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Microevolution in Lower Central America: Genetic Characterization of the Chibcha-speaking Groups of Costa Rica and Panama, and a Consensus Taxonomy Based on Genetic and Linguistic Affinity

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Summary

There is evidence that Amerindians have continuously occupied the lower Central American Isthmus for as long as 10,000 years. There remains some doubt about the relationships of these original colonizers to the resident peoples of this zone at the time of European contact (approximately A.D. 1500). We present new genetic data for up to 48 genetic loci for 570 members of six Chibcha-speaking tribes of lower Central America—the Boruca, Bribri, Cabecar, and Guatuso of Costa Rica and the Kuna and Teribe of Panama—and delineate the genetic affinities among the various groups (these six tribes and the Guaymi and Bokota) of lower Central America. We convert standard genetic distance metrics into a form that is linear with the effective time since divergence, and we compare the genetic distances with linguistic distances for the same groups ($r = .74$, $P < .001$). Geographic affinity accounts for some of the genetic divergence among groups ($r = .49$, $P < .084$) and for some of the linguistic divergence ($r = .53$, $P < .037$), but the correspondence between geographic position and taxonomic affinity is not high. We combine all of the genetic and linguistic data to construct a synthetic overview taxonomy of the lower Central American Chibcha. Both the genetic and linguistic data exhibit hierarchical organization of tribal groups, showing a general east-to-west pattern of grouping, with greater affinities between close neighbors. The presence of private genetic variants of some antiquity within the region and their absence outside the zone, coupled with the essential absence of the DI*A polymorphism of mongoloid origin that is widespread outside the zone, argue for a relatively isolated development of the Central American Chibcha. Our results do not support the old view of lower Central America as a frontier between more advanced cultures to the north and south. Any such explanation would require recent waves of migration from outside the region, migration that is not compatible with either the genetic or linguistic data or with the archaeological history of the region.

Introduction

The complex array of transmitted information we commonly term "language" evolves in such a way as to provide a taxonomic structure of human populations that is, in its way, as detailed as any provided by the genetic data thus far employed for such purposes by human geneticists. While the broad parallelisms of genetic and linguistic evolution have been evident for some time and have received recent attention at the macroscopic level of human taxonomy (Cavalli-Sforza et al. 1988), there has been almost no exploration of the parallelism at the microlevel that would permit precise statements

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about the relative rates of genetic and linguistic divergence, in spite of the availability of an almost exactly parallel theory for the two fields.

Our own work among the Chibcha-speaking groups of lower Central America presents an unusual opportunity to mount a formal comparison of the parallelism of genetic and linguistic divergence at the microtaxonomic level. In the present paper, we will provide a synthetic overview taxonomy of these Central American Chibcha groups, using methods designed to permit a detailed comparison of genetic, linguistic, and geographic information from this region. We will (1) present new genetic data on six Chibcha-speaking tribes of lower Central America—the Boruca, Bribri, Cabecar, and Guatuso of Costa Rica and the Kuna (Cuna) and Teribe of Panama—updating our genetic coverage of this region, (2) delineate the genetic affinities among the various groups of lower Central America (these six tribes and the Guaymi and Bokota), using genetic distance techniques on all of the accumulated data, (3) convert these genetic distances into a time-linear form, (4) compare the genetic data with similarly time-linearized linguistic data for the same groups, using new methods to be described here, (5) compare both with the pattern of geographic isolation among the groups, and (6) attempt to match our findings with what is known of the archaeology of the region. We will argue that these tribal groups (and their languages) have been differentiating in situ for some 7,000 years, with little outside infiltration, despite their strategic position astride the corridor between North and South America. Our ability to accomplish these objectives derives from an almost unique situation, the availability of genetic and linguistic data of comparable detail on the same set of populations.

The Chibcha Populations of Lower Central America

There have been claims that humans first crossed the Isthmus of Panama over 30,000 years ago (Irving 1985; Lewin 1987), but most authorities agree that a date of about 12,000 years ago is more reasonable (Irving 1985; Greenberg et al. 1986). There is undisputed archaeological evidence of continuous occupation of the lower Central American region for as long as 10,000 years (Lange and Stone 1984; Ranere and Cooke, in press). There remains considerable doubt about the relationships of the original colonizers of Central America to the people residing in this region at the time of European contact (approximately A.D. 1500), people referred to by their collective linguistic affiliation as "Chibcha." There will probably never be compelling evidence of a direct link between the original colonizers, characterized in strictly archaeological terms, and the corresponding groups of the post-Columbian period (defined in ethnographic [Stone 1966], linguistic [Constenla 1985], and genetic [Barrantes et al. 1982] terms). The Central American archaeological series contains no record of the language or genotypes of these groups, and any inference we choose to draw is necessarily a bit circumstantial. Notwithstanding the philosophical difficulties, the prehistory of this zone is an intriguing story, and the archaeological/linguistic/genetic reconstruction has recently been the object of much discussion (Meyers 1978; Constenla 1981; Barrantes et al. 1982; Cooke 1982, 1986).

Linguistic reconstruction shows that the Central American Chibcha languages, both those still extant and those extinct since the colonial period, can be traced to a common linguistic ancestor, perhaps dating to 7,000–8,000 years ago (Swadesh 1967; Constenla 1981, 1985; Greenberg 1987). There remains some doubt about the accuracy of linguistic dating for these purely verbal languages (e.g., see Hymes 1960), but even were that time depth accurate, the divergence need not have developed within the current geographical context.

Accumulating archaeological evidence suggests that, subsequent to the initial peopling of this region, there were outside cultural influences penetrating the intermediate zone (lower Central America and northern South America) from Mesoamerica (Wolf 1959; Lothrop 1966; Swadesh 1967; Ferrero 1975; Stone 1977; Linares 1979; Constenla 1981), starting about 600–800 B.C. Later cultural influences from northern South America (Kieder 1940; West 1964; Stone 1966, 1977), where related Chibcha-speaking peoples still exist today, date to the latter half of the first millennium A.D. The available data are, however, compatible with the thesis that the groups first contacted by the Spaniards in lower Central America may have developed in situ over a very long period of time, with these later cultural influences from both north and south being the results of gradual cultural diffusion (Cooke 1984, 1986) rather than of large-scale infiltration or replacement.

In figure 1*a* we present the current tribal distributions of the eight groups with which we are concerned, and in figure 1*b* we present our best reconstruction of the precontact distributions of these same groups, garnered from the available literature (Stone 1966, 1977; R. Cooke, personal communication). This latter map is necessarily a bit conjectural, but it will have no mate-

