.0730	.1466	.1202	.1225	.0940	.1125	.1573	.1828	.1421	.0957
69	.1201	.1919	.1347	.1703	.1217	.1679	.1920	.2136	.2039	.1377
70	.3055	.3441	.2558	.2977	.2873	.3057	.3294	.3363	.3728	.2982
71	.2279	.2893	.3230	.2839	.2704	.2917	.2734	.2914	.2707	.2732
72	.0667	.1018	.1582	.1419	.1092	.1390	.0771	.1687	.1061	.1241
73	.0906	.1360	.1876	.1155	.1514	.1246	.0935	.1383	.1676	.1236
74	.1900	.1944	.2934	.2857	.2401	.2865	.1665	.3406	.2049	.2622
75	.1595	.1842	.2466	.2402	.1932	.2471	.1385	.2858	.1879	.2185
76	.2280	.2805	.3422	.2580	.2809	.3059	.1978	.2994	.2418	.2735
77	.3116	.3586	.4638	.3922	.4128	.3362	.3522	.4249	.3733	.3671
78	.3443	.2677	.4341	.4410	.3686	.3772	.3300	.4740	.2315	.3912

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 2 (*cont.*)

sample nos.	41	42	43	44	45	46	47	48	49	50
1	.0303	.1531	.0129	.1854	.2568	.1413	.1456	.1681	.1441	.2009
2	.1278	.0357	.1447	.0575	.0982	.0213	.2309	.2688	.1014	.1090
3	.0160	.0754	.0256	.1142	.1603	.0811	.1169	.1583	.0935	.1326
4	.1090	.0607	.1297	.0811	.1589	.0366	.2249	.2641	.0967	.1176
5	.1180	.0299	.1302	.0469	.0807	.0101	.2067	.2406	.0767	.0951
6	.0774	.0655	.0774	.1178	.1879	.0780	.1037	.1432	.1044	.1409
7	.1333	.0170	.1273	.0304	.0495	.0141	.2278	.2601	.0554	.0511
8	.0230	.0911	.0159	.1201	.2134	.0912	.1240	.1667	.1083	.1520
9	.0910	.0194	.0850	.0351	.0918	.0094	.1930	.2294	.0363	.0498
10	.0409	.1714	.0113	.1779	.2426	.1445	.1886	.1933	.1339	.1800
11	.1890	.0521	.2075	.0485	.1429	.0392	.2483	.2872	.1541	.1283
12	.1556	.0270	.1550	.0679	.0641	.0295	.1970	.2202	.0790	.0838
13	.0908	.0601	.0902	.1084	.1938	.0774	.1188	.1576	.1071	.1312
14	.0976	.0127	.0909	.0395	.0945	.0133	.1553	.1884	.0442	.0558
15	.1236	.0486	.1290	.0870	.1493	.0683	.2117	.2644	.1022	.1074
16	.0268	.1070	.0116	.1440	.1926	.0967	.1142	.1383	.0782	.1325
17	.1428	.0618	.1511	.0530	.1604	.0286	.2403	.2771	.1208	.1092
18	.1430	.1668	.1510	.1426	.2236	.1253	.2634	.2819	.2063	.2130
19	.2384	.1450	.2645	.1477	.2673	.1122	.3481	.3923	.2416	.2352
20	.1946	.1777	.2248	.1647	.2039	.1408	.2628	.2963	.2468	.2448
21	.2225	.1358	.2345	.1191	.2649	.1169	.3176	.3610	.2233	.2006
22	.0157	.1419	.0100	.1595	.2164	.1245	.1445	.1723	.1054	.1594
23	.1509	.0568	.1577	.0398	.1590	.0321	.2481	.2866	.1128	.0959
24	.0327	.0805	.0254	.0917	.1799	.0718	.1168	.1348	.0810	.1119
25	.1209	.0469	.1404	.0629	.1520	.0379	.2401	.2793	.0921	.1055
26	.0217	.0941	.0372	.1089	.2137	.0883	.1244	.1845	.1266	.1555
