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Intestinal Helminths in Lowland South American Indians: Some Evolutionary Interpretations

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Abstract   Data on intestinal parasite infections for South American Indians in prehistoric times as revealed by coprolite analysis are being used to support transoceanic migration routes from the Old World to the New World. These same findings on modern semi-isolated aborigines, considered persisting prehistoric patterns, are also of great importance as indicators of pre-Columbian peopling of South America. This is the case for the Lengua Indians from Paraguay, studied in the 1920s, and the Yanomami and the Salumã from Brazil, studied in the 1980s. The intestinal parasitic profile of these groups can be empirically associated with culture change, but no clear correlations with the population biology of their hosts can be made at present because of scarcity of data.

It is well known that parasitologic knowledge can be applied to problems of Amerindian anthropology concerned with both prehistoric and contemporaneous groups. With prehistoric populations parasitology has thrown light on the controversy about the peopling of the American continent, supporting some alternative views on migration routes. With modern groups some studies have tried to detect a relationship between the parasitic profile, mainly that of intestinal helminthiasis, and the stages of cultural change of tribal groups in Amazonia.

Here we first comment on the most important results of paleoparasitologic research in South America and their implications for the theories explaining population movements to the New World in pre-Columbian times. Next, our data on intestinal parasitism of Amazonian tribes are analyzed along with earlier studies on other lowland South American Indians to detect typical patterns of infections for these groups. In conclusion, we suggest some lines of investigation to extend our knowledge of the nosology of these tribes and to integrate it with bioanthropologic and sociocultural research.

Intestinal Parasitism in Prehistoric Amerindians

Indirect evidence of prehistoric patterns of parasitism in Amerindian populations were obtained by Darling (1921) and Soper (1927) by studying isolated Indian groups in Paraguay. The proportion of the two hookworm species found in the Indians compared with those from the surrounding white population led Darling and Soper to suggest a transpacific origin for some South American tribal groups. This hypothesis was supported by archeologic theories proposed by Rivet (1926).

However, as discussed by Manter (1967) and Fonseca (1972), this indirect evidence could be innacurate because the contact of these groups with non-Indians was sufficient for the introduction of new parasites into the communities.

The finding of eggs and larvae of parasitic helminths in archeologic material started a new approach to this subject. Through radiocarbon dating and the study of the archeologic context, it has become possible to detect parasitic infections for specific times in geographic regions, and thus paleoparasitologic studies have become a standard set of data on prehistoric infection patterns.

The oldest known human parasitic infection is caused by *Enterobius vermicularis*, recorded by Fry and Moore (1969) in coprolites dated from 10,000 years ago. Since 1969 this parasite has been reported from archeologic sites of North and South America (Wilke and Hall 1985; Horne 1985; Araújo et al. 1985; Faulkner et al. 1989; Ferreira et al. 1989), suggesting its introduction through human prehistoric migrations across the Bering land bridge. The parasite can be directly transmitted from host to host without needing development in the soil; thus the parasite and its accompanying infection could have been maintained within the migration groups under the extremely cold conditions of Siberia and Alaska.

In South America the only finding of *E. vermicularis* in archeologic material is in the western Andean Mountains and in Argentina. It seems to have been a common infection in prehistoric times in Chile and Peru (Patrucco et al. 1983; Araújo et al. 1985; Ferreira et al. 1989). However, human coprolites from archeologic sites from Brazil have never revealed *Enterobius* infection. Paleoparasitologic data suggest an introduction dated from up to 10,000 years ago from North to South America along the west coast and a further southward migration of infected people to Argentina.

Human hookworm infection was recorded only in South America. Allison et al. (1974) found *Ancylostoma duodenale* adult worms in the intestine of a Peruvian mummified body, dated 900 B.C. Ferreira et al. (1980, 1983) found hookworm eggs and larvae in human coprolites, dated

2800 years B.P., from Brazilian archeologic sites. Ferreira et al. (1987) published the finding of hookworm eggs in human coprolites, dated 7230 years B.P., from an archeologic site in northeastern Brazil. This site is the oldest documented human settlement in the Americas, dated 48,000 years B.P. (Guidon and Delibrias 1986; Delibrias et al. 1988).

