THE ISLAND MODEL OF POPULATION DIFFERENTIATION: A GENERAL SOLUTION

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ABSTRACT

The island model deals with a species which is subdivided into a number of discrete finite populations, races or subspecies, between which some migration occurs. If the number of populations is small, an assumption of equal rates of migration between each pair of populations may be reasonable approximation. Mutation at a constant rate to novel alleles may also be assumed.——A general solution is given for the process of population divergence under this model following subdivision of a single parental population, expressed in terms of the observed average frequency of heterozygotes within and between subpopulations at a randomly chosen set of independently segregating loci. No restriction is imposed on the magnitude of the migration or mutation rates involved, nor on the number of populations exchanging migrants.——The properties of two fundamental measures of genetic divergence are deduced from the theory. One is a parameter related to ϕ, the coefficient of kinship, and the other, γ, measures the rate of mutational divergence between the sub-populations.

THE process of genetic differentiation in a subdivided population due to mutation, migration and random genetic drift, has recently been discussed by a number of authors (BODMER and CAVALLI-SFORZA 1968; MAYNARD SMITH 1970; IMAIZUMI *et al.* 1970; MARUYAMA 1970). The basic theoretical models involved in these studies are (*i*) the *island model*, in which each island exchanges genes equally with every other island; (*ii*) *stepping stone* models, which assume the rate of migration between colonies to be a function of the distance between them; (*iii*) models of *isolation by distance*, which deal with populations uniformly distributed throughout a continuum, with individual migration defined by a continuous probability distribution; and (*iv*) a *migration matrix* model, designed to deal with a general migration pattern involving a finite number of colonies. Renewed interest in these models has been stimulated by the discovery of extensive allozyme variability in natural populations of Drosophila, mice and man (LEWONTIN 1967; HARRIS 1969), and by suggestions that selectively neutral mutant alleles may be largely responsible for the observed levels of heterozygosity in these species (KIMURA 1969; KING and JUKES 1969).

Of the basic models, the island model is the most realistic for the study of differences in allelic frequencies between the major racial groups of man or the races and subspecies of other organisms, and for tests of the compatibility of

these differences with the neutral allele hypothesis. WRIGHT (1943) defined the island model to be one "in which the total population is assumed to be divided into subgroups, each breeding at random within itself, except for a certain proportion of migrants drawn at random from the whole". He dealt only with the case of a large number of subgroups in equilibrium, and MAYNARD SMITH (1970) and MARUYAMA (1970) have recently extended the theory to deal with the equilibrium structure of an arbitrary number of colonies. The present paper deals with the complete process of population divergence, providing expectations for the mean frequency of heterozygotes within populations, and in population hybrids, at a randomly chosen set of independently segregating loci.

If the number of races or subspecies is small, the assumption of equal and constant migration rates between each pair of such subgroups may be a reasonable approximation. Mutation at a constant rate to alleles not currently represented in the species can also be assumed, in keeping with modern concepts of the nature of the mutational process (CROW 1969), leading to non-zero mean levels of heterozygosity at equilibrium. With these assumptions, two fundamental measures of the rate of genetic divergence can be defined in terms of the mean frequency of heterozygotes within and between populations. One is a parameter related to ϕ, the coefficient of kinship, and the other, γ, measures the rate of mutational divergence between the populations (LATTER 1972).

1. THE MODEL AND RECURRENCE RELATIONS

The theory deals with a diploid monoecious species subdivided into k populations each of effective size N. The gene pool of the jth population is supposed to contain a proportion $1-m$ of gametes derived at random from adults resident in the jth population in the previous generation, and a proportion $m/(k-1)$ of gametes derived at random from adults resident in each of the remaining $k-1$ populations. Random mutation at a rate μ per generation gives rise to an average of $2N\mu$ novel alleles per locus in each population. All alleles are considered to be selectively neutral. We consider arbitrary values of $k > 1$, $0 \leqslant \mu \leqslant 1$, and $0 \leqslant m \leqslant (k-1)/k$. It is convenient at the outset to redefine the migration parameter as

$$m' = mk/(k-1) \tag{1}$$

where the possible range of values of the parameter is $0 \leqslant m' \leqslant 1$. The value $m' = 1$ corresponds to panmixia involving all Nk breeding individuals.