27	.0999	.0366	.1040	.0626	.1434	.0249	.1706	.2021	.0649	.0845
28	.0392	.1128	.0633	.1071	.2530	.0993	.1606	.2235	.1343	.1552
29	.1007	.0393	.1025	.0617	.1189	.0248	.1289	.1543	.0577	.0828
30	.0508	.0338	.0649	.0694	.1306	.0346	.1396	.1874	.0652	.0956
31	.0727	.0316	.0758	.0463	.1231	.0156	.1473	.1821	.0471	.0708
32	.0311	.1122	.0094	.1564	.1959	.1073	.1230	.1489	.0900	.1431
33	.0268	.0968	.0337	.1094	.1808	.0884	.1084	.1527	.1230	.1480
34	.1324	.0489	.1486	.0578	.1182	.0189	.2416	.2765	.1025	.1091
35	.0271	.0643	.0265	.0993	.1488	.0655	.1258	.1710	.0787	.1187
36	.1272	.0439	.1241	.0543	.0946	.0189	.2485	.2792	.0689	.0684
37	.0196	.1176	.0200	.1606	.2065	.1106	.1622	.1858	.0997	.1646
38	.1838	.0503	.2028	.0592	.0895	.0394	.3136	.3504	.1270	.1160
39	.0616	.1194	.0454	.1778	.2481	.1257	.1351	.1766	.1235	.1838
40	.0990	.0298	.0970	.0498	.0706	.0077	.1907	.2174	.0506	.0655
41	.0000	.1166	.0147	.1581	.2014	.1126	.1387	.1865	.1093	.1743
42	.1166	.0000	.1215	.0506	.0827	.0317	.1933	.2370	.0740	.0849
43	.0147	.1215	.0000	.1502	.1798	.1061	.1431	.1643	.0807	.1339
44	.1581	.0506	.1502	.0000	.1237	.0226	.2225	.2531	.0960	.0712
45	.2014	.0827	.1798	.1237	.0000	.0790	.3165	.3245	.0694	.0768
46	.1126	.0317	.1061	.0226	.0790	.0000	.1878	.2118	.0478	.0531
47	.1387	.1933	.1431	.2225	.3165	.1878	.0000	.0183	.2260	.2780
48	.1865	.2370	.1643	.2531	.3245	.2118	.0183	.0000	.2393	.2904
49	.1093	.0740	.0807	.0960	.0694	.0478	.2260	.2393	.0000	.0219
50	.1743	.0849	.1339	.0712	.0768	.0531	.2780	.2904	.0219	.0000
51	.1795	.0868	.1475	.0539	.1262	.0422	.2505	.2643	.0705	.0460
52	.1647	.0546	.1671	.0721	.1275	.0711	.2820	.3225	.1045	.1010
53	.1377	.0758	.1155	.0797	.1095	.0396	.2673	.2829	.0419	.0447
54	.1474	.2171	.1593	.2568	.3555	.2184	.0003	.0298	.2580	.3162
55	.1500	.0602	.1440	.0311	.1364	.0297	.2359	.2628	.1110	.0853
56	.2854	.1460	.2560	.1589	.1761	.1392	.4302	.4301	.1530	.1341
57	.1233	.0508	.1121	.0304	.1236	.0199	.1731	.2050	.0708	.0576
58	.1750	.0886	.1590	.0783	.0743	.0326	.2355	.2453	.0717	.0715
59	.1727	.1081	.1369	.0629	.1069	.0436	.2723	.2810	.0719	.0532
60	.1485	.0637	.1184	.0629	.0320	.0349	.2334	.2470	.0252	.0304
61	.1407	.0781	.1116	.0481	.1244	.0299	.1620	.1811	.0509	.0434
62	.1270	.0701	.1522	.1333	.1526	.0590	.2033	.2329	.1338	.1804
63	.1314	.1172	.1501	.1386	.2061	.0984	.1832	.2215	.1653	.1895
64	.1454	.1035	.1700	.1440	.1815	.0759	.2236	.2557	.1578	.1930
65	.2376	.2042	.2719	.2493	.2635	.1620	.3351	.3693	.2650	.3208
66	.3031	.4143	.2933	.4159	.4402	.3710	.5114	.5398	.3781	.4324
