THE IMPACT OF RANDOM AND LINEAL FISSION ON THE
GENETIC DIVERGENCE OF SMALL HUMAN GROUPS:
A CASE STUDY AMONG THE YANOMAMA

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ABSTRACT

Most of the genetic divergence that currently separates populations of
Homo sapiens must have arisen during that long period when the local
village (or band) was the basic unit of biological evolution. Studies of tribally
intact Amerindian groups exhibiting such small-group organization have
demonstrated marked genetic divergence between nearby villages. Some of
this genetic radiation can be attributed to the effects of random genetic drift
over time within these small demes. Some of it, however, might be better
ascribed to the consequences of nonrandom genetic assortment at the time of
village fission, a recurring event for such groups. Even random genetic assortment
at the time of fission would lead to some genetic divergence, due to the
finite size of the parent gene pool. We term the genetic consequences of random
assortment the random fission effect. Routinely, village fission occurs along
family lines, leading to even greater genetic divergence between the daughter
villages. We use the term lineal fission effect to describe the genetic conse-
quences of nonrandom assortment and contrast these results with those
derived from random assortment.—A formal treatment of random and lineal
fission effects is developed, first for the single-locus case, then for the multiple-
locus extension. Using this formulation, three Yanomama fission events were
examined. Fission in the Yanomama often involves a great deal of mutual
hostility between the two factions, so that subsequent gene flow between the
two daughter villages is minimal. The first two examples are typical of the
Yanomama behavior norm, and are accompanied by a minimum of subsequent
gene flow between the daughter villages. In these two cases, the observed di-
vergence values are very large and are also very unlikely under random fis-
sion. The lineal fission effect is pronounced. The net impact of lineal fission
is to reduce the effective size of the village at the time of fission by a factor of
four, relative to expectation from random fission. The third example, however,
involved an unusually amicable split of a village, followed by free genetic ex-
change between the fission products. This "friendly fission" yields an observed
divergence value not much in excess of the expectation from random fission.
—The long-term consequences of such fission bottlenecks in effective popu-
lation size are discussed for both intra- and inter-tribal genetic diversity. It
appears that the rate of genetic divergence for tribal and subtribal groups
may have been somewhat greater than would be expected from classical drift
arguments.

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THE origin, amount and significance of the genetic divergence that separates populations of *Homo sapiens* have been matters of enduring anthropological interest for more than a century. Quite apart from a continuing controversy concerning the similarities that bind us and the differences that divide us (e.g., Lewontin 1972; Nei and Roychoudhury 1972, 1974; Cavalli-Sforza 1974; Mitton 1977; Smouse and Spielman 1977), our interest is fanned by continuing confusion about how we got to be the way we are. It is obvious that most of the diversity that currently separates populations must have arisen before *H. sapiens* became a cosmopolitan and collectivist organism, i.e., during that long period when the local village (or band) was the basic unit of hominid social organization. This consideration has been a prime motivation for our own studies (cf., Neel 1976, 1978; Smouse 1981) on modern day "primitive" groups. (We use the appellation "primitive" advisedly and mean to imply tribal groups whose social organization and cultural level are still somewhat reminiscent of that which must have characterized the whole species in the not too distant past.)

A notable characteristic of tribally intact and essentially unacculturated Amerindians is marked genetic divergence between villages, even between closely related villages (Ward and Neel 1970, 1976; Neel and Ward 1972; Spielman, Migliazza and Neel 1974; Spielman and Smouse 1976; Salzano *et al*. 1977; Smouse and Ward 1978). Even greater are the differences between tribes, some of which live in close proximity (Neel and Ward 1970; Smouse and Spielman 1977). Our results are consistent with those of other authors, working in other parts of the world (cf., Kirk *et al*. 1971; Friedlaender 1975; Szathmary and Ossenberg 1978), and extensive microdifferentiation within largely undisturbed tribal groups is a general finding (see, however, Harpending and Jenkins 1974). We have argued that much of this genetic divergence may be attributed to the stochastic aspects of tribal social organization, primarily small village size and complex demography (Neel *et al*. 1964; Chagnon *et al*. 1970; MacCluer, Neel and Chagnon 1971; Neel and Weiss 1975). Genetic drift is the rule in such populations, and has almost surely played a significant role in the evolution of tribal and subtribal diversity.

There is an additional set of social factors, however, that received insufficient attention in the past and that should also contribute (perhaps strongly) to further genetic divergence. A critical feature of any rainforest Amerindian village, either as a social unit or as a gene pool, is that it has a half-life of no more than about two generations; villages periodically undergo fission. The genetic products of the fission usually become independent villages, although if one fragment is too small to form a stable social unit, or if it comes upon hard times, it may fuse with a pre-existing village in the same general area. It is probable that fission contributes substantially, perhaps even disproportionately, to the genetic differentiation between the resulting daughter villages.

There are two aspects of fission that warrant comment. First, the sampling involved in the construction of daughter villages from an already small (125 < N < 250) parent village should contribute an initial genetic disparity between them; depending upon the subsequent fate of the daughter villages, this initial
divergence may be more significant that the sheer genetic drift that will occur before the next fission. To the extent that social fission is genetically random, we use the term *random fission effect* to denote the divergence produced by the sampling aspects of the process.