Let p_{ij} denote the frequency of allele A_i in the gene pool of the jth population at time t. Progress from one generation to the next can conveniently be considered in two steps: (i) a random sampling of $2N$ gametes from the gene pool of the jth population, giving a frequency of A_i among the sample individuals equal to

$$p_{ij}^* = p_{ij} + \delta_{ij} \tag{2}$$

where δ_{ij} is a random variable with zero mean and variance $p_{ij}(1-p_{ij})/2N$; and (ii) mutation and migration to give a frequency of A_i in the following generation of

$$p'_{ij} = (1-\mu) \; [(1-m) \; p^*_{ij} + m\bar{p}^*_{ij}] \tag{3}$$

where

$$\bar{p}^*_{ij} = \frac{1}{(k-1)} \sum_{h \neq j} p^*_{ih} \; .$$

Corresponding to these two steps, the following expressions for the expected frequency of heterozygotes can be derived. Let H denote the mean frequency of heterozygotes prior to random sampling, *i.e.*,

$$H = 1 - \frac{1}{k} \sum_j \sum_i p^2_{ij} \tag{4}$$

and let H_B represent the corresponding frequency of heterozygotes in the set of all possible hybrid populations, *i.e.*,

$$H_B = 1 - \frac{1}{k(k-1)} \sum_j \sum_{h \neq j} \sum_i p_{ij} \, p_{ih} \tag{5}$$

so that

$$H_B - H = \frac{1}{k(k-1)} \sum_j \sum_{h \neq j} \sum_i \tfrac{1}{2} (p_{ij} - p_{ih})^2 \tag{6}$$

Let H^*, H^*_B and H', H'_B also be defined by equations 4 and 5, when the frequencies p_{ij}, p_{ih} are replaced by p^*_{ij}, p^*_{ih} and p'_{ij}, p'_{ih} respectively. Then

$$E(H^*) = H(1 - \frac{1}{2N}) \tag{7}$$

and

$$E(H^*_B - H^*) = H_B - H + \frac{H}{2N}. \tag{8}$$

Similarly it can be shown that

$$E(H') = 1 - (1-\mu)^2 \; [(1-H^*) - (H^*_B - H^*)m(2-m')] \tag{9}$$

and

$$E(H'_B - H') = (1-\mu)^2 \; (1-m')^2 \; [H^*_B - H^*] \tag{10}$$

Note that for k indefinitely large and $\mu = 0$, equations 9 and 10 are equivalent to the familiar recurrence relation (WRIGHT 1951)

$$F' = (1-m)^2 \; [\frac{1}{2N} + (1 - \frac{1}{2N})F].$$

Equations 7–10 give expectations over repeated passages from generation $t \to t+1$, for a single locus with current levels of heterozygosity specified by H and H_B. However, the equations are linear in the variables H and H_B, and hence may also be used to predict changes in the average levels of heterozygosity observed over a large sample of independently segregating loci. Note that identical recurrence relations expressed in terms of coefficients of kinship can be derived from equation 1 of IMAIZUMI, MORTON and HARRIS (1970). The expres-

sions given by MARUYAMA (1970) appear to be in error because of the omission of a term in calculating the probability of sampling two genes from the same population.

2. GENETIC DIVERGENCE AFTER POPULATION SUBDIVISION

In this section we obtain a general algebraic solution for the continuous process of population differentiation, following splitting of a parental population into k identical sub-populations each of effective size N (generation 0). Let $x = H_B - H$, and $y = H$, with initial values $x_0 = 0$, and y_0. The recurrence relations 7–10 can then be written

$$x' = (1-\mu)^2 (1-m')^2 [x + \frac{y}{2N}]$$ (11)

and

$$1-y' = (1-\mu)^2 [(1-y+\frac{y}{2N}) - m(2-m') (x+\frac{y}{2N})]$$ (12)

Progress from one generation to the next can be expressed in terms of the partial differential equations

$$\frac{\partial x}{\partial t} = ax + by \quad ; \quad \frac{\partial y}{\partial t} = dx + ey + f$$

where

$$a = (1-\mu)^2(1-m')^2 - 1$$
$$b = \frac{1}{2N} (1-\mu)^2(1-m')^2$$
$$d = (1-\mu)^2 m'(2-m') (1 - \frac{1}{k})$$
$$e = -\mu(2-\mu) - \frac{(1-\mu)^2}{2N} [1-m'(2-m')(1 - \frac{1}{k})]$$
$$f = \mu(2-\mu)$$