67	.2172	.3171	.2048	.3183	.3519	.2812	.4078	.4350	.2843	.3626
68	.1324	.1223	.1462	.1414	.2224	.0972	.1909	.2348	.1449	.1905
69	.1665	.1552	.1817	.1759	.2435	.1492	.2430	.2961	.2013	.2285
70	.2671	.3491	.3166	.3973	.4179	.3238	.3835	.4462	.4095	.4431
71	.2886	.2332	.3206	.3549	.3913	.2954	.4085	.4656	.2871	.3597
72	.1123	.1142	.1106	.1554	.2444	.1167	.2216	.2317	.0953	.1601
73	.1340	.1367	.1410	.1759	.2395	.1272	.2899	.2841	.1303	.1953
74	.2310	.2568	.2057	.2897	.3586	.2421	.2988	.2603	.1976	.2415
75	.1824	.2198	.1803	.2579	.3354	.2099	.3146	.3112	.1794	.2231
76	.2741	.2829	.3078	.3517	.4469	.2729	.3993	.4351	.2933	.3448
77	.4116	.3505	.3810	.3741	.4718	.3416	.4992	.5128	.2803	.3076
78	.3654	.3578	.3162	.4428	.4034	.3710	.4261	.4417	.3116	.3783

sample nos.	51	52	53	54	55	56	57	58	59	60
1	.1953	.2100	.1694	.1558	.1636	.2868	.1470	.2173	.1807	.1812
2	.0723	.0984	.0543	.2575	.0562	.1808	.0486	.0395	.0827	.0901
3	.1305	.1335	.1046	.1274	.1005	.2518	.0793	.1418	.1395	.1178
4	.0775	.1135	.0441	.2470	.0570	.1765	.0547	.0646	.0993	.1247
5	.0897	.0931	.0725	.2351	.0681	.1972	.0477	.0460	.0973	.0574
6	.1376	.1363	.1331	.1114	.1097	.2531	.0790	.1766	.1666	.1278
7	.0471	.0588	.0517	.2593	.0543	.1404	.0390	.0502	.0612	.0359
8	.1498	.1471	.1297	.1325	.1182	.2654	.0911	.1719	.1569	.1351
9	.0593	.0776	.0420	.2203	.0495	.1583	.0312	.0578	.0684	.0372
10	.1777	.2096	.1529	.2087	.1589	.2639	.1507	.1999	.1524	.1693
11	.0835	.1084	.0898	.2718	.0404	.1754	.0515	.0743	.1016	.1183
12	.0746	.1035	.0646	.2208	.0786	.1827	.0546	.0481	.0993	.0610
13	.1304	.1360	.1285	.1296	.0849	.2245	.0730	.1720	.1462	.1286
14	.0484	.0659	.0407	.1794	.0436	.1487	.0219	.0577	.0675	.0460
15	.1190	.1056	.1178	.2346	.0699	.1895	.0759	.1598	.1338	.1099
16	.1434	.1596	.1195	.1256	.1325	.2428	.1011	.1658	.1396	.1211
17	.0462	.1014	.0449	.2671	.0303	.1519	.0371	.0602	.0631	.1209
18	.1831	.2069	.1702	.2864	.1298	.2909	.1402	.1563	.1729	.1836
19	.1543	.2092	.1378	.3750	.1130	.2489	.1291	.1404	.1596	.2370
20	.2370	.2560	.2225	.2709	.1638	.3643	.1626	.1575	.2207	.1846
21	.1214	.1781	.1277	.3455	.1026	.2434	.1015	.1487	.1308	.2187
22	.1764	.1829	.1436	.1566	.1498	.2770	.1279	.1885	.1596	.1417
23	.0439	.0964	.0484	.2756	.0337	.1522	.0330	.0669	.0602	.1079
24	.1003	.1198	.0892	.1364	.0804	.2187	.0649	.1414	.1133	.1129
25	.0822	.0911	.0616	.2613	.0460	.1293	.0608	.0871	.0944	.1097
26	.1359	.1452	.1219	.1290	.0923	.2629	.0748	.1581	.1356	.1429