Archeologic data point to this ancient occupation of the region as a source of diffusion of cultural traits and art manifestations (Pessis 1987). It is still impossible to trace the parasite's dispersion route in prehistoric South America but, knowing the origin of the infection in the Old World through historical texts (Hoeppli 1959), we consider two ways of introduction. Because the parasite needs to pass through the soil, the Beringia route was discarded because the temperatures were too low (less than 22°C). Transpacific or transatlantic contacts of prehistoric Old World populations with the Americas emerged as a possible means of the parasite's introduction (Araújo et al. 1988). By the transpacific route the parasite may have come to South America with Asiatic fishermen long before the proposed contacts, based on cultural archeologic data from 3000 years B.C. (Meggers and Evans 1966). Transatlantic contacts were proposed by Alcina-Franch (1969), but these seem to have been possible only in the last 4000 years.

Trichuris trichiura is another parasite commonly found in South American human corpolites. This parasite has also been found in North American pre-Columbian coprolites (Reinhard et al. 1987; Reinhard 1988), and, as proposed by Confalonieri (1983), it could have been introduced by transpacific routes. As with the hookworm species, *T. trichiura* eggs also need a passage through the soil to become infective. On the other hand, *Ascaris lumbricoides* seems to have been a North American Indian infection that did not reach South America (Horne 1985; Reinhard et al. 1987; Faulkner et al. 1989).

As stressed by Reinhard (1988), animal parasite infections can be acquired by humans through peculiar feeding habits. For example, Patrucco et al. (1983) and Ferreira et al. (1984) found *Diphyllobothrium pacificum*, a sea lion parasite, in human coprolites; fish apparently acted as intermediate hosts.

As shown by paleoparasitologic data, most of the common intestinal helminths of modern humans were present in paleo-Indians. Their presence suggests past transoceanic movements of people from the Old World to the New World at times earlier than usually acknowledged (Araújo et al. 1988).

Another important consequence of these findings is that they indicate that in some regions of America specific host-parasite relationships have existed for thousand of years, resulting in a probable state of equilibrium with the Indian hosts before contact with outsiders. This must be

taken into consideration when interpreting morbidity and the new adaptations that occurred after the interruption of the original geographic isolation of the tribes.

Kliks (1990) discussed some aspects of the antiquity of humans and their host-parasite relationships based on paleoparasitologic data, and Reinhard (1988) pointed to the need to synthesize the current knowledge of paleoparasitology of prehistoric populations with different lifestyles. However, for a real assessment of the possible impact of these infections in past populations, a greater number of findings that could indicate prevalence or even parasite load are needed.

In the same sense, a broader knowledge of the spatial and chronologic distribution of these infections in precolonial times would contribute to the study of migration routes toward the interior of South America. Until now, paleoparasitologic data has shown different distributions of human helminths in North and South America, suggesting different migration movements and contacts among groups in the past.

Parasitism in Contemporaneous Indian Populations

Although more numerous than the prehistoric studies, we could find only 16 parasite surveys among lowland South American Indians in the literature. These results were appropriately summarized by Salzano and Callegari-Jacques (1988). To these we can add seven more investigations: Genaro and Ferraroni (1984), Kameyama (1985), Bourée et al. (1984), Penot et al. (1978), Chernela and Thatcher (1989), Confalonieri et al. (1989), Confalonieri (1983) (Table 1). The careful examination of these works shows a great diversity of objectives and research methods, which makes comparison difficult. However, the data reveal some general trends and allow some interpretations of the patterns of parasitism among the Indians.

The first is the high frequency of findings in the feces of Indians of rare (e.g., *Capillaria*) or unidentified helminth eggs. These findings can be attributed to the peculiar feeding habits of these people and to the close and continued contact with soil contaminated with wild animal feces.

Another trend observed is the high frequency of polyparasitism, (i.e., multiple-species infection in individual hosts) and the unexpected global absence of some species. However, a quantitative comparison of the findings of polyparasitism by the different researchers is difficult because some articles include commensal protozoan species of the intestines.

Although not typical of the Indian populations, multiple-species infections in these groups could have a special meaning as an indicator

Table 1. Prevalence (in percent) of Intestinal Parasites Observed in South American Indians

Parasite	Unknown (Colombia) (N=219)[a]	Cashibo (Peru) (N=165)[b]	Tukano/Maku (Brazil) (N=498)[c]	Xingu Indians (Brazil) (N=242)[d]	Nadeb/Maku (Brazil) (N=49)[e]	Yanomama (Brazil) (N=65)[f]	Salumá (Brazil) (N=57)[g]
Helminths							
Ascaris lumbricoides	52	55	75	18.5–75.7	61.2	6.6–14.3	–
Trichuris trichiura	37	55	77	0.0–13.1	67.3	20–43.4	–
Ancylostomid	32	72	96	80.7–91.6	95.9	30–74.2	66.6
Strongyloides stercoralis	37	5	3.5	10.4–36.4	12.2	0–3.3	–
Enterobius vermicularis	–	–	6	–	–	0–13.3	–
Taenia sp.	–	–	–	–	–	–	–
Hymenolepis nana	–	–	–	–	–	–	–
Capillaria sp.	–	–	–	–	–	2.8–6.6	–
Protozoans							
Entamoeba coli	19	50	63	74.1–77.6	32.6	–	57.8
Giardia lamblia	14	17	5	12.1–25.2	8.1	2.8–3.3	3.5
Entamoeba histolytica	26.5	24	6.6	49.5–52.6	36.7	28,5–40	43.8
Endolimax nana	8.6	50	5	16.8–31.1	16.3	–	33.3
Todamoeba butschlii	1.3	–	12	29.9–33.3	–	–	38.5
Chilomastix mesnili	–	–	30	14.1–26.2	4.0	–	14.0
Trichomonas hominis	–	6	6	–	2.0	–	–
Balantidium coli	–	6	6	–	–	–	–
Entamoeba hartmanni	8.6	–	–	–	–	–	–
Enteromonas hominis	–	–	3	–	–	–	–
Dientamoeba fragilis	1.8	–	–	–	–	–	–

a. Penot et al. (1978).
b. Bourée et al. (1984).
c. Chernela and Thatcher (1989).
d. Kameyama (1985).
e. Genaro and Ferraroni (1984).
f. Confalonieri et al. (1989).
g. Confalonieri (1983).

of culture change, as attempted by Lawrence et al. (1980). This study is possible if we assume that, because of the low density of prehistoric groups and their wide dispersion in a vast territory with only occasional contacts among them, the geographic distribution of the worm species at that time had wide regional variations and that this pattern persisted until just before contact. In this regard an example is the result obtained by Kameyama (1985) in four ethnic groups in central Brazil that were not infected by *T. trichiuna*. Because the other common nematodes (*Ascaris*, hookworms, *Strongyloides*) were present, the most parsimonious explanation is that the four groups were never-parasitized by this worm species, and, because of their relative isolation, no chance for the introduction of it occurred.

Although our results from the Yanomama should be considered preliminary because of the small number of samples, they show an interesting pattern in the distribution of *Ascaris*. In the central area of the Yanomama territory, where most villages at that time were semi-isolated or even completely isolated from outsiders, *Ascaris* was found in 2 of the 5 villages studied, with a low prevalence (2.5%). On the other hand, the prevalence was 43% in a community with frequent contact with non-Indians at the periphery of the formerly vast and untouched Yanomama territory. A more comprehensive investigation of these groups could confirm the existence of a progressive centripetal diffusion of *Ascaris*, which started with the end of isolation.

Even more revealing are our own findings on the Salumã, a small Indian group from the Amazon first contacted about 15 years ago. Since then they have been almost completely isolated, having only sporadic contacts with a few missionaries. Among the samples examined, of one-third of the village inhabitants, two-thirds were infected by hookworms and no other intestinal helminths were present. This is a remnant of a prehistoric pattern of infection and confirms the paleoparasitologic findings mentioned before, in which hookworm eggs and not *Ascaris* eggs were found in South American archeologic material.

With regard to the different prevalences for the three most common intestinal nematodes (*Ascaris, Trichuris*, and ancylostomids) obtained in the previous investigations, we can group the known factors that govern the occurrence of these infections in the three classical categories: factors related to the parasites, to the environment, or to the hosts. Among these the environmental factors probably have the least influence on patterns of occurrence, because the majority of the communities are situated in areas in which the climate is adequate for the development of the soil forms. The almost universal lack of sanitation facilities, which could reduce fecal pollution of the soil, must also be considered.

Concerning the factors related to the parasites, the most important are their life cycles, especially the life span of the adult worms, and the

minimal duration of the development of infective eggs and larvae in the soil and their maximum resistance. This is important if we consider the great mobility of some groups. For a continued reinfection to take place, the immature forms in the environment must evolve rapidly and the adults must live long in their hosts' bodies. In this way they would not be lost during the frequent changes of settlements. This could perhaps be taken as one possible explanation for the predominance of ancylostomids. Ancylostomids are the worms most commonly found in Indian groups in South America, as reported in 17 of the 23 studies analyzed. It must be remembered that most parasite surveys undertaken among rural and urban populations in the Third World reveal a striking predominance of *Ascaris* as the species with the highest prevalence in several different settings.

The role played by the hosts in the determination of the frequency and level of infection by intestinal worms is a complex one that is difficult to evaluate because of the interaction of a number of biologic, behavioral, and social factors. The most important biologic aspect is immunity, both innate and acquired. Although some groups of Amerindians have been fairly well studied with respect to their genetic aspects (Neel and Ward 1970; Layrisse et al. 1973; Neel and Weiss 1975; Salzano 1975; Long and Smouse 1983; Salzano and Callegari-Jacques 1988), because of the lack of specific studies on the genetic control of immune responses, particularly those to intestinal helminths, we cannot yet assert the existence of differential susceptibilities of some Indian groups to these infections.

In discussing the behavioral and social factors, which are closely linked to the cultural systems of the tribes, we must acknowledge that they have a strong influence on the patterns of acquisition, dispersion, and maintenance of the parasites in the communities. These factors are summarized in Table 2, with emphasis on how cultural changes can modify long-established host-parasite relationships.

Unfortunately, few of the studies mentioned tried to establish correlations between the parasitic profile and acculturation. But they observed the effects of environmental sanitation, sedentism, and physical isolation on parasitism and morbidity (Schwaner and Dixon 1974; Lawrence et al. 1980; Chernela and Thatcher 1989). However, these data should be considered carefully because no uniform criteria and quantitative methodologies were applied; comparison of results by different researchers is to a large extent not valid.

To obtain useful data, we must improve the research designs for fieldwork, including appropriate sampling techniques and statistical processing of the data. Also fundamental is the standardization of laboratory techniques and, for the cultural studies, the use of quantifiable analysis of cultural changes, a necessity already stressed by Salzano (1985).

Table 2. Acculturation Factors Influencing the Occurrence of Intestinal Helminth Infections in Amerindians

Factor	Effect
Disruption of geographic isolation	Introduction of formerly inexistent species
Sedentism and increase in population density	Increase in soil contamination
Changes in housing pattern and environment	Differential exposure to infection
Changes in patterns of individual and environmental hygiene	Increase chance of transmission
Social stress and malnutrition	Greater susceptibility to infection
Introduction of modern medicine	Use of antihelminthics
Genetic changes	Imbalance of long-established host-parasite relationships

Future Investigations

The study of infectious diseases in general and of parasitic diseases in particular has much to offer when integrated with the analysis of biologic and cultural variation of the hosts. What we need now are methodologic refinements for new and more comprehensive correlations. One example is the population analysis of human helminth infections. We presently know, thanks to the work of Anderson (1986), Bundy et al. (1987), Haswell-Elkins et al. (1989), and others, that the intestinal nematodes of humans have peculiar dynamics in their distribution within the host communities. It has been repeatedly demonstrated for several parasite species that they are not uniformly distributed. A small number of the individual hosts harbor the greater part of the parasite population, or, in other words, a few hosts are more susceptible to heavy parasite loads. They are the famous "wormy persons." The result is the so-called overdispersed distribution, which has important implications in morbidity, transmission, and control strategies.

What we still do not know clearly is how much of this general phenomenon is due to a genetically determined individual, group-enhanced susceptibility, or differential exposure to the infective forms in the environment. Irrespective of the predominating factor in a given context, if we want to obtain better results, parasitologic studies in tribal groups must go beyond the qualitative survey and analyze the spatial and individual distribution of the worm loads. This would enable us to elucidate the factors responsible for the clustering of the infections. Only in this way will we be able to compare the infectious profiles with demographic

aspects, genetic pools, patterns of space occupation, and social and individual behavior—factors that change rapidly with acculturation.

A potentially rich line of investigation is the combination of genetic studies with epidemiologic studies of helminthiasis. With this approach we will perhaps be able to demonstrate empirically through population studies—even without experimental immunologic evidence—the existence of genetic susceptibility to these parasites, so long as specific parasite profiles can be correlated with genetically homogeneous groups. This could be complemented by studies of the social and cultural factors that are responsible for marriage practices and kinship ties. Because kinship may influence the genetic composition of groups and subgroups, we would thus have an indirect relationship between culture and the infectious profiles mediated by the genetic pool and the immune response.

South American Indian groups are particularly suited for these integrated studies because of their special characteristics, for example, the relative geographic isolation of many groups, which makes them almost closed to the reintroduction of macroparasites, and because of the small size of their communities. Other characteristics are the better possibilities for the study of the processes of genetic differentiation, a greater correlation between household occupation and the genetic structure of the groups, and the opportunities for following the progressive biologic, behavioral, and social changes that occur after contact with non-Indian national societies.

Literature Cited

Alcina-Franch, J. 1969. Origen transatlantico de la cultura indígena de America. *Rev. Esp. Antropol. Am.* 4:9–64.

Allison, J.M., A. Pezzia, I. Hasegawa, and E. Guerszten. 1974. A case of hookworm infestation in pre-Columbian America. *Am. J. Phys. Anthropol.* 41:103–106.

Anderson, R.J. 1986. The population dinamics and epidemiology of intestinal nematode infections. *Trans. R. Soc. Trop. Med. Hyg.* 80:686–696.

Araújo, A.J.G., L.F. Ferreira, U.E.C. Confalonieri, and M. Chame. 1988. Hookworms and the peopling of America. *Cadernos de Saúde Pública* (Rio de Janeiro) 40:226–233.

Araújo, A.J.G., L.F. Ferreira, U.E.C. Confalonieri, L. Nuñez, and B.M. Ribeiro Filho. 1985. The finding of *Enterobius vermicularis* eggs in pre-Columbiam human coprolites. *Mem. Inst. Oswaldo Cruz* 80:141–143.

Bourée, P.D., D. Basset, O. Coco, B. Beauvais, M.C. David-Julien, and A. Pugnet. 1984. Enquete épidémiologique sur les parasitoses intestinales en Amazonie péruvienne. *Bull. Soc. Pathol. Exot. Filiales* 77:690–698.

Bundy, D.A.P., E.S. Cooper, D.E. Thompson, J.M. Didier, and I. Simmons. 1987. Epidemiology and population dynamics of *Ascaris lumbricoides* and *Trichuris trichiura* infection in the same community. *Trans. R. Soc. Trop. Med. Hyg.* 81:987–993.

Chernela, J.M., and V.E. Thatcher. 1989. Comparison of parasite burdens in two native Amazonian populations. *Med. Anthropol.* 10:279–285.

Confalonieri, U.E.C. 1983. Paleoparasitologia do gênero *Trichuris* Roederer, 1761 com um estudo paleoepidemiológico sobre a origem do *Trichuris trichiura* (Linn.; 1771) na América. D.Sc. dissertation, Universidade Federal Rural do Rio de Janeiro.

Confalonieri, U.E.C., A.J.G. Araújo, and L.F. Ferreira. 1989. Enteroparasitos em Índios Yanomami. *Mem. Inst. Oswaldo Cruz* 84(suppl. 4):111–113.

Darling, S.T. 1921. Observations on the geographical and ethnological distribution of hookworms. *Parasitology* 12:217–233.

Delibrias, G., N. Guidon, and F. Parenti. 1988. The Toca do Boqueirão do Sítio da Pedra Furada: Stratigraphy and Chronology. In *Early Man in the Southern Hemisphere*, J.R. Presco, ed. Supplement to Archaeometry, Australian Studies 1988, Adelaide, 3–11.

Faulkner, C.T., S. Patton, and S.S. Johnson. 1989. Prehistoric parasitism in Tennessee: Evidence from the analysis of desiccated fecal material collected from Big Bone Cave, van Buren County, Tennessee. *J. Parasitol.* 75:461–463.

Ferreira, L.F., A.J.G. Araújo, and U.E.C. Confalonieri. 1980. The finding of eggs and larvae of parasitic helminths in archaeological material from Unaí, Minas Gerais, Brazil. *Trans. R. Soc. Trop. Med. Hyg.* 74:798–800.

Ferreira, L.F., A.J.G. Araújo, and U.E.C. Confalonieri. 1983. The finding of helminth eggs in a Brazilian mummy. *Trans. R. Soc. Trop. Med. Hyg.* 77:65–67.

Ferreira, L.F., A.J.G. Araújo, U.E.C. Confalonieri, and J.M.D. Lima. 1989. *Trichuris trichiura* eggs in human coprolites from the archaeological site of "Furna do Estrago," Brejo de Madre de Deus, Pernambuco, Brasil. *Mem. Inst. Oswaldo Cruz* 84:581.

Ferreira, L.F., A.J.G. Araújo, U.E.C. Confalonieri, and L. Nuñez. 1984. The finding of eggs of *Diphyllobothrium pacificum* in human coprolites (4100–1950 B.C.) from northern Chile. *Mem. Inst. Oswaldo Cruz* 79:175–180.

Ferreira, L.F., A.J.G. Araújo, U.E.C. Confalonieri, M. Chame, and B.M. Ribeiro Filho. 1987. Encontro de ovos de Ancilostomídeos em coprólitos humanos datados de 7232 ± 80 anos. *An. Acad. Bras. Cienc.* 59:280–281.

Fonseca, O. 1972. *Parasitismo e migrações humanas pré-históricas.* Rio de Janeiro: Mauro Familiar Editor.

Fry, G.F., and J.G. Moore. 1969. *Enterobius vermicularis*: 10,000 years of human infection. *Science* 166:1620.

Genaro, O., and J.J. Ferraroni. 1984. Estudo sobre malária e parasitoses intestinais em indígenas da tribo Nadéb-Maku, Estado do Amazonas, Brasil. *Rev. Saude Publica* 18:162–169.

Guidon, N., and G. Delibrias. 1986. Carbon 14 dates point to man in the Americas 32,000 years ago. *Nature* 324:769–771.

Haswel-Elkins, M., D. Elkins, and R.M. Anderson. 1989. The influence of individual, social group, and household factors on the distribution of *Ascaris lumbricoides* within a community and implications for control strategies. *Parasitology* 98:125–134.

Hoeppli, R. 1959. *Parasites and Parasitic Infections in Early Medicine and Science.* Singapore: University of Malaya Press.

Horne, P.D. 1985. A review of the evidence of human endoparasitism in the pre-Columbian New World through the study of coprolites. *J. Archeol. Sci.* 12:299–310.

Kameyama, I. 1985. Parasitoses intestinais entre os Índios do Parque Nacional do Xingu: Alguns aspectos epidemiológicos e ecológicos. M.Sc. dissertation, Universidade de São Paulo.

Kliks, M.M. 1990. Helminths as heirlooms and souvenirs: A review of the New World paleoparasitology. *Parasitol. Today* 6:93–100.

Lawrence, D.N., J.V. Neel, S.H. Abadie, L.L. Moore, L.J. Adams, G.R. Healy, and I.G. Kagan. 1980. Epidemiologic studies among Amerindian populations of Amazonia. III. Intestinal parasitoses in newly contacted and acculturating villages. *Am. J. Trop. Med. Hyg.* 29:530–538.

Layrisse, A., M. Layrisse, I. Malavé, P. Terasaki, R.H. Ward, and J.V. Neel. 1973. Histocompatibility antigens in a genetically isolated American Indian tribe. *Am. J. Trop. Med. Hyg.* 29:493–509.

Long, J.G., and P.E. Smouse. 1983. Intertribal genetic flow between the Ye'cuana and Yanomama: Genetic analysis of an admixed village. *Am. J. Phys. Anthropol.* 61:441–442.

Manter, H.W. 1967. Some aspects of the geographical distribution of parasites. *J. Parasitol.* 53:1–9.

Meggers, B.J., and C. Evans. 1966. A transpacific contact in 3000 B.C. *Sci. Am.* 214:35–38.

Neel, J.V., and R.H. Ward. 1970. Village and tribal genetic distance among American Indians, and the possible implications for human evolution. *Proc. Nat. Acad. Sci. USA* 65:323–330.

Neel, J.V., and K.M. Weiss. 1975. The genetic structure of a tribal population, the Yanomama Indians. XVII. Biodemographic studies. *Am. J. Phys. Anthropol.* 42:25–32.

Patrucco, R., R. Tello, and D. Bonavia. 1983. Parasitological studies of coprolites of pre-Hispanic Peruvian populations. *Curr. Anthropol.* 24:393–394.

Penot, C., H. Pigot, and M.L. Grillot. 1978. Exercicie de la Médicine chez les Indiens d'Amazonie Colombienne: Épidémiologie des parasitoses intestinales. *Bull. Soc. Pathol. Exot. Filiales* 71:334–341.

Pessis, A. 1987. Art rupestre pré-historique: Prémieres registres de la mise en scene. Thèse pour le Doctorat d'Etat, Université de Paris.

Pizzi, T., and H. Schenone. 1954. Hallazgo de huevos de *Trichuris trichiura* en contenido intestinal de un cuerpo arqueologico incaico. *Bol. Chil. Parasitol.* 9:73–75.

Reinhard, K.J. 1988. Cultural ecology of prehistoric parasitism on the Colorado Plateau as evidenced by coprology. *Am. J. Phys. Anthropol.* 77:355–366.

Reinhard, K.J., R.H. Hevly, and G.A. Anderson. 1987. Helminth remains from prehistoric Indian coprolites on the Colorado Plateau. *J. Parasitol.* 73:630–639.

Reinhard, K.J., U.E.C. Confalonieri, B. Herrmann, L.F. Ferreira, and A.J.G. Araújo. 1987. Recovery parasite remains from coprolites and latrines: Aspects of paleoparasitological technique. *Homo* 37:217–239.

Rivet, P. 1926. Les Malayo: Polinésiens en Amerique. *Journal de la Societé de Americanistes de Paris*, n.s., 18:141–278.

Salzano, F.M. 1975. Padrões de variação biológica e cultural em Índios sulamericanos. *Cienc. Cult.* 27:1202–1208.

Salzano, F.M. 1985. Parasitic load in South American tribal populations. Paper presented at the 98th Symposium on The Health and Disease of Populations in Transition, October 19–27, 1985, Santa Fe, New Mexico.

Salzano, F.M., and S.M. Callegari-Jacques, eds. 1988. *South American Indians: A Case Study in Evolution*. Oxford: Oxford University Press.

Schwaner, T.D., and C.F. Dixon. 1974. Helminthiasis as measure of cultural change in the Amazon Basin. *Biotropica* 6:32–37.

Soper, F.C. 1927. The report of a nearly pure *Ancylostoma duodenale* infestation in native South American Indians and a discussion of its ethnological significance. *Am. J. Hyg.* 7:174–184.

Wilke, J.P., and H.F. Hall. 1985. Analysis of ancient feces: A discussion and annoted bibliography. Archeological Research Facility, Department of Anthropology, University of California, Berkeley.