reveal that from 32% to 42% of their genes have an Amerindian origin (Schanfield *et al.*, 1984). Thus, the only remaining evidence of the early presence of Caribs and Arawaks on St. Vincent Island is found among the genes of the highly admixed Black Caribs. The same is true for Dominica, where Afro-Amerindian populations exist to this very day.

There are a number of lessons to be learned from the three examples of New World depopulation provided in this chapter. The impact of imported diseases varied according to the form of subsistence of the affected population, the population density, the degree of geographic isolation, the nature of the conquest, and unique historical events that accompanied European contact. On the surface, the most severely affected population was on St. Vincent Island, where a combination of events including warfare, slavery, and epidemics almost annihilated the native population. However, some of the genes from the original Amerindian population were preserved in the Afro-Amerindian Black Carib population. In fact, St. Vincent's Amerindian component was transplanted to the coast of Central America, where it is currently found in almost 100 000 Garifuna distributed over a large geographic expanse. So, evolutionarily, St. Vincent's indigenous population was in fact successful, with the propagation and spread of its genes in new combinations through a colonizing group (see Figs. 17 and 18). Other island populations of the Caribbean were not as evolutionarily 'fortunate' and simply disappeared.

The Tlaxcaltecans were 'least affected' by their contacts with the Spanish, even though it is ludicrous to view the death of at least 200 000 Indians from a single valley as signaling the least affected! The mortality patterns of the Eskimos of St. Lawrence Island dramatically illustrate the results of synergistic effects of disease, starvation and cultural disruption all interacting and reducing the population from over 4 000 to 200 individuals in less than 50 years.

## 2.5 EVOLUTIONARY CONSEQUENCES OF POPULATION REDUCTION

The Conquest and its sequelae squeezed the entire Amerindian population through a genetic bottleneck. The reduction of Amerindian gene pools to from 1/3 to 1/25 of their previous sizes implies a considerable loss of genetic variabilty in New World populations. Who survived the epidemics? It is highly unlikely that survivorship was genetically random. Dubos (1965) reported that in the 1890s the annual death rate from tuberculosis was 9000 per 100 000 population. The Qu'Appelle Valley Indian reservation of Saskachewan experienced a tuberculosis epidemic in which half the families were eliminated, with some 50% of all children dying. Those families who

survived were likely to have been near the top of the normal range of variability in magnitude of protective response to the tuberculin bacillus. This epidemic is particularly perplexing, since recent molecular genetic evidence has demonstrated that pre-columbian mummies from Peru contained in nodules of their lung tissue a DNA sequence that is found only in TB bacteria, *Mycobacterium tuberculosis*. Thus, tuberculosis was not a disease introduced into the New World but was present there at Contact (Salo *et al.*, 1994). In addition to the question of who survived the epidemic of Qu'Appelle, the most interesting question concerns what precipitated such an epidemic of this New World disease. Most likely the answer is contained in the living conditions experienced by the Indians on the Qu'Appelle reservation. In early colonial times, the Amerindians lived under crowded conditions, with their immune systems weakened or compromised by malnutrition and poor sanitation.

If Amerindians of today are different from their pre-Conquest ancestors with respect to many genetic systems, most likely those genetic traits that confered some selective advantage under the conditions of the Conquest are more numerous among contemporary Amerindians. Thus, the present gene-frequency distributions of Amerindian populations may be distorted by a combination of effects stemming from genetic bottlenecks and natural selection. In addition, the gene frequencies of the native populations were further modified by the massive gene flow or admixture with Europeans and Africans, thus possibly obscuring the pre-Conquest patterns. As a result, great care should be exercised in the interpretation of sophisticated multivariate analyses of gene-frequency distributions among New World populations based upon samples collected by various researchers utilizing a diversity of sampling techniques.

## 2.6 IMPACT OF OLD WORLD DISEASES

The Amerindian populations of the New World evolved for centuries in relative isolation from Old World populations, who numerically constituted the world's majority. The cultural and demographic encounter between the Old and New Worlds is one of the most dramatic events in the history of humanity (Ramenofsky, 1982, 1987). The population of the New World was reduced from over 44 million persons down to 2 or 3 million in fewer than 100 years and was eventually conquered by a small group of Europeans.

Given the immense size of the aboriginal population of the New World at Contact, how could comparatively small numbers of settlers or Spanish conquistadores subjugate it? The primary weapon was disease. This was one of the first uses of 'biological warfare' on a massive scale. As Stewart (1960) concluded, 'smallpox and not Spanish armor was the decisive factor in the fall of Mexico in 1520.' In many cases, the Old World diseases preceded organized European invasions by as much as a century. Cook

(1973) points out that the New England coast was known to explorers from 1497 on and that European fishermen were off the coast of Newfoundland and Nova Scotia throughout the sixteenth century. Indeed, as indicated by Cook, an epidemic in 1617, three years before the settlement at Plymouth, had 'softened up' the local Natives. Percy Ashburn (1947) has argued that English settlement may not have been possible had disease imports not paved the way. Without the effects of smallpox, Francisco Pizarro would probably not have succeeded in his conquest of the Inca Empire of Peru. The first smallpox epidemic started in Vera Cruz, Mexico, during Cortez' first contact in 1519. This disease spread into Guatemala, and then into what is now northern Peru in 1524–26. The Inca ruler and his entourage, including the only legitimate heir, all contracted smallpox and died. The result of their demise was the division of the Empire between rivals, thus lessening Inca resolve and facilitating the conquest of the Empire. Disease imports were thus the Europeans' best weapons against the indigenous populations of the New World and probably served as lethal 'advance men' time and time again in the Conquest of the Americas. Marshall Newman, in lectures at the University of Washington used to stress that 'the West was won in the United States by giving Indians blankets infected with smallpox.'