27	.0524	.0948	.0362	.1894	.0518	.1561	.0349	.0657	.0761	.0910
28	.1185	.1385	.1064	.1695	.0872	.2408	.0778	.1641	.1285	.1693
29	.0497	.0905	.0376	.1522	.0697	.1695	.0413	.0440	.0831	.0821
30	.0815	.0854	.0592	.1553	.0648	.1944	.0409	.0910	.1073	.0889
31	.0594	.0839	.0414	.1706	.0479	.1788	.0233	.0636	.0756	.0667
32	.1454	.1739	.1137	.1346	.1469	.2629	.1102	.1564	.1544	.1337
33	.1383	.1518	.1314	.1177	.1026	.2722	.0800	.1505	.1312	.1239
34	.0707	.1073	.0493	.2689	.0490	.1724	.0460	.0374	.0803	.0961
35	.1260	.1216	.1080	.1406	.0990	.2443	.0717	.1414	.1300	.0958
36	.0420	.0968	.0242	.2800	.0492	.1530	.0356	.0291	.0483	.0672
37	.1691	.1535	.1279	.1776	.1354	.2180	.1317	.1813	.1543	.1495
38	.0957	.1031	.0858	.3468	.0606	.1556	.0806	.0592	.0928	.0935
39	.1871	.1964	.1609	.1393	.1714	.2978	.1321	.2119	.2019	.1669
40	.0518	.0841	.0343	.2176	.0449	.1509	.0312	.0320	.0566	.0461
41	.1795	.1647	.1377	.1474	.1500	.2854	.1233	.1750	.1727	.1485
42	.0868	.0546	.0758	.2171	.0602	.1460	.0508	.0886	.1081	.0637
43	.1475	.1671	.1155	.1593	.1440	.2560	.1121	.1590	.1369	.1184
44	.0539	.0721	.0797	.2568	.0311	.1589	.0304	.0783	.0629	.0629
45	.1262	.1275	.1095	.3555	.1364	.1761	.1236	.0743	.1069	.0320
46	.0422	.0711	.0396	.2184	.0297	.1392	.0199	.0326	.0436	.0349
47	.2505	.2820	.2673	.0003	.2359	.4302	.1731	.2355	.2723	.2334
48	.2643	.3225	.2829	.0298	.2628	.4301	.2050	.2453	.2810	.2470
49	.0705	.1045	.0419	.2580	.1110	.1530	.0708	.0717	.0719	.0252
50	.0460	.1010	.0447	.3162	.0853	.1341	.0576	.0715	.0532	.0304
51	.0000	.0915	.0188	.2870	.0494	.1093	.0335	.0480	.0157	.0779
52	.0915	.0000	.0951	.3197	.0721	.0669	.0822	.1341	.1104	.1027
53	.0188	.0951	.0000	.3033	.0639	.1140	.0442	.0322	.0362	.0739
54	.2870	.3197	.3033	.0000	.2695	.4742	.1988	.2720	.3113	.2675
55	.0494	.0721	.0639	.2695	.0000	.1044	.0278	.0812	.0423	.0872
56	.1093	.0669	.1140	.4742	.1044	.0000	.1538	.1673	.0919	.1625
57	.0335	.0822	.0442	.1988	.0278	.1538	.0000	.0577	.0315	.0610
58	.0480	.1341	.0322	.2720	.0812	.1673	.0577	.0000	.0458	.0603
59	.0157	.1104	.0362	.3113	.0423	.0919	.0315	.0458	.0000	.0621
60	.0779	.1027	.0739	.2675	.0872	.1625	.0610	.0603	.0621	.0000
61	.0212	.1052	.0332	.1933	.0563	.1532	.0193	.0435	.0258	.0540
62	.1483	.1627	.1015	.2231	.1237	.2757	.0940	.0856	.1717	.1480
63	.1529	.1829	.1473	.1971	.0943	.2778	.0960	.1608	.1521	.1566
64	.1832	.1846	.1576	.2449	.1108	.2426	.1207	.1428	.1518	.1529
65	.2891	.2960	.2521	.3562	.1888	.3338	.2260	.2144	.2412	.2503