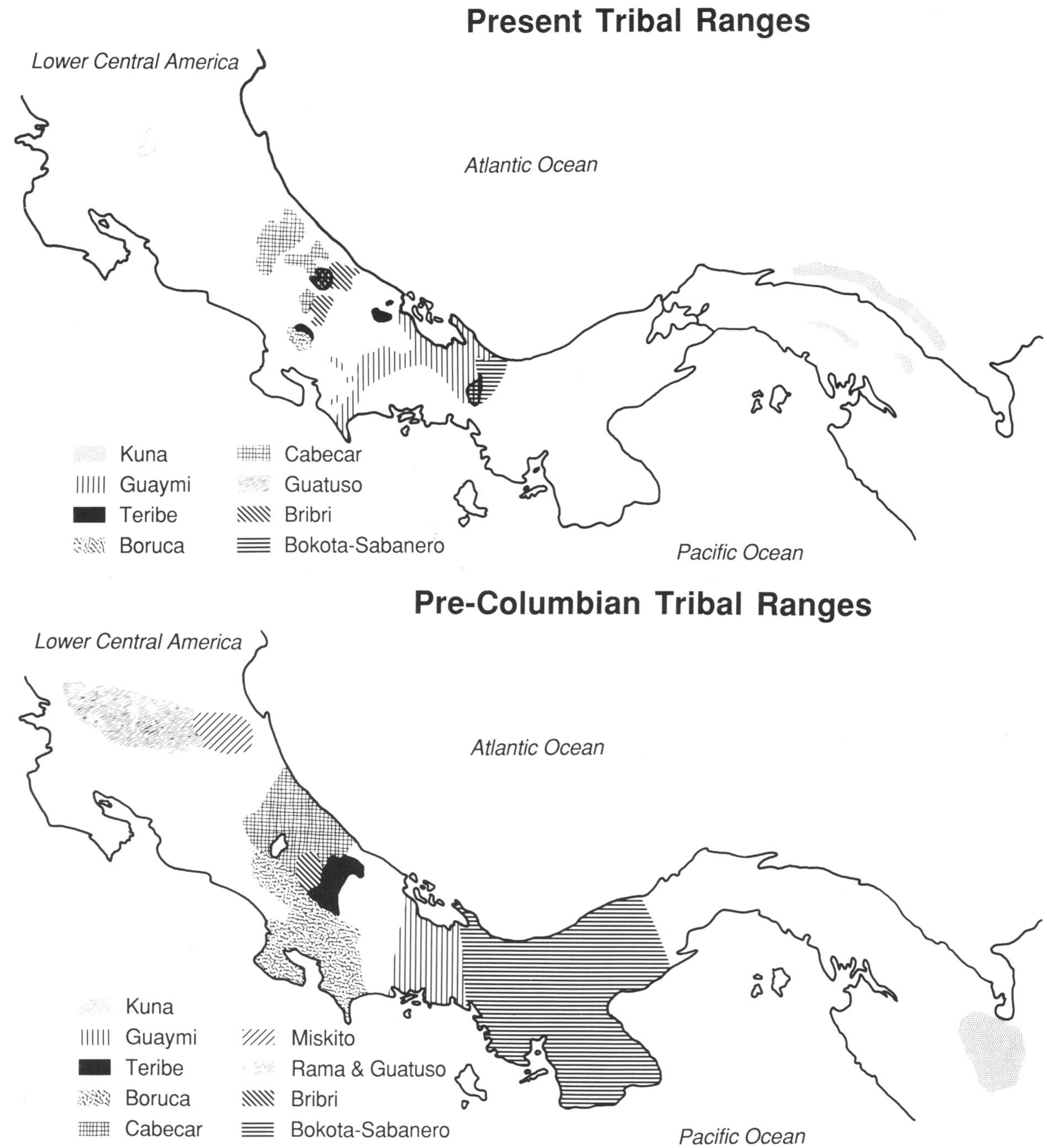

Figure 1 Present (*top*) and Pre-Columbian (*bottom*) distributions of Chibcha-speaking tribes of lower Central America

rial impact on the geographic analyses we report. Some history for each of the groups should set the stage for what follows.

Kuna

There are currently about 55,000 Kuna (also Cuna) inhabiting 50 islands of the San Blas Archipelago along Panama's northeastern coast and some locations in Darien Province. Much has been written about the post-Columbian ethnography and socioeconomy of the Kuna, but their pre-Columbian provenance remains unclear (Costello 1983; Howe 1986). According to Romoli (1987), the pre-Columbian Kuna populations inhabited northwestern Colombia, near current Chocó territory.

In the early colonial period (16th century), the Kuna began to migrate westward through the lands of the recently extinct Cueva, occupying the Tuira River region by about 1600. As late as the 19th century, the Kuna inhabited the mountains and coastal plains of Darien (Torres de Arauz 1980), but they have subsequently moved to more coastal locations and most recently to their current island territory, partly because of outside pressures and partly because of the development of new sources of trade and subsistence in these places (Bort and Helms 1983). Unlike other native Panamanian groups, the Kuna have a strong political and social organization, reaching beyond the extended family, with a clear political hierarchy (Howe 1974, 1976), leading to both territorial conservation and political autonomy.

Guaymi

The Guaymi (also Ngawbé) are widely distributed in western Panama, mainly in Bocas del Toro Province on the Atlantic side and on the Pacific slopes of Panama in Chiriqui and Veraguas provinces. These people speak the Ngawbere language of the Chibcha family. Ethnohistorical accounts clearly show geographical and cultural continuity of the Guaymi in the region that they inhabit today (Young 1970, 1971; Linares and Ranere 1980; Gordon 1982). Archaeological and ecological evidence supports the view that the Guaymi are the cultural descendants of the people who have inhabited the western part of Panama for several thousand years (Cooke 1984, 1986).

Bokota-Sabanero

The neighboring group, the Bokota-Sabanero (also Buglé), live in the extreme eastern area of Bocas del Toro Province and in the highlands of Veraguas and Chiriqui provinces. There is also a small group of recent Bokota immigrants—approximately 40 people—in Coto Brus, Costa Rica. The Bokota speak the Buglere language. The Guaymi and Bokota have traditionally been lumped under the generic name of Guaymi (see discussion in Wássen 1952; Young 1971; Levinshon 1975), but recent genetic (Spielman et al. 1979; Barrantes et al. 1982), linguistic (Levinshon 1975; Gunn 1980; Constenla 1985), ethnological (Gordon 1982), and archaeological (Cooke 1982, 1984, 1986) studies show large differences between them, indicating very early divergence. Where they overlap in Panama, intermarriage is now common, as it is in the small, mixed community in Costa Rica (Barrantes et al. 1982).

Bribri and Cabecar

The Bribri and Cabecar of Costa Rica are closely related groups, currently located on both sides of the Talamancan mountains, in both the lowlands and adjacent highlands. Ethnohistorical evidence demonstrates temporal, cultural, and geographic continuity and contiguity of the Bribri and Cabecar societies in the Talamancan region from the pre-Columbian period (Fernández 1886; Ibarra 1984; Barrantes-Cartin 1986). The relations between them have alternated between amicable and bellicose (Gabb 1875; Stone 1962; Bozzoli de Wille 1979), relationships reflected in the sociocultural, linguistic, and genetic affinities of the two groups to this day. At either the end of the 18th century or the beginning of the 19th century, the Bribri and Cabecar populations in the Talamancan region split, with members of both groups migrating to the Pacific flank of the Talamancan mountains and settling localities near Cabagra and Ujarras. There are presently about 1,300 Bribri and 700 Cabecar on the Pacific side of Costa Rica (Barrantes and Azofeifa 1983; Bozzoli de Wille 1986). There is documented contact across the Talamanca mountains with other Amerindian groups for at least the past 400 years (Bozzoli de Wille and Wing Ching 1980). There is also documentary evidence that both the Bribri and Cabecar have occupied Pacific sites for at least 300 years (Thiel 1900). Whether (and to what extent) the current Pacific populations have incorporated the remnants of any earlier populations is not clear, but a long history of contact across the central cordillera is evident; the Atlantic and Pacific populations have not evolved in complete isolation.

Teribe

The geographic origins of the contemporary Teribe (also known as Terraba, Naso, Texbi, or Tojar) are unclear, but there is documented evidence from the early 1600s of Teribe settlements in the Talamanca region, between the Sixaola and Changuinola Rivers, as well as on Tojar Island (now Isla Colon) in Bocas del Toro Province, Panama (Fernández-Guardia 1975; VonChong and Ortiz 1982). About 1700, part of the Teribe population was relocated by the Spanish to southeastern Costa Rica, and the remaining Panamanian group began a retreat into the mountains, moving along the Teribe River (Gabb 1875; Peralta 1938; Stone 1962). The Costa Rican Teribe have since suffered drastic demographic decay, with remnants merging into Bribri, Cabecar, and Boruca communities. The Panamian population, now spread along the Teribe, San-San, and

Changuinola rivers, and currently numbering about 1,200 inhabitants, shows demographic growth during the 20th century (VonChong and Ortiz 1982) and has begun to intermarry with the neighboring Guaymi.

Boruca

The Boruca are found at two locations, Boruca and Curré, in the Terraba River Valley and neighboring the Bribri, Cabecar, and Teribe localities of the Pacific side of Costa Rica. They have occupied the southeastern region of Costa Rica since before the colonial period (Stone 1949). It is not clear, however, whether the current population is a localized remnant of a more extensive population or a collection of otherwise extinct tribal groups from the Diquis region (Coto Brus, Turucaca, Quepo), as indicated in historical registers (Pittier 1938; Stone 1949; Lothrop 1963; Ferrero 1975). The Boruca have a long history of contact and admixture with Talamancan and Panamanian Indians, as well as with Spaniards, Caribbean blacks, and mestizos, over a very long period of time. The Diquis Valley was a strategic trade route even in precolonial times, and the exchange pattern reflects this fact.

Guatuso

The Guatuso historically inhabited the plains of northern Costa Rica, occupying the upper portions of the Rio Frio drainage. Today they inhabit three small localities or "palenques" (Margarita, Tonjibe, and El Sol), with a total population of roughly 250 individuals (Bozzoli de Wille 1972). During colonial times and even as late as the 18th century, the group had a larger and more stable population (Thiel 1900). The ethnographic and linguistic affiliations of the Guatuso are confusing. They have been considered to be (1) related to the Nicaraguan Rama (Conzemius 1932), (2) a subgroup of the now-extinct Corobici (Peralta 1938; Mason 1950; Ferrero 1975), (3) a branch of the Huetar (Guetar) of Central Costa Rica (Gabb 1875; Johnson 1948), (4) a remnant group of the Costa Rican Voto (Gagini 1917), and (5) a refugee mix of Voto and Huetar (Fernández 1884). Linguistically, the Guatuso are classified as belonging to the Chibcha family, but there is divergence of opinion concerning their exact position within the classification. Some authors have classified Guatuso as an isolated language, but others place it in either the Talamanca or Rama subfamilies (Constenla 1985; Greenberg 1987). Ethnographic accounts are scanty and limited to a short description of marriage practices and kinship (Bozzoli de Wille 1972) and of language (Constenla 1982).

Genetic Characterization

Previous Work

Matson and his colleagues (Matson et al. 1965; Matson and Swanson 1965*a*, 1965*b*) sampled various Chibcha groups in the 1960s. The number of genetic systems available at that time was limited, and the precise ethnic composition of Matson's samples remains unclear. Our own efforts over the past decade, with more extensive typings, have concentrated on the Guaymi (Ngawbé) and Bokota-Sabanero (Buglé) of Panama and immediately adjacent Costa Rica (Tanis et al. 1977; Spielman et al. 1979; Barrantes et al. 1982; Mohrenweiser and Novotny 1982*a*, 1982*b*). There have also been some preliminary studies of genetic markers of pharmacological importance (Inaba and Arias 1987; Arias et al. 1988*a*, 1988*b*; Inaba et al. 1988). We have shown that the Guaymi and Bokota are more closely related to each other than is either to any other Chibcha group (Barrantes et al. 1982), being genetically intermediate between the Costa Rican tribes to the west and the Kuna to the east, as might be expected from their relative geographic positions along the lower Central American corridor. The Talamancan subgroup of Costa Rica and adjacent Panama (Bribri, Cabecar, Teribe, and Boruca) clustered together. The Kuna, the eastern member of the collection, showed affinities with the Chibcha groups of northern South America. There are no extant genetic data from the Guatuso, and their genetic affinities remain unknown.

New Accessions

We report here on the examination of the products of 48 genetic loci from six of these groups—the Kuna, Teribe, Bribri, Cabecar, Boruca, and Guatuso—with two collections each from the Bribri and Cabecar, straddling the central cordillera. These new data on 570 individuals, when coupled with the earlier Guaymi and Bokota collections, permit a depth of genetic analysis not previously possible on the native peoples of this region. Some of the genetic assays were done in the labs of R.B. at INISA, Universidad de Costa Rica, and some were done in the labs of H.W.M. and H.G. at the Department of Human Genetics, University of Michigan. Assay procedures were the same in both places and are fairly standard, and most are merely referenced below.

Blood Group Systems

Typings were performed on red cells that had been preserved in glycerol/sorbitol solution and frozen in liquid nitrogen. The systems investigated were ABO, rhesus (RH), MNS, P, Kell (K), Kidd (JK), Duffy (FY), Diego (DI), and Lewis (LE). All bloods were tested with the following antisera: anti-A, -B, -M, -N, -S, -s, -C, -c, -CW, -D, -E, -e, -P1, -K, -FYA, -FYB, and -DIA. As reagents were available, bloods were also tested with anti-JKA, -JKB, -LEB (and, where negative, and anti-LEA), -(P1+P2), -MG, -VW, -LUA, and -KPB. In the early part of the study, R1R2 bloods were all tested with anti-f and were found to be negative. That additional testing was discontinued for the later part of the study. The procedures employed are the same as those described by Gershowitz et al. (1972).

Plasma Protein Systems

Albumin (ALB), transferrin (TF), haptoglobin (HPT), and ceruloplasmin (CRPL) typings were performed with PAGE, using the procedures of Maurer and Allen (1972) and the staining methods of Tanis et al. (1973). The immunoglobulin (GM and KM) typings were done with the protocols described by Gershowitz and Neel (1978).

Red Cell Protein Systems

The following red cell protein systems were examined for variants by means of starch or PAGE: hemoglobin A and A_2 (HBA and HBA2); acid phosphatase (ACP-1); adenosine deaminase (ADA); adenylate kinase (AK1); carbonic anhydrase I and II (CA1 and CA2, respectively); esterases A, B, and D (ESA, ESB, and ESD, respectively); galactose-1-phosphate uridyl transferase (GALUT); glutamate-oxaloacetate transaminase (GOT); glucose-6-phosphate dehydrogenase (G6PD); glutamic-pyruvate transaminase (GPT); glyoxolase (GLO-1); isocitrate dehydrogenase (ICD); lactate dehydrogenase (LDH); malic dehydrogenase (MDH); nucleoside phosphorylase (NP); peptidases A, B, C, and D (PEPA, PEPB, PEPC, and PEPD, respectively); 6-phospho-gluconate dehydrogenase (6PGD); phosphoglucomutase I and II (PGM1 and PGM2, respectively); phosphoglucose isomerase (PGI); and triosephosphate isomerase (TPI). The methods used have been described in our earlier publications (Tanis et al. 1973; Neel et al. 1977*a*, 1980; Mohrenweiser et al. 1987).

Removing the Admixture

The first task was to minimize the effects of European and African genetic infiltration over the past 500 years. We removed from the sample all individuals possessing an allele that could clearly be attributed to such admixture (alleles *A1, *A2, and *B of the ABO locus, *K of the Kell system, *R of the rhesus system, *S and *C of the β-globin locus, *3A of the PEPA locus, *C of the ACP locus, *2 of the CA2 locus, *2 of the ADA locus, *2 of the PEPD locus, *A of the G6PD locus, and *F or *B specificities of the GM system). Not all African or European ancestry is detectable in this fashion, of course, and there are some subtle biases that can arise. In our situation, almost all such marker alleles occur in individuals who have already admitted either European or African ancestry, most of it within the most recent several generations. The next step was to remove all individuals who admitted either European or African ancestry, regardless of whether it was genetically evident. Finally, all relatives of both types of individuals who were thus also identified as admixed were removed from the sample, thus removing even small amounts of African or European descent. We cannot be certain that we have removed *all* the effects of more ancient gene flow, but inasmuch as admixture seems to have been on the increase in the 20th century, we have probably purged these Amerindian gene pools rather thoroughly.

We have also arbitrarily removed from the sample those individuals with an admitted history of intertribal admixture. Tribal breakdown is an increasingly important process in lower Central America, being the usual consequence of increasing assimilation into the regional population, but it is not the subject of the present paper; we will report on that matter elsewhere. Our effort to "retribalize" these Amerindian gene pools is based on our desire to compare them in their pre-Columbian state—to the extent that is possible. It is clear that our efforts to retribalize these Amerindian gene pools removes only the effects of fairly recent gene flow among tribes, but since intermarriage has been increasing steadily during the 20th century, we have probably removed the largest effects. Earlier (probably limited) genetic exchange is not extricable and may be evident in some of our results. These removals have reduced the number of new acquisitions from 961 people sampled to the 570 mentioned earlier.

In table 1 we present the allele (haplotype) counts for each of the genetic loci assayed. Note that ESA apparently involves four different loci (ESA1, ESA2, ESA3, and ESAC) in this material (Neel et al. 1986, 1988), that LDH involves two loci (LDHA and LDHB), and that HBA and HBA2 involve four loci (two α-globin [treated as one], β-globin, and δ-globin). We report the results for each locus separately. The estimation techniques for allele and haplotype frequencies, described by Barrantes et al. (1982), are the standard likelihood methods used for allele frequency estimation. All frequencies are converted to allelic (haplotypic) counts for tabular economy. For the codominant systems, the tallies are obtained by gene-counting methods and take only integer values; for the dominant systems, standard maximum likelihood procedures yield equivalent fractional counts. We present these fractional counts, rather than allele frequencies, to condense a frequency tabulation that would otherwise be egregious. For comparative purposes, in table 1 we have also included, for the Guaymi and Bokota, tribal summaries from our earlier characterizations (Tanis et al. 1977; Spielman et al. 1979; Barrantes et al. 1982; Mohrenweiser and Novotny 1982*a,* 1982*b;* Wurzinger and Mohrenweiser 1982), after removal of the interracial and intertribal gene-flow effects, as described earlier for the new accessions. The Kidd frequencies for the Teribe, marked with an asterisk (*), are derived from Matson and Swanson (1965*a*), who sampled the Costa Rican community, rather than the Panamanian community represented in our typings. Because we have no Kidd typings for our accession, we report the Matson and Swanson figures as the best available estimates. These values are *not* used in subsequent analyses.

Genetic Affinities

Our genetic marker frequencies for all groups are quite similar to those reported by Fuentes (1961) and Matson (Matson et al. 1965; Matson and Swanson 1965*a,* 1965*b*), both of whom had admixed samples, with the sole exception of the Teribe (Matson's Terraba). Our sample is from the Atlantic side of Panama, near the Guaymi, with whom recent admixture has been considerable, though individuals known to be of recent admixed origin have been removed from the data reported here. Matson's sample was drawn from the Pacific side of Costa Rica and was largely admixed with Bribri, Cabecar, Boruca, and settlers of European ancestry. That group is no longer separately identifiable in the area, although heavily intermarried remnants still exist. The differences in allele frequencies probably reflect different admixture histories. Our samples are ethnically better characterized and "cleaner" than are Matson's, so we shall use only our own data for analysis.

From that subset of 41 loci (64 alleles) for which all accessions have been typed, we have computed all 45 pairwise genetic distances between populations. For the small levels of genetic divergence discussed here, there is very little to choose among the available distance measures (Felsenstein 1973); we have elected to use Nei's (1972) "standardized gene identity" measure, because it is theoretically convertible into an approximate measure of the *effective time* since divergence. Consider the Xth and Yth populations, for which the frequencies of the *i*th allele for the ℓth locus are denoted by $P_{X\ell i}$ and $P_{Y\ell i}$, respectively. Nei's genetic identity measures for the ℓth locus, both those within ($j_{XX\ell}$ and $j_{YY\ell}$) and between populations ($j_{XY\ell}$), are defined as

$$j_{XX\ell} = \sum_i p^2_{X\ell i} \quad j_{XY\ell} = \sum_i P_{X\ell i}P_{Y\ell i} \quad j_{YY\ell} = \sum_i P^2_{Y\ell i}\,, \tag{1}$$

and the averages of the values across loci are defined as

$$J_{XX} = \sum_{\ell=1}^{L} j_{XX\ell}/L \quad J_{XY} = \sum_{\ell=1}^{L} j_{XY\ell}/L \quad J_{YY} = \sum_{\ell=1}^{L} j_{YY\ell}/L\,. \tag{2}$$

Using these multiple-locus gene identity measures, we compute the gene identity of the Xth and Yth populations:

$$I_{XY} = \frac{J_{XY}}{(J_{XX} \cdot J_{YY})^{1/2}}\,, \tag{3}$$

distance measures that can be translated into a statement of the time since divergence. Nei and Feldman (1972) have shown that under standard neutral drift assumptions, the expectation of the logarithm of I_{XY} takes the form

$$D_{XY} = -\log I_{XY} \approx 2\alpha t\,, \tag{4}$$

where α is a rate parameter describing the exponential decay rate for gene identity after effective separation and where *t* is the time, measured in generations, since that divergence. As always with such time translations, there are a pair of obvious reservations. First, we do not know α. Second, the course of genetic divergence is periodically interrupted by episodes of genetic exchange, only the most recent of which can usually be documented with any certainty. Even for these autonomous tribal populations, there must also have been some gene flow in pre-Columbian times. The rate of genetic exchange undoubtedly increased in colonial times, and it has been considerable since the turn of the century. While the individuals known to be the descendants of the more recent intertribal marriages have been removed from the data presented here, at least some earlier gene flow may be evident in the frequencies of the rarer alleles, usually restricted to a single tribe in unadmixed groups (Neel 1978*a,* 1978*b*). Of course, these shared rare alleles may represent mutations occurring before the separation of the groups in question. Whether the shared rare alleles are a remnant of ancient fission or

Table 1

Allelic Counts for 48 Genetic Loci in Eight Amerindian Tribes of Panama and Costa Rica: Kuna, Bokota, Guaymi, Boruca, Bribri (Pacific and Atlantic populations), Cabecar (Pacific and Atlantic populations), Teribe, and Guatuso

LOCUS AND					BRIBRI		CABECAR			
ALLELE	KUNA	BOKOTA	GUAYMI	BORUCA	Atlantic	Pacific	Atlantic	Pacific	TERIBE	GUATUSO
Rhesus:										
R1	145	200	938	88	36	108	54	56	52	82
R2	81	23	158	30	39	84	50	40	69	66
R0	2	7	22	6	5	6	2	24	4	8
RZ	0	0	0	0	0	0	0	0	1	2
MNS:[a]										
MS	98	46	378	37	18	86	47	51	58	6
Ms	44	96	399	49	55	96	51	66	41	74
NS	5	26	18	15	3	6	5	3	5	31
Ns	81	62	260	23	4	10	3	0	22	47
HPT:										
1	32	131	605	62	172	77	50	62	82	68
2	194	105	521	62	156	121	114	56	42	98
ESD:										
1	211	229	1,076	107	292	186	160	120	87	119
2	17	1	46	17	40	12	6	0	39	47
PGM1:										
1	194	224	1,036	87	311	183	152	109	116	160
2	34	6	68	37	21	15	14	11	10	6
Duffy:										
FYA	152	142	481	74	62	127	73	97	47	61
FYB	76	88	637	50	18	71	33	23	79	55
P:[a]										
1	137	127	672	82	34	59	54	54	45	6
2	91	103	446	42	46	139	52	66	81	132
Diego:[a]										
DIB	217	230	1,118	122	80	198	106	120	120	118
DIA	11	0	0	2	0	0	0	0	0	0
TF:										
C	228	238	1,051	117	271	169	138	114	100	166
DCHI	0	0	73	0	55	0	8	0	26	0
DGUA	0	0	0	7	2	29	18	4	0	0
PEPA:										
N	132	230	1,106	124	308	198	150	120	100	116
F	96	0	4	0	24	0	16	0	26	50
ACP1:[a]										
B	183	203	876	112	290	172	149	111	113	152
A	34	9	67	12	42	26	15	9	13	14
GUA	11	18	175	0	0	0	0	0	0	0
GOT:										
1	186	12	162	124	75	186	104	117	120	166
2	42	0	2	0	5	7	2	0	4	0
3	0	0	0	0	0	3	0	3	2	0
TPI:										
1	238	230	1,100	124	315	198	158	120	126	162
3BRI	0	0	0	0	17	0	8	0	0	4
6PGD:										
A	228	224	995	124	332	198	166	120	126	166
C	0	6	103	0	0	0	0	0	0	0
LDHB:										
1	228	230	1,021	124	332	198	166	120	126	166
GUA	0	0	101	0	0	0	0	0	0	0

(*continued*)

Table 1 (continued)

Locus and Allele	Kuna	Bokota	Guaymi	Boruca	Bribri		Cabecar		Teribe	Guatuso
					Atlantic	Pacific	Atlantic	Pacific		
ESA2:										
1	228	229	1,116	124	332	198	166	120	126	166
BOK	0	1	0	0	0	0	0	0	0	0
Kidd:[a]										
JKA	75	27	122	49	59	130	50	70	21[b]	...
JKB	153	203	996	75	21	68	56	50	59[b]	...
GM:[a]										
AG	119	202	699	77	57	149	72	92	...	...
AXG	109	30	423	47	23	49	32	28	...	...
Lewis:[a]										
LE	47	21	322	61	33	85	62	69	...	...
LE(−)	181	209	796	63	47	113	44	51	...	...
KM:										
3	86	150	589	68	48	127	78	64	...	...
1	142	82	533	56	32	71	28	56	...	...
GALUT:										
N	201	203	975	111	77	188	92	118	...	...
DUARTE	27	27	125	13	3	2	14	0	...	...
GPT:										
2	172	8	99	54	69	178	77	88	...	...
1	56	4	65	70	11	20	29	32	...	...
GLO1:										
1	173	17	261	58	44	123	51	76	...	...
2	55	5	123	6	36	75	55	44	...	...
ADA:										
1	228	230	1,074	124	332	198	166	120	126	166
Kell:										
K(−)	228	230	1,118	124	80	198	106	120	126	160
CRPL:										
B	228	238	1,126	124	328	198	164	118	126	166
PEPB:										
N	228	230	1,116	124	332	198	166	120	126	166
ABO:										
O	228	230	1,118	124	80	198	106	120	126	166
ALB:										
N	228	238	1,126	124	328	196	164	120	126	166
ESA1:										
A	228	230	1,116	124	332	198	166	120	126	166
ESA3:										
A	228	230	1,116	124	332	198	166	120	126	166
ESAC:										
A	228	230	1,116	124	332	198	166	120	126	166
PGI:										
N	228	230	1,114	124	332	198	166	120	126	166
ICD:										
N	228	230	1,116	124	332	198	166	104	126	166
NP:										
N	228	230	1,074	124	332	194	166	120	126	166
LDHA:										
N	228	230	1,122	124	332	198	166	120	126	166
MDH:										
N	228	230	1,116	124	332	198	166	120	126	166

(*continued*)

Table I (continued)

Locus and Allele	Kuna	Bokota	Guaymi	Boruca	Bribri		Cabecar		Teribe	Guatuso
					Atlantic	Pacific	Atlantic	Pacific		
α-Globin:										
N	228	230	1,114	124	332	198	166	120	126	166
β-Globin:										
N	228	230	1,114	124	332	198	166	120	126	166
δ-Globin:										
N	228	230	1,102	124	332	198	166	120	126	166
PGM2:										
N	228	230	1,090	124	80	198	106	120	126	166
CA1:										
N	228	230	1,104	122	332	198	166	120	126	166
CA2:										
1	228	230	1,100	122	332	198	166	120	126	166
AK:										
1	228	230	1,104	124	332	198	166	120	126	166
PEPC:										
N	228	22	416	124	332	198	166	120	126	166
PEPD:										
1	228	22	416	124	332	198	166	120	126	166
G6PD:										
B	200	9	124	108	284	155	130	97	99	130
ESB:										
1	228	12	166	124	332	198	166	120	126	166

. . . Missing data, assays not attempted.

[a] Estimated by maximum likelihood procedures for dominant systems and rounded to the nearest whole allele for purposes of tabulation.

[b] Data from Matson et al. (1965).

the natural consequence of subsequent gene flow, the result is a series of estimates of "effective time" since divergence.

These reservations (generic to the exercise) notwithstanding, we shall use D_{XY} as our best estimate of the relative time since divergence, and we shall present the values above the diagonal in table 2. As anticipated from the history of the various groups, the two Bribri collections are very similar, as are the two Cabecar collections. In spite of a certain amount of local gene flow between the two tribes over the past 200–300 years, neither the Atlantic nor the Pacific communities are particularly cohesive across tribes. The Teribe appear to have separated first (i.e., diverged the most) from the other members of the Talamancan subgroup (Bribri, Cabecar, and Boruca). The Talamancan trio (Bribri, Cabecar, and Boruca) shows affinity with both the Guatuso to the west and the Guaymi and Bokota to the east. The Guaymi and Bokota are quite similar and show affinities with both the Talamancan trio to the west and the Kuna to the east. These are the same patterns of affinity we reported elsewhere (Barrantes et al. 1982), patterns based mostly on the Matson data available at that time (Matson et al. 1965; Matson and Swanson 1965*a*, 1965*b*). The new Guatuso acquisition fits into the pattern as the westernmost of the sampled tribes and perhaps has some affinities with the Nicaraguan Rama (Conzemius 1932; Greenberg 1987) or with the Huetar (now extinct) from central Costa Rica (Gabb 1875; Johnson 1948). The overall picture is that of a general east-to-west chain of affinity. The chain extends in both directions, beyond the boundaries of the present study; the western groups have affinities with the Nicaraguan Rama and Sumo, while the Kuna have affinities with the South American Chibcha, with whom they were neighbors until late in the pre-Columbian period (Barrantes et al. 1982).

Linguistic Analysis

A Linguistic Analogue

There are extensive lexicostatistical data on these same groups (Constenla 1981, 1985; Vargas 1986), data providing an unusual opportunity to obtain indepen-

Table 2

Nei's Genetic Distance Metric (D_{XY} × 10) for 10 Central American Groups (above the diagonal) and $\tilde{D}_{XY}$ × 10 (below the diagonal)

					BRIBRI		CABECAR			
	KUNA	BOKOTA	GUAYMI	BORUCA	Atlantic	Pacific	Atlantic	Pacific	TERIBE	GUATUSO
Kuna		.096	.095	.071	.127	.081	.059	.107	.178	.200
Bokota	.097		.021	.039	.088	.077	.081	.067	.145	.158
Guaymi	.096	.021		.042	.115	.087	.089	.097	.117	.183
Boruca	.072	.039	.043		.081	.073	.060	.063	.118	.179
Bribri:										
Atlantic	.128	.089	.116	.082		.037	.036	.028	.095	.116
Pacific	.082	.078	.088	.074	.037		.019	.031	.088	.099
Cabecar:										
Atlantic	.060	.082	.090	.061	.036	.019		.032	.105	.137
Pacific	.108	.068	.098	.064	.028	.031	.032		.126	.157
Teribe	.180	.146	.118	.119	.096	.089	.106	.127		.102
Guatuso	.202	.160	.184	.181	.117	.100	.138	.159	.103	

NOTE.—See text for definitions of distance metrics.

dent estimates of the affinities of the various groups and of their times since divergence. In brief, consider two populations—as before, the *X*th and *Y*th—and imagine a standard lexical item list of length *W*, each item the informational equivalent of a single genetic locus. Two languages are said to be cognate for a particular item if they are recognizably "the same" (allowing for regular phonemic shifts between the two languages). For the *w*th item, define an identity measure h_{XYw} as

$$h_{XYw} = \begin{cases} 1 \text{ if } X \text{ and } Y \text{ are cognate} \\ 0 \text{ otherwise} \end{cases} \qquad (5)$$

and obtain an average for the whole word list:

$$H_{XY} = \frac{\sum_{w=1}^{W} h_{XYw}}{W} = \frac{\text{No. (cognates)}}{\text{Total}} . \qquad (6)$$

The usual convention is to assume that only one form of the item is found in each population; if there are alternatives, it is customary to choose that word which predominates. This sacrifice of the linguistic equivalent of multiple alleles entails some loss of information but permits reduction of the linguistic identity measures within the two populations to the trivial forms

$$H_{XX} = 1 \text{ and } H_{YY} = 1 , \qquad (7)$$

by analogy with equation (2). By analogy with the equation (3), we therefore define an index of linguistic affinity between the *X*th and *Y*th languages as

$$K_{XY} = \frac{H_{XY}}{(H_{XX} \cdot H_{YY})^{1/2}} , \qquad (8)$$

which is simply the cognate fraction, since the denominator is unity.

The lexicostatistical data we shall use are gleaned from table II of Constenla (1985) and table II of Vargas (1986). Vargas (1986) provides contrasts among the Atlantic and Pacific dialects of both Bribri and Cabecar, but Constenla compares each of these languages with others on the basis of the average cognate frequencies for the two dialects. As was the case with genetic identity I_{XY}, the measure K_{XY} can be translated into an approximately time-linearized measure, of the form

$$C_{XY} = -\log K_{XY} \approx 2\beta t . \qquad (9)$$

Above the diagonal in table 3 we present data on C_{XY} for pairs of populations. There are various forms of C_{XY} found in the literature (Swadesh 1955, 1967; Hymes 1960; Dyen 1962*a*, 1962*b*, 1963; Lehman 1962; Greenberg 1987), but most can be directly translated into equation (9). All of the evolutionary and inferential reservations we expressed earlier for D_{XY} apply to C_{XY} as well. The theory for the decay of linguistic affinity is quite analogous to that for the decay of genetic affinity. As a consequence, we should expect the two processes to run in parallel. For these populations, in-

Table 3

Linguistic Distrance Matrix for 10 Central American Indian Groups: C_{XY} (above the diagonal) and $\tilde{C}_{XY}$ (below the diagonal)

					Bribri		Cabecar			
	Kuna	Bokota	Guaymi	Boruca	Atlantic	Pacific	Atlantic	Pacific	Teribe	Guatuso
Kuna		1.666	1.709	1.709	1.709		1.709		1.864	1.760
Bokota	.096		1.201	1.496	1.386		1.423		1.864	1.814
Guaymi	.101	.034		1.619	1.537		1.619		1.814	1.814
Boruca	.101	.065	.084		1.423		1.386		1.864	1.988
Bribri:										
Atlantic	.101	.051	.071	.055		.128	.582	.573	1.580	1.580
Pacific					.001		.646	.627		
Cabecar:										
Atlantic	.101	.055	.084	.051	.008	.009		.163	1.580	1.580
Pacific					.007	.009	.001			
Teribe	.139	.139	.125	.139	.077		.077			2.048
Guatuso	.112	.125	.125	.179	.077		.077		.202	

Note.—See text for definitions of distance metrics; raw data are drawn from Constenla (1985) and Vargas (1986).

asmuch as linguistic affinity is less than genetic affinity, we might anticipate that $\beta >> \alpha$, so that the "linguistic clock" would tick at a higher rate than would the "genetic clock."

Linguistic Relationships

The two dialects each of Bribri and Cabecar, each pair representing 200–300 years of documented separation, show measurable but minimal divergence. The next most similar languages are Bribri and Cabecar themselves. On the basis of these same linguistic data and standard decay rates, these two languages are thought to have diverged about 1,400 years ago (Constenla 1985; Vargas 1986). The next most similar languages are Guaymi (Ngawbere) and Bokota (Buglere), said to be mutually nonintelligible (Spielman et al. 1979; Gunn 1980)—but more similar to one another than is either Bribri or Cabecar to Boruca, another Talamancan language. Teribe is quite divergent from the other languages of the "Talamancan group," a result in keeping with its genetic divergence but *not* with the conventional taxonomy. Kuna and Guatuso are quite divergent both from each other and from all the other languages in our collections (Loukotka 1968; Greenberg 1987). The loose affinities of the Guatuso, in particular, lend little credence to the suggestion that they are closely allied to the Cabecar.

It is customary to scale linguistic affinity relative to some standard, frequently $K_{XY} = .85$ for 1,000 years of divergence, based on the calibrated decay rate for *written* European languages (Hymes 1960; Greenberg 1987), thus permitting an estimate of a "minimal time of divergence" for any pair of languages. This particular standard may not be applicable to these strictly verbal languages; we note that the dialectic divergence within the Bribri ($K_{XY} = .88$) and within the Cabecar ($K_{XY} = .85$), both probably representing less than 300 years of effective separation, argue for an accelerated decay rate for affinity of strictly verbal languages. We cannot settle the issue without an extraneous time reference, but we note here that, whatever the decay rates (α and β), D_{XY} and C_{XY} should be colinear in time if the theory is correct. The next step is to determine whether it is.

Genetic/Linguistic Relationships

The comparison of genetic and linguistic affinity is not a new activity, having been done several times and in a number of different fashions in past 20 years (e.g., see Spielman et al. 1974; Chakraborty et al. 1976; Long et al. 1986; Sokal et al. 1986). Using no more than knowledge of the family to which a language belongs (see Smouse 1982; Salzano et al. 1986), we have found the exercise to be instructive, and we have been even more successful where quantification has been possible (Spielman et al. 1974, 1979; Smouse et al. 1986; Sokal et al. 1986). To our knowledge, no one has ever had the opportunity to compare such detailed genetic and lexicostatistical data on the same groups; the matching data sets available here provide us with an unusual (perhaps unique) opportunity to make such a comparison.

Our approach to the analysis is correlational. We plot D_{XY} (table 2, above the diagonal) against C_{XY} (table 3, above the diagonal) in figure 2*a*. For this analysis, we average genetic distances of tribe *X* to each of the Bribri dialects, and we do so similarly for the Cabecar dialects, reducing the genetic distance matrix to the same form as the linguistic distance matrix. We maintain the full set of genetic distances within the Bribri-Cabecar complex, where we also have a linguistic contrast. The correlation between the two sets of measures is high ($r_{DC} = .69$), demonstrating a strong correspondence between the processes leading to decay of genetic and linguistic affinity. There is nevertheless an obvious departure from linearity; the interdialect points for the Bribri and Cabecar, as well as the contrasts between these closely related languages, show a steeper slope with regard to the genetic distances than do the contrasts of either Bribri or Cabecar with other languages. The relationship is better described by a saturation curve than by a straight line.

Rate Heterogeneity

The essential time linearity of C_{XY} has been documented (Swadesh 1967) for time periods of 1,000–2,000 years, but there are suggestions that the very early stages of dialectic divergence are more rapid than the later decay of affinity. One feature of linguistic decay that could easily cause such an apparent slowdown over time is the fact that some items are more resistant to change than are others (Hymes 1960; Greenberg 1987). Thus, more labile items would change rapidly during the early phases of divergence, while the more conserved items would change at a slower rate and later in the process. A similar situation exists with genetic loci, where some loci show more variation and evolve more rapidly than do others. Heterogeneity of the α value has been dealt with explicitly for genetic data. If the rate constant α varies among genetic loci, then the relationship between *D* and *t* is no longer linear. Nei et al. (1976) have shown that, if the variation of α among loci is described by a gamma distribution (with mean $\bar{\alpha}$ and coefficient of variation *a*), then the relationship between I_{XY} and $\bar{\alpha}$ takes the form

$$\tilde{I}_{XY} \cong \left[\frac{a}{a + 2\bar{\alpha}t}\right]^{a} \cdot \qquad (10)$$

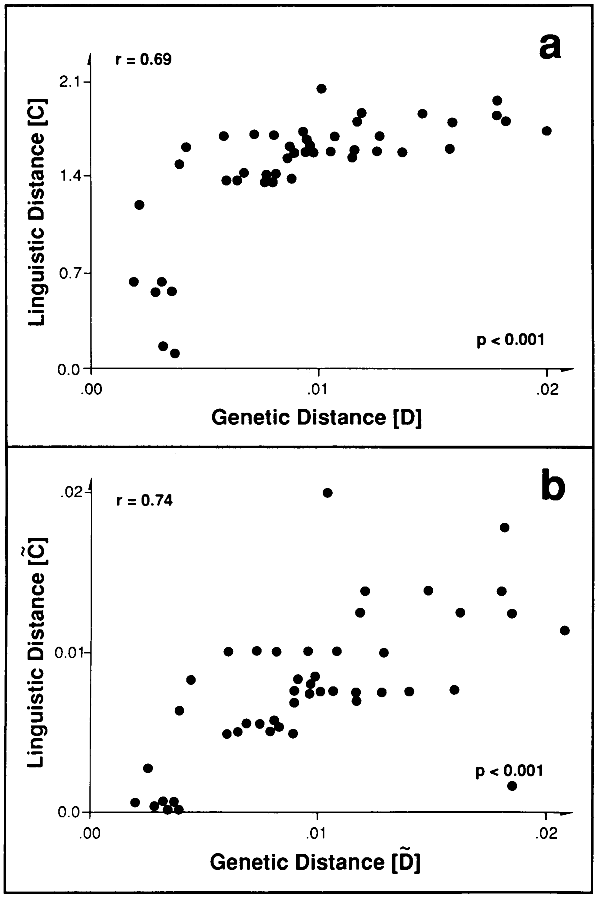

Figure 2 Bivariate plots of genetic and linguistic distances between pairs of groups of lower Central American Indians. *a*, Correlation of D_{XY} and C_{XY}, drawn from matching cells of the upper triangular portions of tables 2 and 3. *b*, Correlation of $\tilde{D}_{XY}$ and $\tilde{C}_{XY}$, drawn from matching cells of the lower triangular portions of tables 2 and 3.

Fortunately, this formula can be translated into a distance measure $\tilde{D}_{XY}$ that is linear with time (*t*):

$$\tilde{D}_{XY} = [1 - \tilde{I}_{XY}^{-a}]/a \cdot [\tilde{I}_{XY}^{-a}] \propto 2\bar{\alpha}t \, . \qquad (11)$$

The coefficient of variation in α values is thought to be about .8 in human studies (Nei et al. 1976), but D_{XY} and $\tilde{D}_{XY}$ are almost perfectly correlated for our data over the range ($0.0 \leqslant a \leqslant 2.0$). For populations as similar as ours ($\bar{\alpha}t$ small), the nonlinearity of *D* is not evident. Using a convenient value of $a = 1.0$ for equation (11), we present calculated values of $\tilde{D}_{XY}$ below the diagonal in table 2; the differences from D_{XY} are clearly trivial.

Given that rate heterogeneity is also suspected for the β coefficient of linguistic decay (Hymes 1960; Greenberg 1987), we use the same sort of gamma-distribution arguments concerning the average rate constant $\bar{\beta}$, defining the relationship between $\tilde{K}_{XY}$ and time as

$$\tilde{K}_{XY} \simeq \left[\frac{b}{b + 2\bar{\beta}t} \right]^{b}, \tag{12}$$

where b is the coefficient of variation of β across lexical items. This formula can also be translated into an equation for a time-linear measure $\tilde{C}_{XY}$:

$$\tilde{C}_{XY} = [1 - \tilde{K}_{XY}^{-b}]/b \cdot [\tilde{K}_{XY}^{-b}] \propto 2\bar{\beta}t\ . \tag{13}$$

In contrast to the experience with genetic distances, however, we discover that the degree of nonlinearity is very sensitive to b, and some correction for heterogeneity in β is clearly in order. By using the *same* transformation strategy for both genetic and linguistic distances, we have effectively compressed the linguistic scale, relative to the genetic scale, while preserving both monotonicity and rank order of both sets of measures.

Unfortunately, there is no extraneous information available to tell us what values of b we should use. Having empirically set $a = 1$, we propose to find a value of b such that $\tilde{C}_{XY}$ and $\tilde{D}_{XY}$ are roughly colinear. This is a statistical problem for which there is no ready-made solution, but simple iterative model fitting makes it clear that a value of $b = .5$ (with $a = 1.0$) restores linearity about as well as can be accomplished with these data. We claim no special statistical virtue for this choice of b except that it reduces the plot of $\tilde{C}_{XY}$ and $\tilde{D}_{XY}$ to colinear form (fig. 2*b*). The observed correlation is .74. The computed values of $\tilde{C}_{XY}$, standardized so that the largest value is the same as the largest computed value of $\tilde{D}_{XY}$, are presented below the diagonal in table 3.

Statistical Testing

What remains is to determine whether the correlation is statistically significant. The fact that all pairwise distances among groups are not independent renders most standard tests inappropriate. To circumvent this difficulty, we first place $\tilde{C}_{XY}$ and $\tilde{D}_{XY}$ in symmetric distance-matrix forms. A proper test of the null hypothesis of no correlation can be obtained by permutational analysis. The rows (and corresponding) columns of the $\tilde{D}$ matrix are randomly permuted, while those of the $\tilde{C}$ matrix are held constant. For each permutation, we compute the correlation coefficient between corresponding entries in the two matrices, building an empiric distribution of this criterion over 1,000 replicate permutations (Mantel 1967; Smouse et al. 1986). We discover that the Prob($r_{DC} \geqslant .74$) $< .001$ under the null hypothesis. The relationship is both strong and statistically compelling, entirely as expected from the parallelism of the exponential decay theories for genetic and linguistic affinity. Having forsaken the traditional forms of time relationship (eqq. [4] and [9]), however, we no longer have a convenient external time reference, but the results do confirm that the two decay processes run in parallel; indeed, they are roughly colinear, once allowance is made for differential rate heterogeneity.

A Geographic Perspective

With the exception of the data on the Teribe, both the genetic and linguistic distances are roughly congruent with geography, given the relative positions of the various groups along the Central American corridor. Recall that the pre-Columbian position of the Teribe is a bit tentative. Of course, to one degree or another, all the groups have relocated during the past 400 years; but the correlation between the pre-Columbian and modern localities is in excess of .96. The two sets of geographic distances are reported in table 4, with pre-Columbian distances above the diagonal and modern distances below the diagonal. It turns out that modern geographic positions are very slightly better predictors of genetic and linguistic affinities than are pre-Columbian positions, which presumably reflects a small amount of gene flow among tribes over the past 400 years (recall that we have removed the very recent intertribal gene flow). Although the differences are small, we will use the current locations for all of the formal geographic analyses that follow.

From a theoretical viewpoint, we should also expect a general relationship between genetic affinity and geographic proximity. Standard isolation by distance models (Wright 1943; Malécot 1969; Morton 1969) yield an expected relationship between genetic kinship and geographic separation of the form

$$I_{XY} \propto \phi \exp(-\gamma G_{XY})\ , \tag{14}$$

or (replacing D_{XY} with $\tilde{D}_{XY}$)

$$\tilde{D}_{XY} \propto \gamma G_{XY}\ . \tag{15}$$

Similar reasoning leads to a predicted relationship between linguistic affinity and geographic proximity that takes an analogous form:

Table 4

Pre-Columbian Geographic (G_{XY}) distances (above the diagonal) and Modern Distances (below the diagonal) for Central American Groups

					BRIBRI		CABECAR			
	KUNA	BOKOTA	GUAYMI	BORUCA	Atlantic	Pacific	Atlantic	Pacific	TERIBE	GUATUSO
Kuna		650	788	965	1,000		1,054		968	1,250
Bokota	403		90	320	353		400		306	598
Guaymi	500	30		145	184		234		100	432
Boruca	776	295	189		83		144		72	324
Bribri:										
Atlantic	713	299	100	63		0	50		40	260
Pacific	731	274	156	35	39					
Cabecar:										
Atlantic	750	319	125	90	20	40		0	60	202
Pacific	720	295	191	35	30	22	30			
Teribe	659	241	40	75	59	72	79	105		292
Guatuso	1,000	540	443	279	245	281	220	260	301	

NOTE.—All data are expressed in kilometers and have been computed from the midpoints of geographic ranges.

$$K_{XY} \propto \eta \exp(-\delta G_{XY}) \, , \qquad (16)$$

and, by analogously replacing C_{XY} with $\tilde{C}_{XY}$, we obtain

$$\tilde{C}_{XY} \propto \delta \, G_{XY} \, . \qquad (17)$$

We plot $\tilde{D}_{XY}$ against G_{XY}, the modern geographic distance (below the diagonal in table 4), in figure 3*a*, and we plot C_{XY} against G_{XY} in figure 3*b*. We discover that $r_{DG} = .49$ $(P < .084)$ and that $r_{CG} = .53$ $(P < .037)$. It is clear that there is a general trend toward increasing divergence with increasing geographic separation in both cases, but neither trend is very strong. Careful examination indicates that the genetic and linguistic distances of the Teribe to other groups are either too large or too small, relative to the corresponding geographic distances; moreover, the genetic and linguistic distances involving the Teribe do not behave the same way. Whether their pre-Columbian locale (fig. 1*b*) is misspecified or whether they had moved into the specified area at some earlier date is uncertain. There is also the possibility that the Teribe, more than a little disrupted both by contact with the Spaniards during the colonial period and by pirates and Miskito Indians in the 17th century, have diverged genetically and linguistically from their Talamancan relatives in different directions (Fernández-Guardia 1975; VonChong and Ortiz 1982). At this juncture, we have to wonder whether they should be included within the Talamancan subgroup at all. The question needs further work.

Discussion

A Combination Taxonomy

Although genetic, linguistic, and geographic affinity are meaningfully correlated, the relationships are not so compelling that all three sorts of information could be expected to yield precisely the same taxonomic groupings. This fact is shown in figure 4, where a UPGMA tree (Sneath and Sokal 1973) is constructed from each of the distance matrices, one each for $\tilde{D}_{XY}$, $\tilde{C}_{XY}$, and G_{XY}. All three representations share a pair of features in common: (*a*) tight clustering of the two Bribri and two Cabecar collections and (*b*) similar clustering of the Guaymi and Bokota.

How these two clusters relate to each other and to the other tribes varies somewhat from data set to data set. For genetic distances (fig. 4*a*), we see that the Teribe and Guatuso cluster together, the Boruca cluster with the Guaymi and Bokota, and that this trio then clusters with the Bribri and Cabecar. The Kuna are then attached to the others, with the Teribe and Guatuso being loosely related outliers. For linguistic distances (fig. 4*b*), the Bribri-Cabecar cluster is linked first with the Boruca, then with the Guaymi-Bokota cluster, and then with the Teribe, the Kuna, and the Guatuso. For the

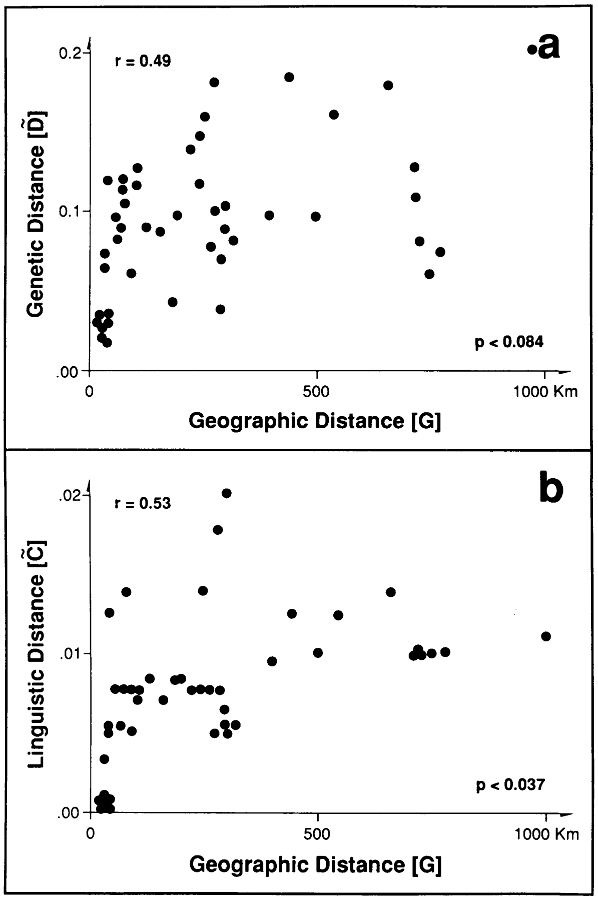

Figure 3 Correlations of genetic and linguistic distances with geographic distance. *a,* Plot of $\tilde{D}_{XY}$ against G_{XY}. *b,* Plot of $\tilde{C}_{XY}$ against G_{XY}. Observed correlations and random probabilities from permutational analysis are indicated.

geographic distances (fig. 4*c*), the Bribri-Cabecar cluster is linked first with the Boruca and then with the Teribe. This "Talamancan" cluster is linked next to the Guaymi-Bokota cluster, then to the Guatuso, and finally to the Kuna. What we see in general is that the shallower links of the tree are basically consistent across data sets but that the deeper links are rearranged. It is worth remembering, however, that the precision on the nodal positions decreases as we move back in time (i.e., deeper into the phylogeny), so that the deeper links are not at all well estimated. It is possible to test whether these various data sets yield trees that are significantly correlated (e.g., see Spielman et al. 1974), but these networks derive from the original distance matrices, and, with our matrix procedures, we have *already* answered that question about correspondence among data sets. There is no additional information in the derivative trees. Basically, they are correlated but not interchangeable.

It would be more useful to devise some means of combining different types of information into a single (joint) taxonomy. On the premise that the current geographic pattern is not highly correlated with either the genetic or linguistic patterns, we will concentrate on combining the genetic and linguistic data into a consensus representation. Since these two distance measures are roughly colinear, we might add them together (element by element) to obtain a consensus distance matrix, from which a consensus taxonomy could be derived. We could easily weight the two matrices differentially, of course, but there is no obvious way to decide what weights to use. Having already adjusted both matrices to the same (relative-time) scale, and lacking any clear reason to do otherwise, we have chosen to weight them equally. Formally, we define the matrix of taxonomic distances, T_{XY}, as

$$T_{XY} = \tilde{D}_{XY} + \tilde{C}_{XY} . \tag{18}$$

From this combination distance matrix (T_{XY}), we extract a combination taxonomy (fig. 4*d*), again using a UPGMA algorithm (Sneath and Sokal 1973). As might have been anticipated, the resulting tree is intermediate between those from genetic (fig. 4*a*) and linguistic (fig 4*b*) analyses. The Bribri and Cabecar cluster together, as do the Guaymi and Bokota. The Boruca and Teribe are tied to the Bribri and Cabecar in ascending order, and the Talamancan group is then connected to the Guaymi-Bokota cluster, which is then linked to the Guatuso, and then finally to the Kuna. Figure 4*d* is the best composite taxonomy available from the combined genetic and linguistic evidence. The tree still does not match the geography well, as regards the positions of the Boruca and Teribe. The Boruca are more similar to the Guaymi and Bokota than to the Bribri and Cabecar, and the Teribe are quite distant from both of these groups, hooking into the dendrogram only after the Kuna are added.

Any time translation of the tree would necessarily represent the imposition of numerous assumptions on the data, so that we should view the amounts of divergence in figure 4 as measures of relative time. Moreover, the tree analysis assumes that the only processes of interest are group fission and genetic and linguistic drift in geographic isolation. The histories of these various groups is such that at least a portion of the pattern observed is due to gene flow and its linguistic analogue. The tree is a representation of the phylogenetic process

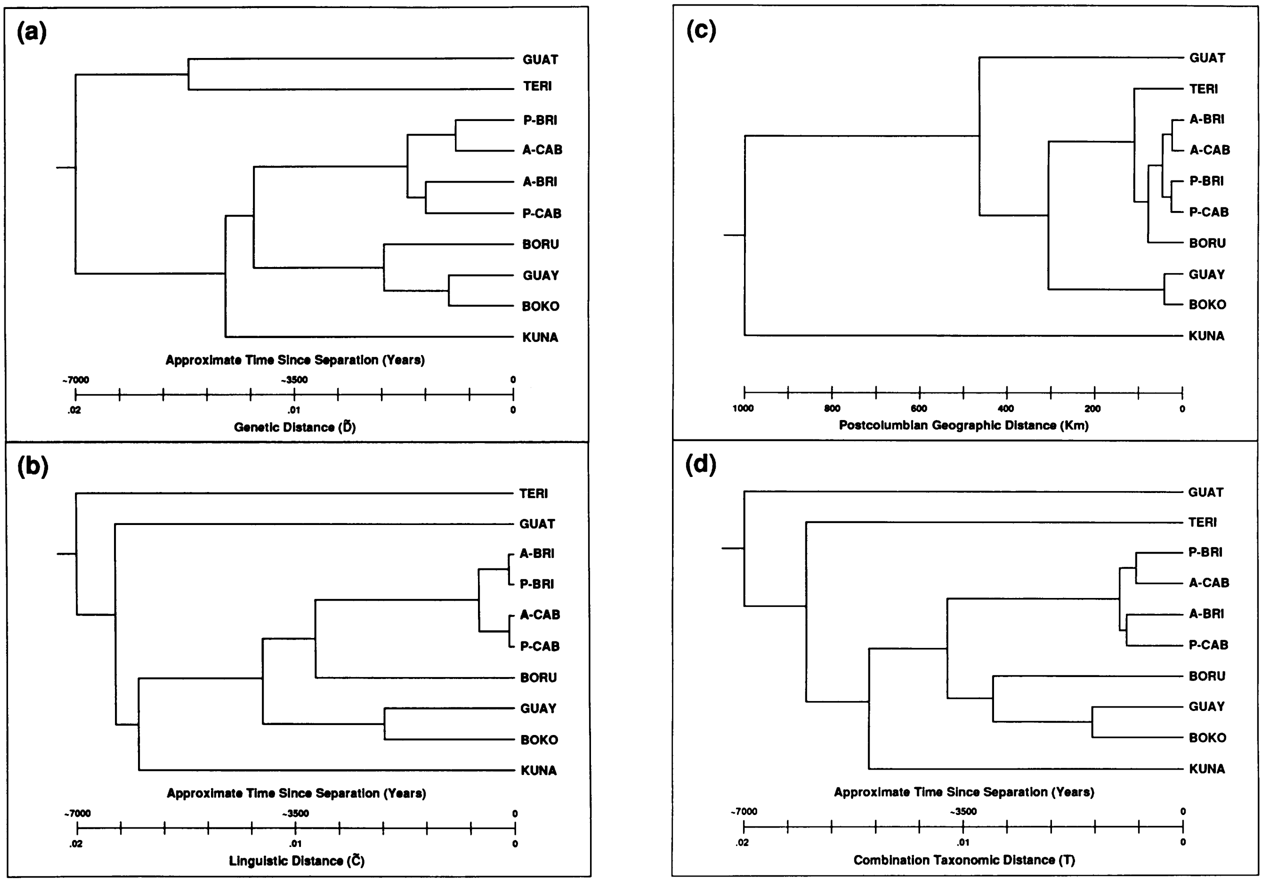

Figure 4 Phylogenetic reconstruction of 10 Chibcha-speaking groups of lower Central America, by using a UPGMA algorithm and (*a*) genetic ($\bar{D}_{XY}$), (*b*) linguistic ($\bar{C}_{XY}$), (*c*) geographic (G_{XY}), and (*d*) combination (T_{XY}) distances.

that would have led to the results we see, had the process been purely one of fission and drift. Any discussion of a time frame is subject to the same proviso—and should be approached with due caution.

Archaeological Perspective

Is there any help available from the archaeological record? A necessarily limited overview of a complex body of literature reveals some relevant observations: (*a*) Archaeological presence of Amerindians can definitely be demonstrated in lower Central America by 9000–8000 B.C., although earlier people must have passed through to South America (Bird and Cooke 1978; Snarskis 1979; Ranere and Cooke, in press). (*b*) Incipient agriculture is evident by 500 B.C. (Piperno et al. 1985), with evolution to widespread sedentary agricultural communities during the first millennium B.C. (Cooke 1984; Snarskis 1984; Hansell 1987). Nevertheless, while steady, demographic growth was slow in this region (at least until the end of the first millennium B.C.), in contrast to contemporary demographic trends in both Mesoamerica and South America. Two regional archaeological studies in western and central Panama (Linares and Ranere 1980; Cooke and Ranere 1984) suggest continuity between pre-Columbian and colonial era Indian populations. Today, these regions are occupied by the modern Guaymi and Bokota, respectively. It is reasonable to assume a similar situation in the neighboring Talamanca and Diquis regions, but the archaeological situation in eastern Panama is not clear at the moment. In central Panama, the in situ development of cultural features (e.g., lithic assemblages) can be traced to 5000 B.C., coincident with the early phases of sedentary horticulture (Cooke and Ranere 1984). (*c*) Hierarchical political societies developed between 300 B.C. and A.D. 500, over much of the isthmus (Linares and Ranere 1980; Cooke 1984; Snarskis 1984, 1987). Population growth was greater, and the pace of cultural change increased. (*d*) While there is evidence, dating to about 7000 B.C., of some cultural contact with people both north and south of the region, there is no evidence of population-sized movements from either zone during the past several thousand years. The available archaeological evidence is most compatible with an early occupation by, and limited migration thereafter of, the peoples in lower Central America.

The archaeological data are thus compatible with a deepest time depth (the deepest node in fig. 4*d*) of anything up to about 10,000 years. By that time, the primeval population of mobile hunter-gatherers had spread throughout the region. Given even the limited cultural, linguistic, and genetic diffusion that must have occurred within the region since that early date, the "effective time depth" must be shallower. Cooke (1984) suggests that division of the major stocks represented here (Guatuso and their kin, proto-Talamancan, proto-Guaymi/Bokota, and proto-Kuna) may have taken place as early as the beginnings of early horticulture (7,000 years ago). On the strength of such evidence, it is not unreasonable to set the deepest node in figure 4 at about 7,000 years ago and then to calibrate all other time depths accordingly. There is inevitably some guesswork involved in setting the time frame, but should later work necessitate either a stretching or a compression of the time scale, none of our inferences about the relationships among the groups would change.

Given the level of exchange that must have characterized these groups in the past, a purely phyletic interpretation of the hierarchical representations in figure 4 is obviously unwarranted. Inasmuch as the groupings run roughly east to west, we might legitimately ask whether a planar model (diffusion) of the relationships might not equally well represent the affinities in question. The answer to that question is implicit in the results of figures 3 and 4. Neither genetic nor linguistic pattern is very smoothly related to geographic pattern. These remnant Amerindian populations are geographically clustered, with large physical gaps in between, but the geographic clustering pattern is poorly correlated with either the genetic or linguistic pattern. Whether we view the east-to-west trend as the consequence of cultural, linguistic, and genetic diffusion over a patchy geography, or whether it represents the result of an imposition of a sequential fission pattern on an essentially linear geography is largely immaterial. The most plausible interpretation is that we have some of both and that a clear distinction would be difficult to make at this late stage of the process. Our conclusions parallel the cultural observations of Meyers (1978, p. 205): "Predictably what we find is that adjacent cultures tend to resemble each other more closely than they resemble more distant cultures. Conceptually, this could be viewed as a series of overlapping culture circles which link the civilizations at each end of the Intermediate Area." Some of the continuity almost surely represents exchange among neighboring groups over the past 10,000 years, but the clustering within the Central American Chibcha is almost certainly due to phyletic fission.

Private Variants

In addition, the Chibcha of lower Central America have genetic characteristics that distinguish them from the groups in Mesoamerica and northern South America—namely, a virtual absence of DI*A in most groups, high frequencies of TF*D-CHI and 6PGD*C, as well as polymorphic frequencies of five regionally restricted variants, TPI*3-BRI, TF*D-GUA, ACP*GUA1, LDHB*GUA1, PEPA*2-KUNA—lending credence to the idea that the peoples of this region have developed in situ over a very long period of time, without major intrusions from the outside (Neel et al. 1977*b*). The frequencies of these allelic variants are included in table 1 and in our analyses above. We will elsewhere discuss at some length how the distributions of these variants can be used to supplement the present treatment (E. A. Thompson, J. V. Neel, P. E. Smouse, and R. Barrantes, unpublished data). For the present, we note that these additional observations also argue for a relatively small founding population and for essential isolation of the Central American Chibcha over a long period. Cultural barriers and geographic isolation have contributed to an essential containment of both genetic and linguistic exchange within the region. Our results do not support the old view of the Intermediate Area (and lower Central America) as a well-traveled "frontier" between "mother cultures" to the north and south. Any such explanation would require recent waves of migration from outside the region. While there have been cultural influences from both directions, waves of migration are not compatible with either the genetic and linguistic data or with the archaeological history of the region.

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