Second, fission is usually not random with respect to genotype (Neel 1967; Chagnon 1968, 1974, 1975, 1979; Fix 1975, 1979). For the Yanomama, the subject of this paper, intravillage political alliances have a strong familial component. A village normally contains no more than four or five extended lineages, each headed by a socially prominent male. These various lineages are linked by marriage, and everyone within the village is related to one extent or another, sharing at least some common ancestors not more than a few generations back. As a village grows, internal social tensions develop; the overt manifestations of such tensions is a struggle for "headmanship" between a pair of prominent men. Eventually, the struggle breaks into the open, and one of the protagonists departs. With him go his political adherents: his wives and their relatives, his brothers and children, and their relatives. Everyone in the village is somewhat related, and the fission cuts across family lines. There is, nevertheless, a strong tendency for genetic cohesion *within* each of the factions. The consequence is that the genetic divergence *between* the two groups should be enhanced, relative to the divergence expected from a genetically random fission. Neel (1967) has termed this enhanced divergence the *lineal (fission) effect*.

The degree of antipathy that persists between the two splinter villages will depend on the detailed circumstances in any given instance. In some cases, the daughter villages will maintain reasonably amicable relations, subsequently exchanging members. In such cases, the initial genetic divergence will be partially diluted by migration. In other cases, the split will lead to prolonged estrangement and minimal gene flow (Chagon 1967). In these cases, the divergence caused by fission is "captured".

The processes we have described in detail for the Yanomama are similar (in broad outline) to those we have observed for other rainforest tribal groups in South America, notably the Xavante (Neel et al. 1964; Neel 1967) and the Makiritare (Ward and Neel 1970; Arvello-Jimenez 1971), and it seems probable that such behavioral components of village formation and dissolution are fairly general social correlates of swidden agriculture. Since fission occurs with some regularity, its consequences for genetic radiation of these small gene pools are potentially important.

Some of the theoretical implications of fission have been dealt with elsewhere (e.g., Rothman, Sing and Templeton 1974; Neel and Thompson 1978; Thompson and Neel 1978), but very little attention has been directed toward an assessment of their actual impact on human genetic variation; most of the available evidence is indirect (e.g., Giles, Walsh and Bradley 1966; Morton et al. 1972; Fix 1975). In the course of our fieldwork among the Yanomama of southern Venezuela and northern Brazil, three pairs of villages that had resulted from recent fission events were encountered. In each of these documented cases, the approximate population of the parent village has been reconstructed.
The purposes of this paper are threefold. (1) We shall develop a formal treatment of the genetic consequences of village fission. (2) We shall determine how much genetic divergence can be expected from genetically random fission. (3) We shall assess the randomness of Yanomama fission from these three example cases, and shall quantify the magnitude of the lineal effect. Having dealt with these matters for the Yanomama, we shall then indicate how this same pattern of social behavior might have influenced the evolutionary radiation of *Homo sapiens* in the lowland rainforests of South America.

**MATERIALS AND METHODS**

*Populations studied:* The first pair of villages, Ironasi (11G) and Mowaraoba (11HI), are the derivatives of the fission, in 1968, of a village that we shall designate Ironasi-Mowaraoba (11GHI). Subsequent to this fission, which was of the usual Yanomama sort, the two daughter villages were situated about a day's travel apart on the headwaters of the Mavaca River. Fieldwork was conducted in 1969, a year later, and the sample sizes were 38 for 11G and 124 for 11HI. [These samples, of course, do not include those members of the parent village who died subsequent to the split (1968) but before our arrival in 1969]. The second pair of villages, Mömariböwei (03D) and Reyaböböwei (03H/11J are the fission products of a parent village that we shall designate Mömariböwei-Reyaböböwei (03DH/11J). Prior to the fission in 1960, this parent village was located near the mid-course of the Mavaca River. Fieldwork in these villages was conducted in 1966 and in 1969, at which times the villages were located about a day's walk apart. Sample sizes (for surviving participants of the fission) were 65 for 03D and 67 for 03H/11J. The daughter villages from both of these fission events were not estranged at the time of sampling, but gene flow had been nil.

The third pair of villages, Ora (03A) and Koro (03B), are derivatives of a single ancestral village that we shall arbitrarily designate as Ora-Koro (03AB), and that fissioned in 1961. At that time, the parent village was located near a missionary home, at the confluence of the Mavaca and Orinoco Rivers. Both the mission and the village were located on the upriver side of the confluence. A second missionary entered the field in 1961 and built his home at the same location, but on the downriver side of the confluence. (It is customary to man each missionary post with two and sometimes three families, allowing for periodic rotation of staff.) At that juncture, the existing village split, presumably on the basis of a decision that there were greater benefits to be derived from close contacts with both missionaries. This “friendly fission” was rather atypical of Yanomama fission in general, and the resulting geographic proximity and amicable relations between the daughter villages permitted easy exchange of members subsequent to the split. At the time fieldwork was conducted in 1966, five years after the fission, most families extended through both villages, and the permanent residence of some family units was none too clear. The “split” we have observed thus reflects the countervailing result of both fission and gene flow processes. We may anticipate that the Ora-Koro divergence is less than is the norm just subsequent to Yanomama fission. The sample sizes (for surviving participants of the fission) are 68 for 03A and 34 for 03B. Each of these situations is a bit different, but each represents a natural experiment of the sort required to assess the real impact of village fission on the genetic divergence of small human groups.

*Genetic markers employed:* We have assayed each of the sampled individuals for 35 blood group, serum protein and erythrocyte enzyme systems. The results of these genetic determinations have been reported elsewhere *in extenso* (Gereshowitz et al. 1972; Weitkamp et al. 1972; Weitkamp and Neel 1972; Tantis et al. 1973; Ward et al. 1975). Most of the loci examined are monomorphic (or nearly so) in these villages, and thus are of no use in assessing the genetic consequences of fission. A number of the polymorphic systems are characterized by alleles that exhibit dominance relations that create statistical difficulties for the treatment we shall describe. We shall therefore ignore all such loci here. We are left with seven co-dominant polymorphic systems. (*RhCc, RhEe, MN, Ss, Fy, Gc, Alb*). The two *Rh* markers may be treated
either as resulting from four alleles at a single locus or as resulting from two alleles at each of two closely linked loci. Similar comments are appropriate for the MN and Ss systems (cf., Smouse and Neel 1977; Smouse and Ward 1978). Following Spielman and Smouse (1976), we have chosen to adopt the two-locus approach, but we find it necessary to allow for the resulting nonindependence between linked marker sets in our analysis. For the samples used here, we list the numbers of the various single-locus genotypes in Table 1. We have used only those individuals assayed for all seven systems (the vast majority of individuals sampled in the field.)