66	.4550	.5057	.3644	.5319	.4511	.6383	.4122	.3614	.4447	.4239
67	.3575	.4005	.2800	.4277	.3508	.5215	.3150	.2845	.3464	.3275
68	.1737	.1907	.1606	.2083	.1526	.3366	.1023	.1708	.1695	.1542
69	.2125	.2169	.2048	.2598	.1700	.3561	.1254	.2228	.1750	.1965
70	.4472	.4646	.3921	.3903	.3905	.6311	.3585	.3447	.4118	.4013
71	.3595	.3287	.2986	.4126	.3540	.4293	.3145	.3836	.4244	.3543
72	.1632	.1529	.1229	.2504	.1615	.2396	.1417	.1969	.1887	.1698
73	.1632	.1639	.1122	.3268	.1703	.2293	.1670	.1656	.1891	.2064
74	.2767	.2682	.2445	.3354	.2952	.3457	.2716	.3276	.3175	.2856
75	.2660	.2370	.2188	.3474	.2492	.3001	.2394	.3064	.2776	.2635
76	.3672	.3224	.3145	.4089	.3023	.3337	.3326	.3899	.3647	.3760
77	.2687	.2475	.2548	.5384	.3401	.2289	.3185	.3688	.3086	.3853
78	.3685	.3862	.3628	.4422	.4652	.4369	.3930	.4295	.4016	.3750

Table 2 (*cont.*)

sample nos.	61	62	63	64	65	66	67	68	69	70
1	.1613	.1699	.1529	.1655	.2556	.3058	.2165	.1689	.2083	.3372
2	.0810	.0259	.1005	.0765	.1468	.3447	.2670	.1203	.1579	.2932
3	.1036	.0963	.0952	.1263	.2098	.3195	.2308	.1019	.1293	.2499
4	.0833	.0333	.0936	.0749	.1440	.3375	.2596	.1181	.1640	.3105
5	.0757	.0296	.1086	.0720	.1508	.3537	.2722	.1024	.1587	.2888
6	.1083	.0868	.0805	.0909	.1976	.3989	.3011	.0968	.1424	.3543
7	.0540	.0781	.1224	.1141	.2159	.4057	.3186	.1275	.1594	.3358
8	.1131	.1234	.1217	.1406	.2402	.3017	.2122	.1172	.1603	.3102
9	.0376	.0720	.1068	.0867	.1826	.3660	.2740	.0990	.1479	.3379
10	.1532	.2064	.1911	.2041	.2981	.3092	.2202	.2039	.2344	.3650
11	.0999	.0726	.1176	.1043	.1786	.4457	.3592	.1592	.1952	.3533
12	.0795	.0462	.1185	.1045	.1526	.3430	.2634	.1007	.1833	.2924
13	.1084	.1052	.0946	.0892	.1908	.4255	.3231	.1185	.1579	.3800
14	.0357	.0645	.0911	.0969	.1967	.3787	.2840	.0987	.1439	.3490
15	.1053	.1159	.1085	.0872	.1854	.4721	.3670	.1338	.1515	.4005
16	.1124	.1342	.1314	.1399	.2420	.3203	.2276	.1337	.1803	.3396
17	.0610	.0566	.0859	.0830	.1498	.3876	.3029	.1205	.1630	.3266
18	.1807	.1609	.1927	.1985	.1157	.2519	.1747	.0994	.2603	.2002
19	.1646	.1051	.1603	.1339	.1934	.4798	.3975	.1880	.2491	.3240
20	.2239	.1620	.2180	.2134	.1549	.3371	.2622	.1492	.2825	.2084
21	.1314	.1528	.1716	.2051	.2946	.5014	.4075	.1811	.2209	.3437
22	.1400	.1782	.1599	.1889	.2832	.3282	.2364	.1646	.1920	.3138
23	.0591	.0875	.1024	.1164	.2138	.4307	.3376	.1301	.1776	.3416
24	.0810	.1183	.1060	.1418	.2369	.3476	.2517	.1061	.1452	.3020
25	.0930	.0751	.1165	.0851	.1646	.4044	.3141	.1476	.1886	.3688