Were the Amerindians genetically more susceptible to Old World diseases? Crosby (1974) quotes a German missionary who stated in 1699 that the Amerindians die so easily that 'the bare look and smell of a Spaniard causes them to give up the ghost.' Centerwall (1968), during an expedition to the Amazon forest, observed a measles epidemic strike a 'virgin soil' Yanomama population of South American Indians. The researchers were able to monitor the effects of this epidemic and concluded that the death toll from measles was no different than what was observed in European populations that had not been repeatedly exposed to the same disease. Malaria and yellow fever were diseases that were equally fatal to both Europeans and Indians when these diseases were brought into the New World by African slaves. In Europe, epidemics caused by smallpox, yellow fever, and influenza were extremely severe with high mortality. The mortality was somewhat higher in the New World because the disease effects were further exacerbated by starvation, slavery and physical exhaustion. Thus, it has been argued that Amerindians did not have any special sensitivity or susceptibility to imported Old World diseases.

If there were no special susceptibility, why then did the Old World disease imports so ravage the indigenous populations at European contact? There have been several explanations offered for this phenomenon.

### Cold screen

Stewart (1960) first explained the susceptibility of Amerindians in terms of his 'cold screen' theory. This theory suggests that the migration of Siberians through the Arctic

(Neel, 1962; Weiss *et al.*, 1984). However, a recent comparison of the three methods used by researchers for assessing Amerindian admixture in Mexican Americans (genealogical approach, skin-color reflectometry, and genetic markers) showed no association of NIDDM disease with degree of admixture in males. These three measures of admixture were also poorly correlated with each other. Mitchell *et al.* (1993) conclude that 'the three measures considered may assess different dimensions of admixture . . . .' Considering the high degree of African admixture reported for northern Mexico, it is surprising that Mitchell *et al.* used only a biracial model of admixture for the Mexican Americans of San Antonio (Crawford, 1976; Crawford *et al.*, 1979). A more appropriate model should have been triracial and included African, Spanish and Amerindian parental populations.

Similarly, Hanis *et al.* (1986) examined the possible relationship between estimates of individual admixture and risk from chronic diseases such as diabetes and gall-bladder disease. The individual admixture estimates were based upon 16 blood-group and protein loci, and a biracial hybrid model was applied to a population of Mexican-Americans from Starr County, Texas. The individual estimates were unrelated to the probability of being diabetic and marginally related to gall-bladder disease. Hanis *et al.* concluded that the independent assortment of loci precludes the use of this method, unless the loci used for estimating admixture are either linked to the disease or involved in its etiology (such as DNA candidate genes). An alternative explanation is that the biracial admixture model that was imposed on a triracially hybridized population caused too much statistical noise for the detection of a significant pattern. Hutchinson and Crawford (1981) also failed to demonstrate a statistically significant relation between risk of hypertension and individual estimate of African admixture (grouped into quartiles).

## 7.5 EPILOG

The 'native' inhabitants of the Americas have been swept along by two turbulent demographic and evolutionary events which have sculpted their gene pools and forever altered their societies. The first of these events was the peopling of the New World, in which Asians expanded into the Americas. Most likely this expansion was fueled by population pressures that forced Siberian groups across Beringia into two unpopulated continents containing a vast assortment of ecological niches as varied as the tundra, tropical forests, and deserts of the Americas. These populations were reproductively and culturally isolated from the remainder of the world for more than 30 000 years. Some gene flow must have continued from the Old World at various times and in varying magnitudes. Following the earliest Asian settlers (Paleo-Indians) came the

Na-Dene-speakers, and finally the Eskimos–Aleuts. In addition, small trickles of Asian Eskimos continued to cross the Bering Strait and intermingle with related groups on St. Lawrence Island, the Diomedes and the Alaskan mainland. Thus, some genes continued to flow from the Old World and may have prevented the further genetic differentiation of the New World populations. Evolutionarily, this peopling of the Americas can be viewed as a natural 'experiment' with genes made in Asia being 'tested' by the geographic diversity and selective forces of the New World.

The second unique historical event was the collision of the two worlds that had evolved separately for thousands of years. This contact resulted in the initial reduction and genetic bottleneck of the indigenous populations. The populations of the Americas were drastically reduced by disease, warfare, and slavery until the extinction of some groups and the attainment of a population nadir towards the end of the nineteenth century. This population reduction has forever altered the genetics of the surviving groups, thus complicating any attempts at reconstructing the pre-Columbian genetic structure of most New World groups. Massive population movements from Europe and Africa followed the Conquest of the New World and created admixed populations of Afro-Americans and Hispanic Americans. From the evolutionary viewpoint, these new combinations of genes 'tested' by environments that differ from their place of origin resulted in some success stories and some failures. The Garifuna (Black Caribs) amalgam of genes and cultures allowed them to be highly successful in their colonization of coastal Central America. However, many other groups quietly and tragically disappeared without much fanfare.

Despite this tragic history of oppression and death, the surviving North Amerindians have rallied and numerically attained pre-Contact population levels. Apparently, the improvement of health facilities and medical care has stemmed the downward spiral of population decline and lowered the morbidity and mortality rates of native Americans. Currently, with the decreases in mortality and increases in fertility, the Amerindians are the fastest-growing ethnic group in the United States. With recent developments in native businesses, successful litigation against the United States government concerning past treaties and rights, and overall improvements in their economic conditions, the future for the natives of the Americas looks much brighter. It is hoped that world opinion will help the Amerindian enclaves in Latin America survive the massive intrusions and destruction of their rain forest. As a species, we will be poorer if we continue to lose the ever-dwindling human biological and cultural diversity: our evolutionary heritage.