SINGLE-LOCUS DIVERGENCE

In this section, we shall devise a single-locus measure of the genetic divergence between daughter villages. We shall then use this measure to gauge the likely impact of random fission and to assess the actual impact of lineal fission. In the next section, we shall extend the analysis to the multiple-locus case.

The measure: Consider three co-dominant genotypes, say \( G_1 = Rh(CC) \), \( G_2 = RH (Cc) \) and \( G_3 = Rh(cc) \), present in numbers \( M_1, M_2 \) and \( M_3 \) in the parent village. In the first daughter village, these genotypes are present in numbers \( N_1, N_2 \) and \( N_3 \), while in the second daughter village, they are present in numbers

### TABLE 1

<table>
<thead>
<tr>
<th>Marker genotype</th>
<th>11Ghi</th>
<th>11HII</th>
<th>03DHH/11J</th>
<th>03AAB</th>
<th>03BHH</th>
<th>03AB</th>
<th>03BIB</th>
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<tr>
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<td>84</td>
<td>39</td>
<td>34</td>
<td>27</td>
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<td>14</td>
<td>34</td>
<td>23</td>
<td>28</td>
<td>32</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>NN</td>
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<td>6</td>
<td>3</td>
<td>5</td>
<td>9</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Ss-SS</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ss</td>
<td>9</td>
<td>28</td>
<td>11</td>
<td>25</td>
<td>12</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>ss</td>
<td>29</td>
<td>95</td>
<td>53</td>
<td>41</td>
<td>55</td>
<td>30</td>
<td></td>
</tr>
<tr>
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<td>30</td>
<td>114</td>
<td>64</td>
<td>65</td>
<td>56</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Cc</td>
<td>6</td>
<td>10</td>
<td>1</td>
<td>2</td>
<td>12</td>
<td>6</td>
<td></td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Rh-EE</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ee</td>
<td>14</td>
<td>48</td>
<td>23</td>
<td>23</td>
<td>25</td>
<td>7</td>
<td></td>
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<tr>
<td>ee</td>
<td>21</td>
<td>70</td>
<td>41</td>
<td>40</td>
<td>42</td>
<td>25</td>
<td></td>
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<tr>
<td>Fy-aa</td>
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<td>72</td>
<td>22</td>
<td>28</td>
<td>31</td>
<td>19</td>
<td></td>
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<tr>
<td>ab</td>
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<td>47</td>
<td>36</td>
<td>29</td>
<td>24</td>
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<tr>
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<td>10</td>
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<td></td>
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<td>Gc-11</td>
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<td>102</td>
<td>58</td>
<td>39</td>
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<td>21</td>
<td>13</td>
<td>20</td>
<td>7</td>
<td>20</td>
<td>11</td>
<td>3</td>
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<tr>
<td>22</td>
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<td>2</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td></td>
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<tr>
<td>Alb-NN</td>
<td>38</td>
<td>119</td>
<td>65</td>
<td>65</td>
<td>51</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>NY</td>
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<td>5</td>
<td>0</td>
<td>2</td>
<td>16</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>YY</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Sample size: 162 132 102
(M_1 - N_1), (M_2 - M_2) and (M_3 - N_3). We estimate the allelic frequencies of the parent village and the two fission fragments by

\[ \bar{p}_1 = \frac{2N_1 + N_2}{2N} = f_1(C) \]  
\[ \bar{p}_2 = \frac{2M_1 + M_2}{2M} = f_2(C) \]  
\[ \bar{p}_3 = \frac{2(M_1 - N_1) + (M_2 - N_2)}{2(M - N)} = f_2(C) \]

where \( M = M_1 + M_2 + M_3 \) and \( N = N_1 + N_2 + N_3 \) are the respective sizes of the parent and first daughter village, respectively. Given these allelic frequencies, we construct a "genetic distance" metric as a gauge of divergence; we prefer the \( \Delta \) measure of SMOUSE and SPIELMAN (1977), a measure that is closely related to the \( F_{ST} \) measure of WRIGHT (1951). The genetic distance between the two daughter villages is given by

\[ \Delta = \sqrt{\frac{(\bar{p}_1 - \bar{p}_2)^2}{S^2}} \]  
\[ S^2 = \frac{M_1(1 - \bar{p}_1)^2 + M_2(1/2 - \bar{p}_2)^2 + M_3(0 - \bar{p}_3)^2}{(M - 1)} \]

Equation (2b) is simply the (additive) genetic variance of the locus of interest within the parent village. Thus, genetic distance is the difference between the two daughter villages, relative to the variation available for the split in the parent village. Any particular split may be represented by a vector \((M, N) = (M_1, M_2, M_3, N_1, N_2, N_3)\) and implies a corresponding value of \( \Delta \).

**Random fission:** To assess the impact of random fission, we must determine the sampling distribution of \( \Delta \). Given a parent gene pool with \( M_1, M_2 \) and \( M_3 \) individuals of genotypes \( G_1, G_2 \) and \( G_3 \), a random sample of \( N \) individuals is drawn to construct the first daughter village. Sampling is without replacement; i.e., an individual removes his/her genotype from the available sampling pool upon leaving the village. The probability of obtaining a daughter village with \( N_1, N_2 \) and \( N_3 \) individuals of genotypes \( G_1, G_2 \) and \( G_3 \) (with \( N = N_1 + N_2 + N_3 \)) is given by the extended hypergeometric distribution

\[ Pr(N_1, N_2, N_3|M_1, M_2, M_3, N) = \frac{\begin{pmatrix} M_1 \\ N_1 \end{pmatrix} \begin{pmatrix} M_2 \\ N_2 \end{pmatrix} \begin{pmatrix} M_3 \\ N_3 \end{pmatrix}}{\begin{pmatrix} M \\ N \end{pmatrix}} \]  

for \( 0 \leq N_1 \leq M_1, 0 \leq N_2 \leq M_2, 0 \leq N_3 \leq M_3 \) and \( 0 < N < M \), and is zero otherwise.

This distribution is conditioned on the sizes of the two daughter villages, \( N \) and \( (M - N) \). The ecological and/or social factors influencing the size at which
a village is “ripe” for fission and the constraints on “viable size” for the daughter villages imply some probability distribution for \( N: (M - N)\). These processes are of interest in their own right (cf., CHAGNON 1975, 1979), but are still poorly understood. We shall thus ignore them here, taking \( N \) and \( (M - N) \) as given for any particular fission.

We have treated our samples as though they were the total populations of the daughter villages, just subsequent to the split. In fact, those individuals who died after the split, but before our arrival, are not included. We have sampled these villages intensively, but a few people are always missed. In addition, there is unavoidably some loss of individuals between field collection and the final analysis. What we have in practice is a two-stage sampling process. The first sampling phase is the fission itself; the second phase is the sampling of individuals from the daughter villages (just subsequent to the split) that reach final analysis. It can be shown that the distribution given as Eq. (3) is the correct formula for this two-stage process, provided that the second stage of sampling is genetically random. (See HALD 1960 for the two-class proof. The extension to multiple classes is obvious, but can be obtained from PES upon request.) As we have no reason to believe the second sampling phase to be other than random, our results should give an unbiased picture of the first stage (fission) sampling.

To construct a random distribution for \( \Delta \), we have computed the \( \Delta \) values for all possible fission vectors \((M,N)\)' that can be constructed from Table 1, using Eq. (2), and have weighted these \( \Delta \) values by their probabilities of occurrence, computed from Eq. (3). The results are presented in Table 2 for the Ironasi-Möwaroba (11GHI) fission. The Mömariböwe-Reyäboböwei (03DH/11J) and Ora-Koro (03AB) fissions yield similar results.

### Table 2

**Probability distribution for \( \Delta \) under random assortment during the fission of Ironasi-Möwaroba (11GHI) for each of seven marker loci**

<table>
<thead>
<tr>
<th>Range of ( \Delta )</th>
<th>( MN )</th>
<th>( St )</th>
<th>( Cc )</th>
<th>( Es )</th>
<th>( FY )</th>
<th>( Gc )</th>
<th>( Alb )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.00 - 0.05</td>
<td>0.1322</td>
<td>0.1659</td>
<td>0.1902</td>
<td>0.2412</td>
<td>0.2623</td>
<td>0.2745</td>
<td>0.4081</td>
</tr>
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<td>0.05 - 0.10</td>
<td>0.2504</td>
<td>0.3047</td>
<td>0.1959</td>
<td>0.1121</td>
<td>0.1192</td>
<td>0.1181</td>
<td>0.0000</td>
</tr>
<tr>
<td>0.10 - 0.15</td>
<td>0.2129</td>
<td>0.1185</td>
<td>0.1484</td>
<td>0.2024</td>
<td>0.2128</td>
<td>0.1257</td>
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</tr>
<tr>
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<td>0.1173</td>
<td>0.1566</td>
<td>0.1610</td>
<td>0.0913</td>
<td>0.1919</td>
<td>0.2495</td>
</tr>
<tr>
<td>0.20 - 0.25</td>
<td>0.0552</td>
<td>0.1531</td>
<td>0.0950</td>
<td>0.1166</td>
<td>0.1350</td>
<td>0.1333</td>
<td>0.2577</td>
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<tr>
<td>0.25 - 0.30</td>
<td>0.0552</td>
<td>0.0454</td>
<td>0.0908</td>
<td>0.0767</td>
<td>0.0865</td>
<td>0.0812</td>
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<td>0.0256</td>
<td>0.0282</td>
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<td>0.0431</td>
<td>0.0736</td>
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<td>0.0280</td>
<td>0.0173</td>
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<td>0.0199</td>
<td>0.0000</td>
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<td>0.0141</td>
<td>0.0080</td>
<td>0.0081</td>
<td>0.0114</td>
<td>0.0080</td>
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</tr>
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<td>0.0046</td>
<td>0.0000</td>
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<td>0.0013</td>
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</tr>
<tr>
<td>0.65 - 0.70</td>
<td>0.0003</td>
<td>0.0003</td>
<td>0.0006</td>
<td>0.0002</td>
<td>0.0001</td>
<td>0.0003</td>
<td>0.0000</td>
</tr>
<tr>
<td>( \geq 0.70 )</td>
<td>0.0001</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
</tbody>
</table>
Three points emerge for an examination of Table 2. First, random fission generally leads to $\Delta > 0$; only if $p_1 = \bar{p} = p_2$, can $\Delta = 0$. Given the small sizes of the parent villages, only rarely will such an event occur by chance. (See, however, the $RhCc$ locus of the Ora-Koro (03AB) fission in Table 1). Second, there is considerable variation from locus to locus in the array of possible $\Delta$-values. Loci for which the second allele is uncommon, such as $RhCc$ and $Alb$, admit of only a few discrete $\Delta$ values, and the probability distribution is "lumpy". Loci for which the second allele is more frequent admit of more possibilities, and their probability distributions are smoother. Third, the probability of achieving a $\Delta$ value in excess of 0.60 is less than 0.01 with random fission, and the probability of randomly achieving a value even as high as 0.40 is never more than 0.05. Thus, the divergence generated by random fission is generally not excessive.

Nonrandom (lineal) fission: In Table 3, we have listed the observed $\Delta$ values for all three fissions and all seven markers, along with the probabilities of achieving (or exceeding) these values by random fission. The variation from locus to locus is rather striking, and no clearcut pattern emerges. For the Ironasi-Möwaraoba (11GHI) fission, two of the loci ($RhCc$ and $Gc$) exhibit very unlikely $\Delta$ values [$Pr(\Delta \geq \Delta) = 0.0111$ and 0.0004, respectively.] The other loci exhibit $\Delta$ values ranging from 0.0647 ($Fy$) to 1.0000 ($MN$ and $Ss$). The evidence is mixed, but there is at least a suggestion of nonrandomness. For the Mömari-böwei-Reyaböböwei (03DH/11J) fission, we again find that two of the loci ($Ss$ and $Gc$) exhibit unlikely $\Delta$ values. [$Pr(\Delta \geq \Delta) = 0.0212$ and 0.0000+, respectively.] The other loci exhibit $\Delta$ values ranging from 0.3191 ($MN$) to 1.0000 ($RhCc$). Again, the evidence is mixed, but there is a suggestion of nonrandomness. For the Ora-Koro (03AB) fission, none of the observed $\Delta$ values is convincingly larger than random expectation; in view of the gene flow following the initial "friendly fission", this is not surprising. Some variation in $\Delta$ values from locus to locus is to be expected, of course, and to obtain a clearcut picture, we need the multiple-locus approach of the next section.

**TABLE 3**

*Observed $\Delta$ values for all seven genetic markers and for each of the three fission events, along with the random probabilities of achieving (or exceeding) these values*

<table>
<thead>
<tr>
<th>Fission village</th>
<th>Genetic marker</th>
<th>$MN$</th>
<th>$Sr$</th>
<th>$Cc$</th>
<th>$Ee$</th>
<th>$Fy$</th>
<th>$Gc$</th>
<th>$Alb$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ironasi-Möwaraoba</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed $\Delta$</td>
<td></td>
<td>0.0046</td>
<td>0.0115</td>
<td>0.4991</td>
<td>0.0704</td>
<td>0.3552</td>
<td>0.6830</td>
<td>0.2324</td>
</tr>
<tr>
<td>$Pr(\Delta \geq \Delta)$</td>
<td></td>
<td>1.0000</td>
<td>1.0000</td>
<td>0.0111</td>
<td>0.7588</td>
<td>0.0647</td>
<td>0.0004</td>
<td>0.3424</td>
</tr>
<tr>
<td>Mömari-böwei-Reyaböwei</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed $\Delta$</td>
<td></td>
<td>0.1979</td>
<td>0.4115</td>
<td>0.0967</td>
<td>0.1375</td>
<td>0.5666</td>
<td>0.7331</td>
<td>0.2434</td>
</tr>
<tr>
<td>$Pr(\Delta \geq \Delta)$</td>
<td></td>
<td>0.3191</td>
<td>0.0212</td>
<td>1.0000</td>
<td>0.4476</td>
<td>0.7956</td>
<td>0.0000+</td>
<td>0.4963</td>
</tr>
<tr>
<td>Ora-Koro</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed $\Delta$</td>
<td></td>
<td>0.2924</td>
<td>0.2162</td>
<td>0.0000</td>
<td>0.1353</td>
<td>0.2798</td>
<td>0.2126</td>
<td>0.4104</td>
</tr>
<tr>
<td>$Pr(\Delta \geq \Delta)$</td>
<td></td>
<td>0.1808</td>
<td>0.4424</td>
<td>1.0000</td>
<td>0.5679</td>
<td>0.2010</td>
<td>0.3754</td>
<td>0.0836</td>
</tr>
</tbody>
</table>
MULTIPLE-LOCUS DIVERGENCE

The measure: The single-locus analysis suffers from two limitations. First, genotypes are not assorted into daughter villages one locus at a time; individuals come “packaged” as multiple-locus genomes. Second, the various loci are not segregating independently within the parent villages. Tight (essentially absolute) linkage ensures nonindependence of the RhCc and RhEe markers and of the MN and Ss markers, but even the unlinked loci do not segregate with complete independence. We have elsewhere explained these departures from panmixia within a village as a general feature of small population demography (Smouse and Neel 1977), but here they constitute a nuisance for the analysis.

For independently segregating loci, we could compute an average (per locus) Δ value as

$$\Delta = \sqrt{\frac{\sum (\Delta^2_i + \Delta^2_j + \ldots + \Delta^2_n)}{J}}$$

where $\Delta^2_i$ is the genetic distance for the jth locus, computed as in Eq. (2a). By using multiple locus extensions of Eq. (2a) and Eq. (2b), we can obtain an average Δ value that allows for the nonindependence of the various loci. This more precise estimate of Δ is given by

$$\Delta = \sqrt{\frac{(\bar{P}_1 - \bar{P}_2)'S^{-1}(\bar{P}_1 - \bar{P}_2)}{J}}$$

The vector $\bar{P}_1$ is the array of J = 7 allele frequencies for the first daughter village, and $\bar{P}_2$ is the corresponding array for the second daughter village, computed as in Eqs. (1a) and (1c). The $$(J \times J)$$ covariance matrix S is constructed as in Spielman and Smouse (1976), and takes the form

$$S = \frac{\sum_{i=1}^{M} (Y_i - \bar{P})(Y_i - \bar{P})'}{(M - 1)}$$

The vector $\bar{P}$ is the array of J = 7 allele frequencies for the parent village, as per Eq. (1b). The vector $Y_i$ contains a set of seven genetic scores, one for each codominant locus. For example, the 7-locus genotype [MNSS, RhCCeE, FY-ab, Gc-11, A1b-YY] has the vector representation $Y'_i = [1/2, 1, 1/2, 1/2, 1, 0]$. The scoring convention is chosen so that $\bar{Y} = \bar{P}$, so that the variances are the genetic variances of the various loci and the covariances are functions of the gametic disequilibria between pairs of loci (Smouse and Neel 1977; Smouse and Spielman 1977). In the event that the disequilibria are all zero, Eq. (4b) degenerates to Eq. (4a), but since we wish to capitalize on the Rh and MNSs complexes, we shall use Eq. (4b).

Random fission: To assess the impact of random fission on genetic divergence, it is again necessary to determine the random probability distribution of Δ. With seven loci, there are routinely 15–30 different genotypes extant within villages of these sizes. A complete enumeration of all possible genetic splits would be prohibitively tedious; we have chosen instead to generate an empirical distribu-
tion. Using a pseudorandom number generator, we drew a sample of N individuals from the parent village (of size M), without replacement, to construct the first daughter village. Using the 7-locus genotypes of the chosen individuals and those of the \((M-N)\) residual individuals, placed in the second daughter village, we computed \(\Delta\) via Eq. (4b). This randomization experiment was conducted 10,000 times for each of the three fission examples. The resulting distributions are presented in Figure 1. On the average, random fission should lead to values of \(\Delta \sim 0.18\); values as low as \(\Delta \sim 0.05\) or as high as \(\Delta \sim 0.35\) are exceedingly rare.

Nonrandom (lineal) fission: The observed divergence values \(\langle \Delta \rangle\) are also indicated in Figure 1, and obviously reflect the histories of the three fissions, as related earlier. The Ironasi-Mőwaraboa (11GHI) and Mőmaribőwei-Reyabóbőwei (03DH/11J) fissions, followed by a minimum of gene flow, show striking genetic divergence. In the first case, \(\Delta = 0.3693\), and none of the 10,000 random fissions yielded a larger \(\Delta\) value. In the second case, \(\Delta = 0.3391\), and only 1 of 10,000 random fissions yielded a larger \(\Delta\) value. We attribute these departures from random expectation to the familial nature of Yanomama fission; the lineal fission effect is quite large. The Ora-Koro (03AB) fission yields a \(\Delta\) value only slightly above the expected value from random fission, indicating the ameliorating influence of subsequent gene flow.

DISCUSSION

The social component of fission: The thrust of this paper has been to demonstrate the genetic consequences of Yanomama fission practice, and we have described the social component of the process only in passing. We have concentrated solely on the genetic consequences, because the social practices leading to Yanomama fission have been described in detail elsewhere (cf., Neel 1967; Chagnon 1968). There is, nevertheless, a point of contact between the social and genetic treatments that we should mention. Chagnon (1975, 1979) quantifies the social consequence of village fission in terms of inbreeding coefficient analogues, derived from a formal pedigree analysis. It develops that \(\Delta\) can be related to \(F_{ST}\) (see below), so that Chagnon’s treatment of the social processes could be made compatible with our empiric measure from the genotypes. We have measured \(\Delta\) directly, but it is the juxtaposition of the two types of analysis that rounds out the picture. Future studies of fission effects should include both social (pedigree) and genotypic analysis.

Effective population size: As mentioned earlier, \(\Delta\) is related to \(F_{ST}\). Let \(\sigma^2_\rho\) be the variance in allele frequency between (a pair of) populations. Then, a bit of algebraic manipulation yields

\[
F_{ST} = \frac{\sigma^2_\rho}{P(1-P)} = \frac{(\bar{P}_1 - \bar{P}_2)^2}{2P(1-P)} = \frac{1}{4} \left[ \frac{(\bar{P}_1 - \bar{P}_2)^2}{P(1-P)/2} \right] = \frac{\Delta^2}{4}.
\]  

If the variance in allele frequencies \((\sigma^2_\rho)\) is viewed as due to genetic drift, then
YANOMAMA FISSION EFFECTS

Figure 1.—Distributions of randomly generated genetic divergence (Δ) measures for three Yanomama fission events: Ironasi-Mowaraoba (11G vs. 11HI), Mowariböwei-Reyaböwei (03D vs. 03H/11J), and Ora-Koro (03A vs. 03B). The Δ values are the observed genetic divergence.

$F_{ST}$ may be converted to an estimate of effective population size ($N_e$), because

$$
\hat{F}_{ST} = \frac{1}{2N_e} \Leftrightarrow \hat{N}_e = \frac{2}{\Delta^2}
$$

Assume that random fission yields $\Delta \sim 0.18$, on the average, while lineal fission yields $\Delta \sim 0.36$. From Eq. (7), these two figures imply effective population sizes of $N_e \sim 61.73$ and $N_e \sim 15.43$, respectively. (Even though lineal fission is a departure from random genetic assortment, we can scale its consequences in terms
of "random equivalents"; lineal fission quarters the effective population size at the time of split.)

**Fission and growth:** The consequences of these differences in effective population size \( (N_e) \) for the rate of genetic divergence can be nontrivial. The Yano-
mama have been expanding for a period of at least 100 years (4 generations) and have approximately doubled in that period (Neel and Chagnon 1968; Neel and Weiss 1975). A doubling of population size would require fission. Consider the implications of a 100-year cycle of growth and fission, and assume no genetic exchange between villages. Assume that a village fissions when it reaches a size of \( M = 150 \) individuals and that the daughter villages are of size \( (N = 75 = M - N) \). Growth produces villages of size \( N_1 = 89, N_2 = 106, N_3 = 126 \) and \( N_4 = 150 = M \). (We denote \( N_0 = 75 = M/2 \).) With typical Yanomama demography (Neel and Weiss 1975) \( N_e \sim N/2 \) under genetic drift, so that \( N_{e1} \sim 44.45, N_{e2} \sim 53, \) and \( N_{e3} \sim 63 \). At the time of fission, we employ \( N_{e1} = N_{e0} \sim 61.73 \) for random fission and 15.43 for lineal fission. Over a 4-generation cycle, the average \( N_e \) value is given by the solution to

\[
\left(1 - \frac{1}{2N_e}\right)^4 = \prod_{i=1}^{4} \left(1 - \frac{1}{2N_{ei}}\right).
\]

These average values are \( \bar{N}_e = 54.48 \) and 32.67 for random and lineal fission, respectively. The genetic divergence to be expected after 4 generations is given by

\[
F_{ST(4)} = 1 - \left(1 - \frac{1}{2N_e}\right)^4 = \frac{\Delta^2(4)}{4}.
\]

These \( \bar{N}_e \) values convert to \( F_{ST(4)} \) values of 0.0362 and 0.0598, respectively, and to \( \Delta^2(4) \) values of 0.3805 and 0.4891, respectively. With multiple cycles of growth and fission, the differences would be even more pronounced.

**Fusion and exogamy:** The Yanomama growth rate over the last century cannot have been maintained indefinitely, of course, since even as short a period as 2,000 years of such expansion would have converted a single village of 75 people into over a million villages and 80 million people. [The whole of lowland South America probably contained no more than 10 million people by 1500 AD (Denevan 1976), and native populations have generally decreased ever since.] Moreover, while the Yanomama have been expanding over the past century, their neighbors have achieved numeric equilibrium or have declined.

In the absence of general growth, fissions must be roughly balanced by fusions (or village extinction). Fusion results in gene flow, which (along with marital exogamy) dissipates some of the genetic divergence caused by fission, as illustrated in Figure 1c. That being the case, does it really matter (over evolutionary time) whether fission generates genetic divergence between neighboring villages? To answer that question, we must deal with some additional aspects of tribal social organization and population structure.

**Growth and fragmentation:** Although the Yanomama are notable for their genetic divergence from neighboring tribes (Ward et al. 1975), they also exhibit
a considerable amount of infratribal genetic radiation. The tribe is fragmented into "dialect groups" or "clusters" (Figure 2) among which genetic divergence is quite large (SMOUSE and SPIELMAN 1977; SMOUSE 1981). These large assemblages differ moderately in language and culture (MIGLIAZZA 1972), and linguistic analysis suggests that they may have been effectively separated for as many as 600 to 1,200 years (SPIELMAN, MIGLIAZZA and NEEL 1974).

Within the Yanomame dialect cluster, we have sampled intensively and have identified "miniclusters" of closely related villages; these subgroups can be traced to a series of village fissions, followed by rapid territorial expansion, before 1900 (WARD 1972). Gene flow between these miniclusters has subsequently been rather limited, and much of the genetic divergence caused by the initial fissions seems to have been "captured" as minicluster differences (cf., SMOUSE and WARD

![Figure 2](image-url)

**Figure 2.**—Territorial extent of four Yanomama dialect clusters (slightly modified from MIGLIAZZA 1972), with extent of Yanomame dialect miniclusters indicated: P = Padamo, O = Ocamo, W = Wanabowetari, N = Namowetari and S = Shamaturi.
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Within the subgroups, fission and fusion are counterbalanced, and there is an active migration network.

This semihistorical reconstruction is reflected in a series of $\Delta$ values. Extensive computation yields average figures as follows:

$$
\bar{\Delta} \text{ (Villages/Same miniclusters)} = 0.33 \\
\bar{\Delta} \text{ (Villages/Different miniclusters)} = 0.58 \\
\bar{\Delta} \text{ (Villages/Different dialects)} = 0.74
$$

What we observe is a hierarchy of variation. Fission effects appear not to have had a pronounced long-term influence on the genetic divergence between villages of the same minicluster, due to counterbalancing fusion and exogamy, but can definitely be implicated in minicluster differences. The evidence on dialect cluster formation is less direct, but we are inclined to postulate that at least some of that divergence also arose as fission effects (cf., SMOUSE 1981).

We mentioned above that the Yanomama have been growing and expanding over the past century, the period during which these Yanomama miniclusters have developed. There are two explanations of this phenomenon. First, the surrounding tribes had been displaced and/or decimated by contact with neo-Brazilians, especially rubber tappers, and the Yanomama expanded into vacated territory after the demise of the rubber trade. Second, the acquisition of metal axes and machetes improved the land-clearing capability of the Yanomama, a fact that probably contributed to the rapidity of the expansion. (The intertribal trade network had permitted passage of such goods for an extended period, but the Yanomama were so isolated that they were relatively late recipients.) In the process of expanding, the population fragmented. A similar (but more ancient) expansion and fragmentation phase can be postulated as the most likely explanation for the dialect cluster differences (SMOUSE 1981).

We do not imply that all of the genetic divergence between miniclusters and between dialect clusters is due to fission effects. It is not possible to partition extant divergence exactly into fission and (subsequent) drift components, and it seems probable that long-term drift has contributed somewhat to the divergence between dialect clusters. It is worth noting, however, that in an expanding group, effective population size is smallest at the outset, a time that corresponds with irreversible fission and fragmentation events. Fission effects are apt to dominate the rate of genetic divergence for some time to come.

Fission effects may also have played a role in the genetic divergence of tribes. We note that Yanomama dialect clusters might alternatively be viewed as closely related tribes. South American groups of comparable ethnological, linguistic and genetic divergence have been classified as tribes of the same language family (cf., SALZANO et al. 1977). The important point here is not so much to establish the proper taxonomic relationships as it is to realize that language families probably begin as dialect clusters in a single tribe; these latter probably began as miniclusters.

In the continuous ebb and flow of supratribal dynamics, some tribes expand at the expense of others. Gene flow across tribal boundaries has been limited in the past (NEEL 1978a), and cultural expansion usually implies spatial and ge-
netic displacement, rather than assimilation (see, however, Chagnon et al. 1970; Neel et al. 1977). In the process of tribal expansion, it is almost inevitable that there would be a breakdown of communication and gene flow, leading to the sort of fragmentation we have described within the Yanomama. Fission effects should contribute materially to the initial genetic radiation. Time and drift (cultural and genetic) would enhance the differences until tribal-level divergence had been achieved. It is obvious that tribal divergence is not primarily due to fission effects, because the realized differences are simply too large (Smouse and Spielman 1977); in the parlance of this paper, \( \Delta \) (tribes) \( \sim 0.85 \) somewhat larger than the \( \Delta \sim 0.36 \) expected from the initial (lineal) fission.

The magnitude of the fission contribution to genetic radiation of tribal groups depends on how active the expansion-replacement-fragmentation dynamic has been. If the initial colonizers of South America had spread rapidly to occupy the entire territory, then evolved \( \text{in situ} \) ever since, the impact of fission effects would long since have been overshadowed by subsequent genetic drift. The ethnographic map of South America, however, is a patchwork of interdigitating linguistic families (Loukotka 1968). An examination of the linguistic tapestry of the continent suggests that tribal expansion, replacement and fragmentation have been localized and episodic (but not necessarily infrequent) occurrences throughout the history of human occupation in South America. If human evolution on the continent is viewed as a semicontinuous process of group displacement, then fission effects become more prominent as an explanation of the extant genetic diversity among tribes. The net consequence is that genetic radiation may have been more rapid (and perhaps substantially so) than would be consistent with classical genetic drift theory.

On a larger scale: The temptation to extrapolate from the South American experience to a planet-wide discussion of the evolution of \( \text{Homo sapiens} \) is almost irresistible. Any such effort must deal with a trio of serious caveats, however. First, even to treat the genetic radiation of South American Indians, we have found it necessary to stray very far from the hard data. The \( \Delta \) values are easily observable, but the matching linguistic, historical and ethnographic evidence leaves a great deal to be desired. At the minicluster level, we can reconstruct events with some confidence; at the dialect cluster level, we can plausibly interpret the clues; at the tribal level, we are speculating. We have indulged our urge to generalize, because a great deal of cultural, historical and linguistic evidence bearing on our postulates can still be collected from South America and analyzed. We offer these conjectures to stimulate future work. To extrapolate on a larger scale and for a much longer time period is truly to “wag the dog by the tail”. While such speculation may be worthwhile, one’s conclusions are not really susceptible to either verification or falsification.

Second, the original human colonizers of South America were hunter-gathers, and their antecedents had been hunter-gatherers for a very large fraction of human evolutionary history. It is possible that the sorts of evolutionary behavior we have documented here for swidden agriculturalists should not be extrapolated to our distant hunter-gatherer ancestors. Many extant hunter-gatherer tribes show large amounts of microdifferentiation (cf. Kirk et al. 1971; Szathmary and
Ossenberg 1978), but it remains unclear whether such groups have been subject to the sort of group displacement dynamics leading to the periodic “capture” of fission effects. A great deal of comparative work with other sorts of social organization is in order before wide extrapolation is appropriate.

Third, because the time of human entry into the New World is (more or less) datable, one might be tempted to use Amerindian divergence measures to calibrate the “evolutionary clock” (cf., Cavalli-Sforza and Bodmer 1971). The fission effects we have described would have been very prominent along the expanding periphery of colonization, and evolutionary radiation could only have been very rapid. How much of the existing variation one should attribute to colonization dynamics, how much to genetic drift in situ and how much to group displacement dynamics is sheer guesswork. Even if one assumes that the population processes were the same in other parts of the world, the respective time periods over which these three processes have operated were different. To use Amerindian variation to calibrate the “clock” seems to us rather risky.

Conclusion: It is clear that much of the variation between extant human populations arose before detribalization. Tribal social organization involves small group dynamics, and the stochastic element of evolution looms large. It seems probable that the genetic infrastructure of present-day tribal populations can be traced to expansion and fragmentation dynamics, processes that involve substantial fission effects. The process of village fission is strongly nonrandom socially, and results in pronounced genetic cohesion within, and great genetic differences between, daughter villages. As a consequence, the rate of human radiation within (and probably among) tribal populations is accelerated, relative to random drift expectation.

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LITERATURE CITED


WARD, R. H. and J. V. NEEL, 1970  Gene frequencies and microdifferentiation among the
Makiritare Indians. IV. A comparison of a genetic network with ethnohistory and migra-
1976  The genetic structure of a tribal population, the Yanomama Indians. XIV. Clines and
their interpretation. Genetics 82: 103–121.

WEITKAMP, L. R., T. ARENS, M. L. GALLANGO, J. V. NEEL, J. SCHULTZ and D. C. SHREFFLER,
1972  The genetic structure of a tribal population, the Yanomama Indians. III. Seven

WEITKAMP, L. R. and J. V. NEEL, 1972  The genetic structure of a tribal population, the Yano-
Human Genet. 35: 433–444.


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