26	.1055	.1216	.1026	.1385	.2196	.3401	.2490	.1079	.1370	.2506
27	.0532	.0488	.0883	.0834	.1766	.3625	.2746	.1021	.1579	.3383
28	.1064	.1479	.1125	.1663	.2682	.3878	.2944	.1397	.1588	.2988
29	.0379	.0479	.0991	.1024	.1980	.3621	.2736	.1063	.1599	.3330
30	.0632	.0481	.0763	.0855	.1830	.3493	.2596	.0834	.1197	.2856
31	.0373	.0493	.0812	.0779	.1702	.3378	.2498	.0730	.1201	.3055
32	.1136	.1329	.1424	.1628	.2642	.2837	.1962	.1466	.1919	.3441
33	.1013	.1280	.1035	.1410	.2351	.3614	.2685	.1202	.1347	.2558
34	.0762	.0275	.1003	.0696	.1346	.3457	.2697	.1225	.1703	.2977
35	.0856	.0976	.0929	.1065	.2080	.3424	.2487	.0940	.1217	.2873
36	.0483	.0570	.1117	.1035	.1662	.3346	.2519	.1125	.1679	.3057
37	.1446	.1372	.1398	.1321	.2201	.3239	.2327	.1573	.1920	.3294
38	.1187	.0771	.1500	.1061	.1704	.4233	.3403	.1828	.2136	.3363
39	.1485	.1386	.1451	.1491	.2542	.3198	.2306	.1421	.2039	.3728
40	.0402	.0385	.0722	.0654	.1459	.3451	.2595	.0957	.1377	.2982
41	.1407	.1270	.1314	.1454	.2376	.3031	.2172	.1324	.1665	.2671
42	.0781	.0701	.1172	.1035	.2042	.4143	.3171	.1223	.1552	.3491
43	.1116	.1522	.1501	.1700	.2719	.2933	.2048	.1462	.1817	.3166
44	.0481	.1333	.1386	.1440	.2493	.4159	.3183	.1414	.1759	.3973
45	.1244	.1526	.2061	.1815	.2635	.4402	.3519	.2224	.2435	.4179
46	.0299	.0590	.0984	.0759	.1620	.3710	.2812	.0972	.1492	.3238
47	.1620	.2033	.1832	.2236	.3351	.5114	.4078	.1909	.2430	.3835
48	.1811	.2329	.2215	.2557	.3693	.5398	.4350	.2348	.2961	.4462
49	.0509	.1338	.1653	.1578	.2650	.3781	.2843	.1449	.2013	.4095
50	.0434	.1804	.1895	.1930	.3208	.4324	.3626	.1905	.2285	.4431
51	.0212	.1483	.1529	.1832	.2891	.4550	.3575	.1737	.2125	.4472
52	.1052	.1627	.1829	.1846	.2960	.5057	.4005	.1907	.2169	.4646
53	.0332	.1015	.1473	.1576	.2521	.3644	.2800	.1606	.2048	.3921
54	.1933	.2231	.1971	.2449	.3562	.5319	.4277	.2083	.2598	.3903
55	.0563	.1237	.0943	.1108	.1888	.4511	.3508	.1526	.1700	.3905
56	.1532	.2757	.2778	.2426	.3338	.6383	.5215	.3366	.3561	.6311
57	.0193	.0940	.0960	.1207	.2260	.4122	.3150	.1023	.1254	.3585
58	.0435	.0856	.1608	.1428	.2144	.3614	.2845	.1708	.2228	.3447
59	.0258	.1717	.1521	.1518	.2412	.4447	.3464	.1695	.1750	.4118
60	.0540	.1480	.1566	.1529	.2503	.4239	.3275	.1542	.1965	.4013
61	.0000	.1327	.1272	.1500	.2608	.4268	.3286	.1254	.1665	.3999
62	.1327	.0000	.1001	.0626	.1232	.3092	.2405	.1012	.1673	.2594
63	.1272	.1001	.0000	.0787	.1617	.4227	.3310	.1126	.1268	.3448
64	.1500	.0626	.0787	.0000	.0764	.3747	.3255	.1165	.1698	.2885