The Laplace transform method of solution (LAPWOOD 1968) leads to the following algebraic equations

$$p\bar{x} \quad\quad = a\bar{x} + b\bar{y}$$
$$p\bar{y} - y_0 \quad = d\bar{x} + e\bar{y} + f/p$$

where $\bar{x}(p)$, $\bar{y}(p)$ denote the Laplace transforms of $x(t)$, $y(t)$ respectively. The general solutions are then obtained by inversion of the expressions

$$\bar{x} = \frac{b(y_0 p + f)}{p [(p-a)(p-e)-bd]}$$
$$\bar{y} = \frac{(p-a)(y_0 p + f)}{p [(p-a)(p-e)-bd]}$$

to give

$$x(t) = \frac{b}{a}(\alpha_1 - \alpha_2)^{-1} \Big[(\alpha_2 \hat{y} - a y_0) \, [1 - exp(\alpha_1 t)]$$

$$- (\alpha_1 \hat{y} - a y_0) \, [1 - exp(\alpha_2 t)] \Big] \tag{13}$$

and

$$y(t) = y_0 + (\alpha_1 - \alpha_2)^{-1} \Big[\{-\alpha_2 (\hat{y} - y_0) - (f + e y_0)\} \, [1 - exp(\alpha_1 t)]$$

$$+ \{\alpha_1 (\hat{y} - y_0) + (f + e y_0)\} \, [1 - exp(\alpha_2 t)] \Big] \tag{14}$$

where

$$\alpha_1, \alpha_2 = \tfrac{1}{2} \left[(a+e) \pm \sqrt{(a-e)^2 + 4bd} \right] \tag{15}$$

and $\hat{y}$ denotes the equilibrium value of y, given by

$$\hat{y} = \frac{-af}{ea - bd} \tag{16}$$

Similarly, the equilibrium value of x, denoted by $\hat{x}$, is

$$\hat{x} = \frac{bf}{ea - bd} \tag{17}$$

Equilibrium levels of heterozygosity

MAYNARD SMITH (1970) has determined the equilibrium values of H and H_B for this model, provided m', μ and N^{-1} are all small. The foregoing general solutions for H and H_B as a function of time allow us to give the following equilibrium relationships for $k > 1$, $0 \leqslant m' \leqslant 1$, $0 < \mu \leqslant 1$. Equations 16 and 17 lead to

$$\frac{\hat{y}}{\hat{x}} = -\frac{a}{b}$$
$$= 4N\lambda$$

where

$$\lambda = \tfrac{1}{2} \left[(1-\mu)^{-2}(1-m')^{-2} - 1 \right] \tag{18}$$

so that

$$\frac{\hat{H}}{\hat{H}_B} = \frac{4N\lambda}{1 + 4N\lambda} \tag{19}$$

The second relationship of interest involves the ratio

$$\hat{\gamma} = \frac{\hat{H}_B - \hat{H}}{1 - \hat{H}}$$

$$= \frac{bf}{ea - bd + af}$$

$$= \left[1 + \left\{ \frac{m'(2-m')}{k\mu(2-\mu)(1-m')^2} \right\} \right]^{-1} \tag{20}$$

and expressions 19 and 20 lead to the equation

$$\hat{H} = \frac{4N\lambda\hat{\gamma}}{1 + 4N\lambda\hat{\gamma}} \tag{21}$$

In the early generations of the process of genetic differentiation following subdivision, *i.e.* for $\frac{t}{2N} \ll 1$, we may replace terms of the form $1 - exp(\alpha t)$ in equations 13 and 14 by $-\alpha t$, leading to

$$x(t) = \gamma_0\, bt \tag{22}$$
$$\gamma(t) = \gamma_0 + (f + e\gamma_0)t \tag{23}$$

3. AN APPROXIMATE SOLUTION

In this section, expressions are derived which describe the continuous process of population differentiation for a restricted range of values of the parameters. The necessary conditions for the equations to give useful predictions are:

    (*i*)   that μ, m', N^{-1} should all be sufficiently small for squares
         and products of these quantities to be ignored; and
   (*ii*)   that $16Nm'/k$ should be small by comparison with $(1 + 4Nm')^2$.

Given (*i*), the expression under the square root sign in equation 15 is given approximately by

$$(a - e)^2 + 4bd = \frac{1}{(2N)^2}\, [(1 + 4Nm')^2 - 16\frac{Nm'}{k}]$$

and if $16Nm'/k$ is small by comparison with $(1 + 4Nm')^2$, equation 15 becomes

$$\alpha_1, \alpha_2 = \frac{1}{2}\left[(a + e) \pm \frac{1}{2N} (1 + 4Nm')\, [1 - \frac{8Nm'}{k(1 + 4Nm')^2}] \right] \tag{24}$$

$$= -\frac{1}{2N}\left[1 + 4N\lambda - \frac{4Nm'}{k(1 + 4Nm')}\ ,\ 4N\mu + \frac{4Nm'}{k(1 + 4Nm')} \right] \tag{25}$$

where $\lambda = \mu + m'$. Equations 13 and 14 can then be evaluated by use of the following expressions:

$$\alpha_1 - \alpha_2 = -\frac{1}{2N}\left[1 + 4Nm' - \frac{8Nm'}{k(1 + 4Nm')} \right] \tag{26}$$

$$a = -2\lambda;\ \ b = 1/(2N);\ \ d = 2m'(1 - 1/k);\ \ e = -\frac{1}{2N}(1 + 4N\mu);\ \ f = 2\mu; \tag{27}$$

together with equations 16 and 25.

    The approximate equilibrium levels of heterozygosity are given by equations 19 and 21, with λ set equal to $\mu + m'$, and $\hat{\gamma}$ evaluated by the expression

$$\hat{\gamma} = \left[1 + \frac{m'}{k\mu} \right]^{-1} \tag{28}$$

For k indefinitely large, the equilibrium level of heterozygosity becomes

$$\hat{H} = \frac{4N\lambda}{1 + 4N\lambda}$$

as given by WRIGHT (1943). In the absence of migration between populations ($m' = 0$), the equilibrium mean frequency of heterozygotes is

$$\hat{H} = \frac{4N\mu}{1 + 4N\mu}$$

for arbitrary k (KIMURA and CROW, 1964), and the approach to equilibrium is given by

$$x(t) = (1 - \gamma_0) [1 - exp(-2t\mu)] - (\hat{\gamma} - \gamma_0) \{1 - exp [-\frac{t}{2N} (1 + 4N\mu)]\}$$

and

$$\gamma(t) - \gamma_0 = (\hat{\gamma} - \gamma_0) \{1 - exp [-\frac{t}{2N} (1 + 4N\mu)]\}$$

For $\mu = 0$, the equations become (MALÉCOT, 1948)

$$\gamma(t) = \gamma_0 [exp (-\frac{t}{2N})] .$$

The initial rate of genetic divergence

For small values of $t/2N$, it may be deduced from equations 22, 23 and 27 that

$$x(t) = \gamma_0 \frac{t}{2N}$$

and

$$\gamma(t) = \gamma_0 (1 - \frac{t}{2N}) + 2\mu t (1 - \gamma_0).$$

A measure of genetic divergence, which is closely related to the coefficient of kinship, can then be *defined* as

$$\phi^*(t) = \frac{x(t)}{x(t) + y(t)}$$

$$= 1 - \frac{E(H)}{E(H_B)} \tag{29}$$

with an equilibrium value given by equation 19 as

$$\hat{\phi}^* = (1 + 4N\lambda)^{-1} \tag{30}$$

and an initial rate of change given by

$$\phi^*(t) = \frac{t}{2N} \left[1 + 2t\mu \left(\frac{1 - \gamma_0}{\gamma_0}\right)\right]^{-1}$$

$$\sim \frac{t}{2N} \tag{31}$$

The second parameter of importance is the measure of genetic distance defined by LATTER (1972), viz.,

$$\gamma(t) = \frac{x(t)}{1 - \gamma(t)}$$

$$= \frac{E(H_B - H)}{1 - E(H)} \tag{32}$$

with an equilibrium value given by equation 28 and an initial rate of change given by

$$\gamma(t) = \frac{t}{2N} \left(\frac{\gamma_0}{1 - \gamma_0}\right) \left[1 - 2\mu t + \left(\frac{\gamma_0}{1 - \gamma_0}\right) \frac{t}{2N}\right]$$

If the average level of heterozygosity in the parental population prior to subdivision is represented as

$$\gamma_0 = \frac{4k^* N\mu}{1 + 4k^* N\mu}$$

the expression for $\gamma(t)$ in the early generations becomes

$$\gamma(t) = 2k^* t\mu \left[1 + 2t\mu (k^* - 1)\right]^{-1}$$
$$\sim 2k^* t\mu \tag{33}$$

provided $k^* t\mu$ is small by comparison with unity.

4. DISCUSSION

Two parameters emerge from the preceding analysis as informative measures of the degree of genetic differentiation among populations, viz. (*i*) the parameter $\phi^*(t)$ defined by equation 29, which is related to the coefficient of kinship, and (*ii*) the measure of mutational divergence $\gamma(t)$ given by equation 32. In practical applications of these two formula, the expectations concerned should be taken to denote mean levels of heterozygosity over a large sample of independently segregating loci. In the calculation of ϕ^*, loci which are monomorphic for the same allele in all populations need not be included in the sample, since they make no numerical contribution to the ratio $E(H)/E(H_B)$. This is not true of estimates of γ, which should be based on gene frequencies at a random sample of both monomorphic and polymorphic loci. Predictions based on equations 20, 28 or 33 cannot be expected to hold for gene frequency data derived from polymorphic loci alone.

The parameter ϕ^* has been shown to have an equilibrium value under general conditions of $(1 + 4N\lambda)^{-1}$, where $\lambda = \mu + m'$ for small values of both μ and m'. Note that ϕ^* is identical with ϕ, the coefficient of kinship, for the pure drift model, $\mu = m' = 0$. By contrast, γ reaches an equilibrium which is independent of N, being a function only of the pressure of mutation tending to differentiate the populations concerned, and the opposing effects of migration (equations 20,
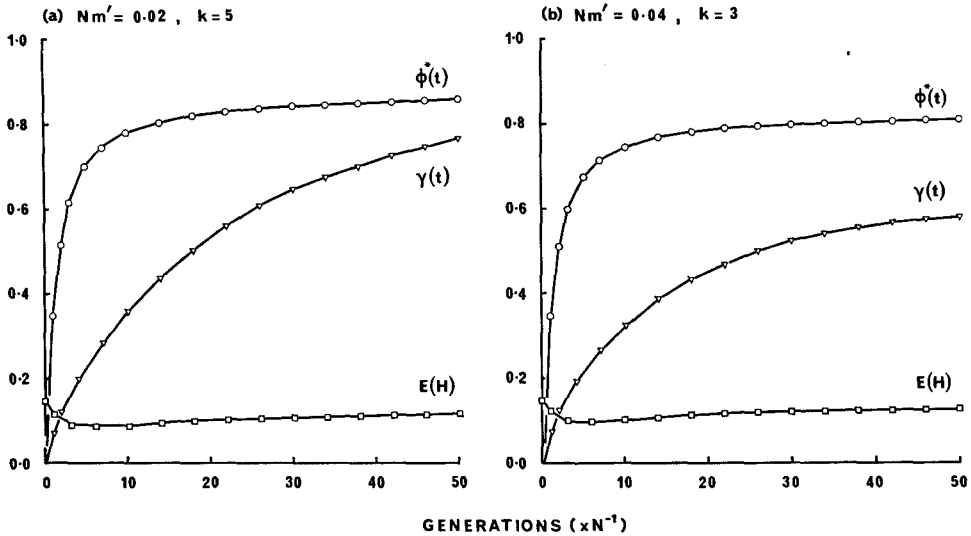
FIGURE 1.—Predicted changes in two measures of genetic divergence following population subdivision, based on equations 13–17. The parameter ϕ^* is defined by equation 29, and is closely related to the coefficient of kinship; γ is a measure of mutational divergence defined by equation 32 (cf. LATTER 1972). The initial level of heterozygosity assumed is $\gamma_0 = 0.15$. In both regimes $N = 2000$ and $N\mu = 0.02$, where N denotes the effective population size of each of k subspecies, races or island populations exchanging migrants at a rate m per generation. The mutation rate to novel alleles is μ per generation. $E(H)$ denotes the mean level of heterozygosity over a set of independently segregating loci.

28). The two parameters also differ intrinsically in their initial behavior following population subdivision. Provided the conditions set out in the first paragraph of section 3 are satisfied, ϕ^* increases initially at a rate proportional to $1/2N$ (equation 31), while the initial rate of increase of γ is proportional to μ (equation 33).

The complete process of change in ϕ^* and γ is illustrated in Figure 1 for a rate of migration equal to the mutation rate (1a), and one equal to twice the mutation rate (1b). The parameters were chosen to give levels of heterozygosity within populations of the order of 0.10–0.15 throughout. The initial rate of change of ϕ^* given by equation 31, and that for γ predicted by equation 33, are realized in both instances up to $t = 0.1N$, with errors less than 4%. The initial level of heterozygosity of $\gamma_0 = 0.15$ corresponds to a value of k^* in equation 33 of 2.2, so that the parental population is one with an average level of heterozygosity appropriate to a population in equilibrium at a size of 4,400. The model envisages a subsequent rapid increase in numbers, followed by subdivision into units of size 2,000 at generation $t = 0$.

The data of Table 1 provide a check on the algebra leading to the derivation of equations 13–17, and indicate the accuracy of the approximate solution based on equations 25–28. The two regimes concerned are identical with those of Figure 1, except that $N = 200$ is used instead of $N = 2000$. The calculations indicate that

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TABLE 1

Predicted heterozygosity and genetic divergence between sub-populations

The three values in each cell of the table are obtained by the use of (*i*) the recurrence relations 11, 12; (*ii*) the general solution given by equations 13–17; and (*iii*) the approximate solution based on equations 25–28.

Regime** Nm'	k	Generations (t)	Solution	Predicted heterozygosity and genetic divergence†			
				$E(H)$	$E(H_B\text{-}H)$	$\phi^*(t)$	$\gamma(t)$
0.02	5	N	(*i*)	0.1192	0.0639	0.3488	0.0725
			(*ii*)	0.1192	0.0638	0.3486	0.0725
			(*iii*)	0.1192	0.0638	0.3487	0.0725
		$10N$	(*i*)	0.0913	0.3253	0.7809	0.3579
			(*ii*)	0.0913	0.3252	0.7808	0.3579
			(*iii*)	0.0913	0.3249	0.7807	0.3576
		$50N$	(*i*)	0.1137	0.6740	0.8557	0.7605
			(*ii*)	0.1137	0.6740	0.8557	0.7604
			(*iii*)	0.1136	0.6737	0.8557	0.7601
0.04	3	N	(*i*)	0.1198	0.0627	0.3435	0.0712
			(*ii*)	0.1198	0.0626	0.3432	0.0711
			(*iii*)	0.1198	0.0625	0.3430	0.0711
		$10N$	(*i*)	0.0997	0.2887	0.7433	0.3207
			(*ii*)	0.0997	0.2887	0.7433	0.3207
			(*iii*)	0.0995	0.2868	0.7423	0.3185
		$50N$	(*i*)	0.1239	0.5062	0.8034	0.5777
			(*ii*)	0.1239	0.5062	0.8034	0.5777
			(*iii*)	0.1237	0.5054	0.8033	0.5767

** $N = 200$, $N\mu = 0.02$, $\gamma_0 = 0.15$, together with the specified values of Nm' and k.

† The measures are defined respectively by equations 4, 6, 29 and 32.

for μ and m' small, quite accurate predictions may be obtained from equations 25–28 with 16 Nm'/k as much as one-sixth the magnitude of $(1 + 4Nm')^2$. Equations 13–17 give precisely the values obtained by repeated application of the recurrence relations 11 and 12.

It has been indicated previously that this analysis of population differentiation according to the island model is of potential interest in the study of the major racial groups of man and other species, where the number of groups may be small, and migration rates are low. The measures of genetic divergence defined in the paper have the advantage of being simple functions of the mean levels of heterozygosity within the groups concerned, and the predicted levels of heterozygosity in the inter-population hybrids. The behavior of these parameters by comparison with others in common use is discussed elsewhere (LATTER 1973).

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