65	.2608	.1232	.1617	.0764	.0000	.3163	.2460	.0991	.2718	.2326
66	.4268	.3092	.4227	.3747	.3163	.0000	.0356	.2760	.4646	.2422
67	.3286	.2405	.3310	.3255	.2460	.0356	.0000	.1953	.3765	.2901
68	.1254	.1012	.1126	.1165	.0991	.2760	.1953	.0000	.1445	.1994
69	.1665	.1673	.1268	.1698	.2718	.4646	.3765	.1445	.0000	.3735
70	.3999	.2594	.3448	.2885	.2326	.2422	.2901	.1994	.3735	.0000
71	.3618	.2464	.3271	.3303	.4552	.6127	.5115	.3281	.3725	.5256
72	.1489	.1395	.1853	.1793	.2916	.4084	.3121	.1607	.2323	.4043
73	.1802	.1180	.2038	.1975	.2786	.3602	.2768	.1964	.2625	.3808
74	.2706	.2673	.3186	.2691	.4325	.3670	.4063	.2924	.3819	.4458
75	.2424	.2374	.2710	.2064	.3569	.3469	.3878	.2526	.3226	.3644
76	.3574	.2577	.2939	.1648	.2670	.4347	.4920	.3235	.3982	.4262
77	.3018	.4533	.4927	.5308	.4856	.5943	.4782	.3216	.5821	.6021
78	.3712	.4134	.4753	.4831	.4470	.4610	.3634	.2780	.5538	.5391

sample nos.	71	72	73	74	75	76	77	78
1	.3384	.1306	.1628	.2227	.1963	.2787	.4177	.3121
2	.2751	.1431	.1153	.2889	.2517	.2779	.4052	.4250
3	.2528	.1058	.1291	.2306	.1954	.2832	.3921	.3815
4	.2259	.0960	.0802	.2334	.1901	.2032	.3319	.4135
5	.2731	.1259	.1202	.2611	.2274	.2748	.4119	.3987
6	.2340	.0968	.1596	.1983	.1844	.2185	.3749	.2928
7	.2755	.1342	.1370	.2645	.2364	.3143	.3609	.3703
8	.2851	.1034	.1468	.2146	.1859	.2708	.3853	.3060
9	.2645	.0946	.1244	.2319	.1875	.2568	.3451	.3601
10	.3889	.1420	.1590	.2240	.2030	.3266	.4162	.3544
11	.3051	.1821	.1686	.3312	.2955	.3013	.4084	.4609
12	.2565	.1446	.1408	.2649	.2597	.3056	.3344	.3074
13	.2530	.0949	.1599	.1962	.1845	.2066	.3520	.3127
14	.2559	.0914	.1201	.2106	.1912	.2614	.3035	.3194
15	.2554	.1269	.1807	.2673	.2184	.2441	.4031	.4186
16	.2835	.0830	.1270	.1668	.1573	.2387	.3358	.2732
17	.2936	.1475	.1309	.2954	.2457	.2656	.3562	.4349
18	.4519	.2327	.1996	.3431	.3298	.3885	.3450	.3690
19	.3201	.2214	.1913	.4254	.3066	.3345	.4032	.4330
20	.4785	.3159	.2863	.4675	.4469	.4679	.4886	.4978
21	.3143	.2039	.1866	.3957	.2979	.4185	.3501	.3830
22	.3250	.1116	.1391	.2124	.1847	.2935	.3853	.3745
23	.2690	.1292	.1235	.2901	.2333	.2983	.3027	.3770
24	.2637	.0698	.0993	.1646	.1525	.2681	.3193	.3435
25	.2242	.0849	.0826	.2184	.1725	.1752	.3094	.4029
26	.2932	.1353	.1658	.2798	.2267	.2960	.4032	.4095
27	.2217	.0720	.0846	.1885	.1692	.2054	.2841	.3189
28	.2862	.1170	.1351	.2585	.2054	.2805	.3520	.4498
29	.2278	.0788	.0814	.1965	.1812	.2484	.2946	.3344
30	.1891	.0792	.0999	.2112	.1747	.2333	.3334	.3667
31	.2279	.0667	.0906	.1900	.1595	.2280	.3116	.3443
32	.2893	.1018	.1360	.1944	.1842	.2805	.3586	.2677
33	.3230	.1582	.1876	.2934	.2466	.3422	.4638	.4341
34	.2839	.1419	.1155	.2857	.2402	.2580	.3922	.4410
35	.2704	.1092	.1514	.2401	.1932	.2809	.4128	.3686
36	.2917	.1390	.1246	.2865	.2471	.3059	.3362	.3772
37	.2734	.0771	.0935	.1665	.1385	.1978	.3522	.3300
38	.2914	.1687	.1383	.3406	.2858	.2994	.4249	.4740
39	.2707	.1061	.1676	.2049	.1879	.2418	.3733	.2315
40	.2732	.1241	.1236	.2622	.2185	.2735	.3671	.3912
41	.2886	.1123	.1340	.2310	.1824	.2741	.4116	.3654
42	.2332	.1142	.1367	.2568	.2198	.2829	.3505	.3578
43	.3206	.1106	.1410	.2057	.1803	.3078	.3810	.3162
44	.3549	.1554	.1759	.2897	.2579	.3517	.3741	.4428
45	.3913	.2444	.2395	.3586	.3354	.4469	.4718	.4034
46	.2954	.1167	.1272	.2421	.2099	.2729	.3416	.3710
47	.4085	.2216	.2899	.2988	.3146	.3993	.4992	.4261
48	.4656	.2317	.2841	.2603	.3112	.4351	.5128	.4417
49	.2871	.0953	.1303	.1976	.1794	.2933	.2803	.3116
50	.3597	.1601	.1953	.2415	.2231	.3448	.3076	.3783
51	.3595	.1632	.1632	.2767	.2660	.3672	.2687	.3685
52	.3287	.1529	.1639	.2682	.2370	.3224	.2475	.3862
53	.2986	.1229	.1122	.2445	.2188	.3145	.2548	.3628
54	.4126	.2504	.3268	.3354	.3474	.4089	.5384	.4422
55	.3540	.1615	.1703	.2952	.2492	.3023	.3401	.4652
56	.4293	.2396	.2293	.3457	.3001	.3337	.2289	.4369
57	.3145	.1417	.1670	.2716	.2394	.3326	.3185	.3930
58	.3836	.1969	.1656	.3276	.3064	.3899	.3688	.4295
59	.4244	.1887	.1891	.3175	.2776	.3647	.3086	.4016
60	.3543	.1698	.2064	.2856	.2635	.3760	.3853	.3750
61	.3618	.1489	.1802	.2706	.2424	.3574	.3018	.3712
62	.2464	.1395	.1180	.2673	.2374	.2577	.4533	.4134
63	.3271	.1853	.2038	.3186	.2710	.2939	.4927	.4753
64	.3303	.1793	.1975	.2691	.2064	.1648	.5308	.4831
65	.4552	.2916	.2786	.4325	.3569	.2670	.4856	.4470
66	.6127	.4084	.3602	.3670	.3469	.4347	.5943	.4610
67	.5115	.3121	.2768	.4063	.3878	.4920	.4782	.3634
68	.3281	.1607	.1964	.2924	.2526	.3235	.3216	.2780
69	.3725	.2323	.2625	.3819	.3226	.3982	.5821	.5538
70	.5256	.4043	.3808	.4458	.3644	.4262	.6021	.5391
71	.0000	.1669	.1929	.3549	.3014	.3478	.3966	.4657
72	.1669	.0000	.0350	.1132	.0939	.1979	.2527	.3015
73	.1929	.0350	.0000	.1353	.1271	.2230	.2752	.3554
74	.3549	.1132	.1353	.0000	.0374	.1421	.3596	.3652
75	.3014	.0939	.1271	.0374	.0000	.0982	.3472	.3485
76	.3478	.1979	.2230	.1421	.0982	.0000	.4879	.5320
77	.3966	.2527	.2752	.3596	.3472	.4879	.0000	.2232
78	.4657	.3015	.3554	.3652	.3485	.5320	.2232	.0000

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES