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Dairying barriers affect the distribution of lactose malabsorption

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Abstract

Most mammals stop drinking milk at weaning, which is also the time when they cease producing lactase, the digestive enzyme that hydrolyzes lactose. Cessation of lactase production and milk drinking also characterize most human populations, especially those of African and Asian descent. However, a genetic mutation that maintains the functionality of lactase production into adulthood occurs commonly among populations from northern Europe, where dairying is practiced routinely. Indeed, the ability to absorb lactose is nutritionally beneficial for adults only if milk consistently is available. What determines the distribution of dairying? We hypothesized that specific environmental circumstances affect where milk-producing ungulates can be raised safely and economically, thus influencing the geographical occurrence of dairying and lactase persistence. To evaluate this hypothesis, we compiled data on adult lactose absorption (LA) and malabsorption (LM) frequencies in 270 indigenous African and Eurasian populations (Appendix A). Partial correlation analyses revealed that, as predicted, adult LM is associated with extreme climates (at high and low latitudes) and, more significantly, with the historical (pre-1900) geographical occurrence of nine deadly, communicable diseases of cattle. These results suggest that areas where adult LM predominates are those where it is impossible or dangerous to maintain dairy herds.

Keywords: Lactase persistence; Lactose malabsorption; Cattle diseases; Dairying barriers; Sleeping sickness; Anthrax; Cholera; Malaria; Nomadism

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1. Introduction

Most mammals stop producing lactase, the enzyme that hydrolyzes lactose, at weaning; thereafter, they are intolerant of milk (Johnson, Kretchmer, & Simoons, 1974). The cessation of lactase production at weaning and adult lactose malabsorption also predominate among humans, particularly peoples of Asian and African descent. However, some populations, particularly those of northern European and Scandanavian descent, exhibit high frequencies of lactase persistence. These people can continue to drink milk throughout life (Flatz, 1989; Flatz & Rotthauwe, 1971; Simoons, 1978, 1982). Considerable information has recently become available about the physiological mechanisms and molecular bases of the adult lactase polymorphism (reviewed by Swallow, 2003; Swallow & Hollox, 2000).

However, the historical ecology and distribution of adult lactose absorption (LA) and malabsorption (LM) have, for decades, intrigued geneticists (e.g., Cavalli-Sforza, 1973; Flatz, 1987, 1989; Flatz & Rotthauwe, 1971) and nutritional ecologists (Durham, 1991; Simoons, 1970, 1971, 1982). Genetic evidence indicates that the lactase polymorphism arose recently (5,000–10,000 years ago) and spread rapidly due to strong positive selection (Bersaglieri et al., 2004; Hollox et al., 2001). Today, lactase persistence occurs far north and south of the equator in Africa and Asia, far from its putative areas of origin (Flatz, 1987; Hollox & Swallow, 2002). Puzzlingly, in some parts of Africa and the Middle East, lactase-persistent populations have lived side-by-side with populations of lactose malabsorbers throughout recorded history (Flatz, 1987, 1989; Simoons, 1978; Swallow, 2003).

The leading hypothesis to explain the geographical distribution of adult LA and LM is that nutritional advantages of lactose digestion confer a selective advantage on lactase-persistent phenotypes in areas where milk is reliably available throughout adult life, that is, where dairying is practiced regularly. This "culture–historical hypothesis" (McCracken, 1971; Simoons, 1970) has received considerable support (Durham, 1991; Hollox et al., 2001; Simoons, 1978, 2001; Swallow, 2003), including, most recently, from (1) a maximum likelihood analysis that used genetic and linguistic trees to control for the effects of relatedness among subject populations (Holden & Mace, 1997) and (2) a study of single-nucleotide polymorphisms covering 3.2 Mb around the lactase gene, which indicated that alleles associated with lactase persistence have been subject to strong selection within the past several thousand years (i.e., in the setting of dairy farming: Bersaglieri et al., 2004).

The culture–historical hypothesis does not address the important antecedent question: Why is dairying practiced in some areas but not in others? Obviously, the geographical occurrence of dairying depends, proximally, on cultural traditions (McCracken, 1971; Simoons, 1970). We hypothesize that, ultimately, it depends on ecological factors that affect whether milk-producing ungulates, particularly cattle, can be raised in a given area. For example, extreme climates could make it impossible to keep dairy herds outdoors year-round, especially where forage is sparse, such as in extremely cold or hot climates (e.g., tundra, deserts, or rain forests). Moreover, in certain locales, endemic pathogens may debilitate or kill the animals, thereby making herding uneconomical, or even hazardous if the disease is transmissible to humans. Indeed, dairy herding is rare in Africa within the range of the tse-tse fly, which is the major vector of sleeping sickness (Simoons, 1982; Smith, 1992).

We evaluated this ecological "dairying barrier" hypothesis by synthesizing information on the frequencies of adult LA and LM among indigenous African, Asian, and European populations. Parallel information from indigenous peoples of North and South America and Oceania is not available. We also compiled data on latitude, climate (temperature), and the historical distributions (before 1900) of communicable and potentially fatal diseases of cattle. Relationships among these variables and lactase phenotypes were examined statistically.

2. Methods

We gathered and synthesized all published data on the frequencies of primary adult LA and LM throughout the world. Data in previous compilations by Flatz (1989), Holden and Mace (1997), Simoons (1970, 2001), and Swallow and Hollox (2000) were verified from original sources and augmented using online databases and searches of the primary literature. Our entire data set, which includes LA/LM information from 270 populations and their associated references, is presented as an electronic appendix (Appendix A) to this paper, to facilitate use by future investigators. We believe that it is the most comprehensive compilation of adult LA/LM information currently available.

For analyses, we subsampled the appendix database (Appendix A) to identify populations that met five criteria of accuracy, completeness, and adequacy of sample sizes: (i) n=≥20 subjects; (ii) subjects were ≥10 years old (i.e., weaned); (iii) subject population was not of "mixed" origin; (iv) subject population lived in its country of origin (i.e., nonimmigrants and nonnomadic); and (v) the country of origin was in Europe, Asia, or Africa. For each population that met all five criteria, we determined the latitude and mean annual temperature using the city where each study took place (or the closest major city) as the point of reference. Data were analyzed using Pearson correlations, partial correlations, and multiple regressions in Statview 2. Before analysis, LM frequency data were transformed (arcsine square root) to achieve normality.

Domesticated, milk-producing ungulates include goats, sheep, camels, and cattle; the latter are, by far, the most common sources of milk (Simoons, 1970, 1971). We synthesized information on the historical geographical occurrence of communicable, deadly diseases of cattle, based on an exhaustive search of the veterinary literature, for each of the countries represented by the populations in our final sample. We used only sources that included a dated map showing the distribution of each disease and included only diseases whose geographical distribution, prior to 1900, was confirmed by ≥2 independent sources. Thus, we took into careful account the changes in the distribution of each disease due to recent spread (since 1900) and eradication efforts (generally beginning in the 1960s). We included in our analyses every disease for which it was possible to obtain appropriate and reliable information.

3. Results

LM data that fulfilled our five criteria of accuracy and completeness were available from 91 populations in 39 countries, ranging latitudinally from southern Africa to southern

Table 1
Mean adult lactose malabsorption frequencies in 39 Eurasian countries (n = number of subjects), and information on latitude, temperature, number of deadly endemic cattle diseases found there historically (pre-1900), and sources of LM data

	n	Average LM	Average lat.	Average temperature (°C)	Number of diseases	Reference
Afghanistan	210	0.85	35.70	12.61	5	Rahimi, Delbrück, Haeckel, Goedde, and Flatz, 1976
Austria	347	0.20	47.65	9.08	2	Rosenkranz et al., 1982
Botswana	22	0.91	24.45	15.61	6	Nurse and Jenkins, 1974
Britain	75	0.05	51.50	11.72	3	Ho, Povey, and Swallow, 1982
China	641	0.85	41.17	5.76	4	Yongfa, Yongshan, and Jiujin, 1984
Denmark	700	0.03	55.80	7.67	2	Busk, Dahlerup, Lytzen, Binder, and Gundmand-Hoyer, 1975; Gudmand-Høyer, Dahlqvist, and Jarnum, 1969
Egypt	654	0.67	28.76	20.50	3	Hussein, Flatz, Kühnau, and Flatz, 1982
Finland	293	0.18	60.10	2.50	1	Jussila, 1969; Jussila, Isokoski, and Launiala, 1970
France	117	0.33	45.95	12.64	3	Cuddenec, Delbrück, and Flatz, 1982; O'Morain, Loubiere, Rampal, Sudaka, and Delmont, 1978
Gabon	20	0.60	0.40	25.50	5	Gendrel et al., 1989
Germany	1226	0.15	51.02	8.67	3	Flatz, Howell, Doench, and Flatz, 1982
Greece	700	0.56	9.00	17.64	3	Kanaghinis et al., 1973
Greenland	106	0.86	66.65	−1.39	0	Gudmand-Høyer, McNair, and Jarnum, 1973
Hungary	558	0.39	47.40	12.21	3	Czeizel, Flatz, and Flatz, 1983
India	100	0.64	18.60	26.89	5	Desai, Gupte, and Pradhan, 1970
Iran	21	0.86	35.40	16.61	4	Sadre and Karbasi, 1979
Ireland	50	0.04	53.20	9.28	1	Fielding, Harrington, and Fottrell, 1981
Israel	67	0.81	32.00	19.39	3	Gilat, Gelman, and Shochet, 1971
Italy	553	0.78	41.09	13.91	3	Burgio et al., 1984; Meloni, Columbo, Ruggiu, Dessena, and Meloni, 1998; Rinaldi et al., 1984; Zuccato et al., 1983
Japan	40	0.73	40.30	10.00	4	Yoshida, Sasaki, and Goto, 1975

Table 1 (*continued*)

	n	Average LM	Average lat.	Average temperature (°C)	Number of diseases	Reference
Jordan	204	0.76	31.40	14.25	3	Hijazi, Abulabin, Ammarin, and Flatz, 1983; Snook, Mahmoud, and Chang, 1976
Lebanon	74	0.78	33.50	20.61	3	Nasrallah, 1979
Namibia	40	0.92	19.60	22.00	6	Jenkins, Lehmann, and Nurse, 1974
Nigeria	72	0.78	8.86	25.75	6	Kretchmer, Ransomek, Hurwitz, Dungy, and Alakija, 1971; Olatunboson and Adadevoh, 1971
Pakistan	480	0.60	30.32	20.82	5	Abbas, 1984; Ahmad and Flatz, 1984
Poland	190	0.38	51.45	7.46	3	Socha and Ksiaszyk, 1984
Rwanda	86	0.77	2.00	21.00	7	Cox and Elliot, 1974
Siberia	61	0.87	61.10	−2.89	0	Lember et al., 1995
South Africa	79	0.76	26.20	16.50	6	Segal, Gagjee, Essop, and Noormohamed, 1983
Spain	265	0.15	37.10	15.22	3	Peña-Yañez, Peña-Angulo, and Juarez-Fernandez, 1971
Sri Lanka	200	0.73	7.00	23.50	5	Senewiratne, Thambipillai, and Perera, 1977
Sudan	321	0.54	14.96	25.88	7	Bayoumi, Saha, Sali, Bakkar, and Flatz, 1981
Sweden	400	0.01	59.20	7.72	1	Dahlqvist and Linquist, 1971
Thailand	315	0.98	14.71	27.67	4	Flatz and Saengudom, 1969; Flatz, Saengudom, and Sanguanbhokhai, 1969; Keusch et al., 1969
Tunisia	43	0.83	34.00	24.40	3	Filiali, Ben Hassine, and Dhouib, 1987
Turkey	480	0.71	39.50	11.39	4	Flatz, Henze, Palabiyikoglu, Dagalp, and Turkkan, 1986
Uganda	52	0.96	0.20	21.22	8	Cook and Kajubi, 1966
Zaire	52	0.95	4.20	24.50	7	Elliott, Cox, and Nyomba, 1974
Zambia	26	1.00	15.28	20.50	7	Cook, Asp, and Dahlqvist, 1973

Greenland (Table 1). Overall, adult LM predominated (Fig. 1). In our sample, the mean frequency of LM was 61±30% (±S.D.; n=9940 subjects), with a range of 2% (Denmark) to 100% (Zambia; Fig. 2).

Historical (pre-1900) distributions of nine deadly cattle pathogens could be determined accurately (American Geographical Society, 1951; Cliff & Haggett, 1988; Odend'hal, 1983; Rodenwaldt, 1952; Scott, 1981; World Anthrax Data, 2003). These diseases were

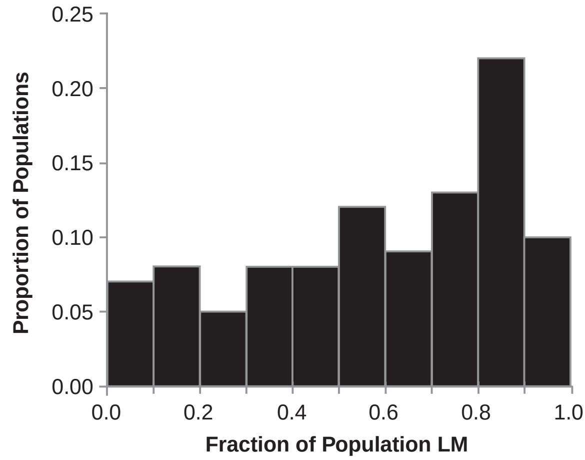

Fig. 1. Frequencies of primary adult LM among 91 indigenous populations ($n = 9940$ people) from 39 countries in Africa, Asia, and Europe (see Table 1).

anthrax, malaria, sleeping sickness, cholera, heartwater, Rift Valley fever, brucellosis, rinderpest, and theileriosis. The first four also are transmissible, and potentially fatal, to humans.

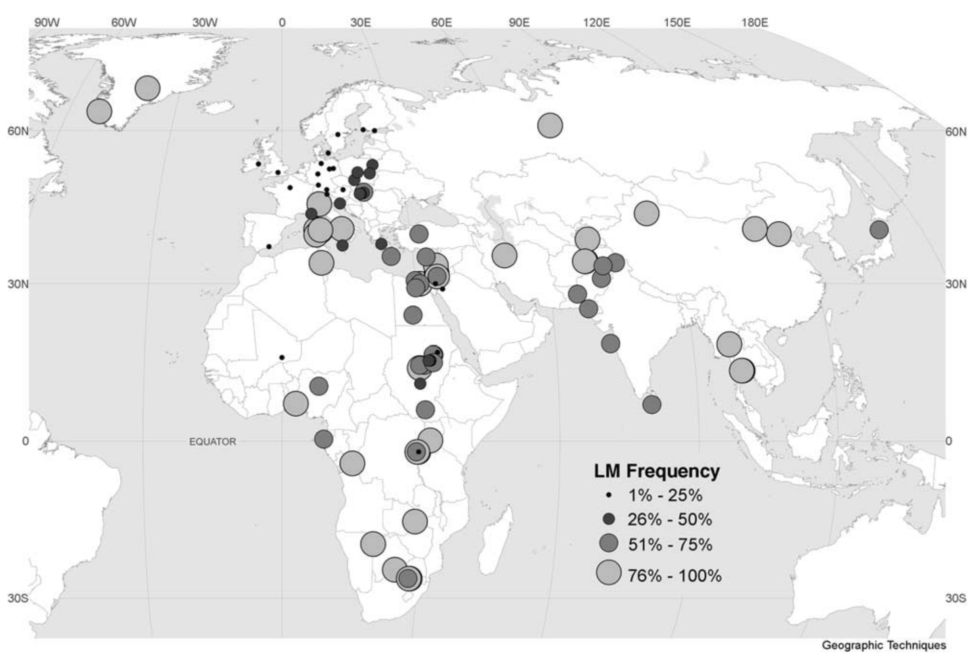

Fig. 2. Distribution of primary adult LM among 91 populations ($n = 9940$ people; see Table 1) plus 9 nomadic, low-latitude, lactose-absorbing populations ($n = 1077$ people; these nomads were analyzed separately).

Our data revealed a significant negative correlation between adult LM frequencies and latitudes (Fig. 3a), with two extreme outliers (i.e., z scores >2.0): Siberia (61° N, in present day Russia) and Greenland (67° N). There was a significant, positive correlation between LM

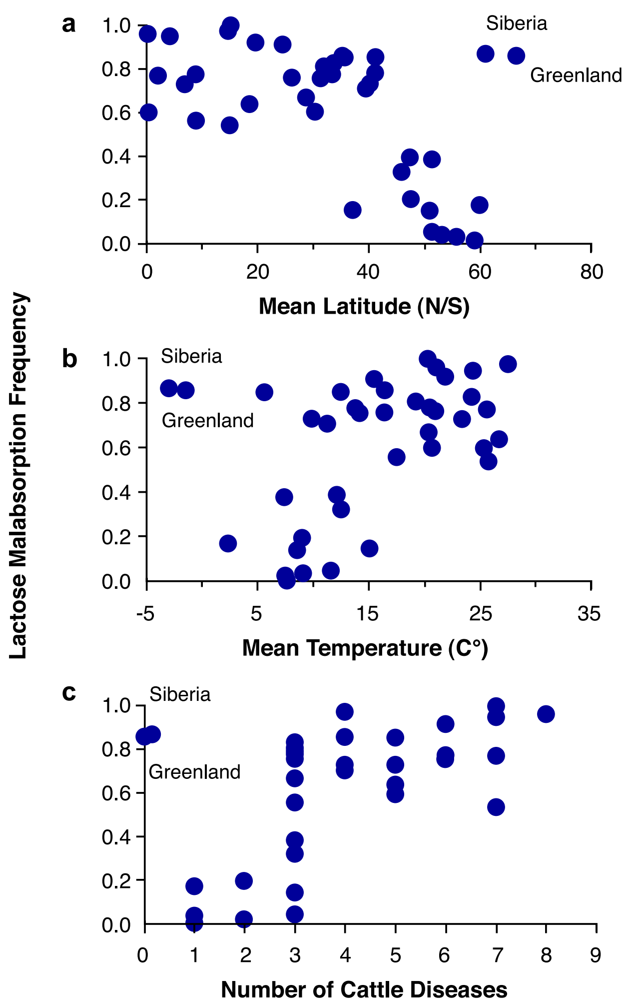

Fig. 3. Occurrence of primary adult LM in relation to climate and historical occurrence of cattle diseases in 91 populations from 39 countries (see Table 1). (a) LM frequency vs. latitude. The negative correlation was highly significant whether the two statistically identified outliers, Siberia and Greenland (z scores >2.0), were included ($r=-.56$, $p<.0002$) or excluded ($r=-.70$, $p<.0001$). (b) LM frequency vs. mean annual temperature. The positive correlation was significant whether the two statistically identified outliers, Siberia and Greenland, were included ($r=.42$, $p<.0086$) or excluded ($r=.61$, $p<.0001$). (c) LM frequency vs. historical (before 1900) occurrence of nine cattle diseases (anthrax, brucellosis, cholera, heartwater, malaria, Rift Valley fever, rinderpest, sleeping sickness, and theileriosis). The positive correlation was significant whether the two statistically identified outliers, Siberia and Greenland, were included ($r=.54$, $p<.0004$) or excluded ($r=.71$, $p<.0001$).

frequencies and mean temperatures (Fig. 3b), with Siberia and Greenland again appearing as statistical outliers. There also was a significant, positive correlation between LM frequencies and historical presence of deadly cattle diseases (Fig. 3c), again with the same two statistically identified outliers.

Multiple regression analyses indicated that adult LM frequencies were well predicted by latitude, temperature, and diseases together, whether Siberia and Greenland were included [r=.59, $F(3,31)$=6.363, p<.0015] or excluded [r=.74, $F(3,29)$=13.15, p<.0001]. Partial correlation analyses revealed that the numbers of diseases had an independent, significant effect on LM frequencies (t=2.14, p<.03), even when latitude and temperature were held constant statistically, whereas neither latitude (t=−.85, p=.40) nor temperature (t=.55, p=.58) significantly affected LM frequencies when diseases were held constant.

4. Discussion

Humans are the only mammals that regularly drink milk as adults. However, populations differ markedly in their physiological capabilities of digesting lactose (Fig. 1). Frequencies of adult LM in populations from Eurasia and Africa decrease with increasing latitude (Fig. 2) and increase with increasing temperature and, especially, with numbers of deadly cattle diseases that were present before 1900 (Table 1, Fig. 3). The implication is that harsh climates and dangerous diseases negatively impact dairy herding, thus also geographically restricting the availability of milk.

Populations from northern Siberia and Greenland are exceptions to the latitudinal trend: Although they live far north of the equator (>60° N), they are predominantly malabsorbers. In light of our dairying barrier hypothesis, both exceptions are instructive because neither cattle nor transmissable cattle diseases can thrive in such extreme climates. As a result, those populations did not predictably have access to fresh milk. Although the now-extinct Greenland Norse population attempted to maintain dairy herds, the animals and their owners always teetered on the brink of starvation (Simoons, 2001) and died out in <500 years. The latter-day Greenland Eskimos (the population in our database), which have persisted much longer, do not keep dairy cattle, and their diet is devoid of milk or dairy products (Simoons, 2001).

Previous investigators (Bayoumi, Flatz, Kühnau, & Flatz, 1982; Durham, 1991; Flatz, 1989; Hussein & Ezzilarab, 1994; Simoons, 1978; Swallow, 2003) identified 13 additional outlier populations, but at the other end of the latitudinal spectrum. These peoples live at low latitudes in Africa and the mid-East, but they are predominantly lactose absorbers as adults (i.e., lactase persistent). Nine of these populations have been sampled adequately to be included in our database and analyses (Fig. 2). Among them, LM frequencies are indeed low (mean=35±25%), and milk and dairy products make up a significant fraction of their diet, raising the question of how these people surmounted ecological barriers to dairying.

The most likely explanation is nomadism. All 13 populations have historically been migratory pastoralists that inhabited borders between major climatic zones in Africa (Mali, Rwanda, Uganda, Congo, Egypt, and Sudan) and the mid-East (Jordan, Saudi Arabia; Griffiths, 1972; Johnson, 1969; Smith, 1992; Swallow, 2003). Seasonal movements of these peoples coincide with the advance and retreat of the intertropical (wind) convergence zone (the ITCZ: Waliser, 2003), enabling them to locate suitable cattle forage and avoid extreme temperatures year-round (Hayward & Ogentoyinbo, 1987; Kraus & Businger, 1994). Moreover, these pastoralists typically maintain small herds, spread their cattle out, and keep them moving (Johnson, 1969), all of which should reduce pathogen transmission rates.

In present-day Africa, some sedentary populations maintain domesticated cattle, particularly among the subequatorial Bantu tribes. Although few have been adequately sampled, those that have are predominantly lactose malabsorbers (Durham, 1991; Fig. 2). These patterns seem to run counter to both the culture–historical and dairying barrier hypotheses. However, these populations traditionally did not maintain dairy cattle or have access to fresh milk. Dairy herding in subequatorial Africa is a recent (20th century) phenomenon, facilitated by control or eradication of the most devastating cattle diseases and introduction of new breeds of cattle that are tolerant of extreme heat and draught (Coetzer, Thompson, & Tustin, 1994). Moreover, even today, adults in these populations rarely drink fresh milk, instead consuming fermented milk products, such as yogurt and cheese, which have minimal lactose and thus do not require lactase to digest (Durham, 1991).

Our dairying barrier hypothesis is complementary, and not an alternative to, the culture–historical hypothesis (McCracken, 1971; Simoons, 1970), which posits that the mutations that maintain lactase into adulthood are positively selected only where dairying flourishes (Bersaglieri et al., 2004; Swallow, 2003). Results of our analyses imply that adults of Asian and African descent typically are lactose malabsorbers because dairy herding was precluded from their ancestral homes by ecological factors. Adult lactose malabsorbers or their recent ancestors were sedentary agriculturalists or hunter gatherers who lived in places that were not conducive to safe and economical maintenance of dairy herds, due especially to lethal pathogens, extreme climates, or both. The historical distribution of dairying, and the resulting distribution of the adult LM phenotype, thus lend support to the assertion of Diamond (1999) that "the different historical trajectories of Africa and Europe stem ultimately from differences in their environments."

Acknowledgments

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Appendix A

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
1	Afghan–mixed urban	Afghanistan	34.3	N	0.77	18–60	34	Rahimi et al. 1976
2	Afghan–Pashtun	Afghanistan	34.3	N	0.79	18–60	71	Rahimi et al. 1976
3	Afghan–Hazara	Afghanistan	34.3	N	0.8	18–60	10	Rahimi et al. 1976
4	Afghan–Tajik	Afghanistan	34.3	N	0.82	18–60	79	Rahimi et al. 1976
5	Afgan–Pasha-I	Afghanistan	38.5	N	0.87	18–60	60	Rahimi et al. 1976
6	Afghan–Uzbek	Afghanistan	34.3	N	1	18–60	16	Rahimi et al. 1976
7	Indians and Eskimos	Alaska	61.1	N	0.94	adults	36	Duncan and Scott 1972
8	Australian whites	Australia	33.53	S	0	adults	23	Bolin and Davis 1969
9	Chinese in Australia	Australia	33.53	S	0.56	3–34	34	Bolin and Davis 1970b
10	Indians in Australia	Australia			0.8	adults	5	Bolin and Davis 1969
11	Australian Aborigines	Australia	17.2	S	0.84	15–75	45	Brand et al. 1983
12	Chinese in Australia	Australia	22.2	N	0.9	adults	30	Bolin and Davis 1969
13	New Guineans	Australia			1	adults	8	Bolin and Davis 1969
14	Austria (west)	Austria	47.2	N	0.15	adults	166	Rosenkranz et al. 1982
15	Austria (east)	Austria	47.2	N	0.25	adults	181	Rosenkranz et al. 1982
16	Aymara (Bolivia)-children	Bolivia	15.3	S	0.774	11–15	31	Balanza and Taboada 1985
17	Herero	Botswana			0.9	≥15	10	Currie et al. 1978
18	‡hua Bushmen	Botswana	24.45	S	0.91	adults	22	Nurse and Jenkins 1974
19	Brazil–caucasoid	Brazil	22.5	S	0.45	20–52	40	Seva-Ereira et al. 1983

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
20	Brazil–Negroid	Brazil	22.5	S	0.85	20–52	20	Seva-Ereira et al. 1983
21	Brazil–Mongaloid	Brazil	22.5	S	1	20–52	20	Seva-Ereira et al. 1983
22	British	Britain	51.5	N	0.05	11–88	75	Ho et al. 1982
23	Jews in Britain	Britain	51.3	N	0.8	adults	10	Neal 1968
24	Greek	Cypriots in Britain	Britain	35.1	N 0.88	ad + child.	17	Mehta and Latham 1977
25	Indians and pakastanis	Britain			0.93	adults	16	Neal 1968
26	Bantu	Cameroon	6	N	1	adults	6	Elliott et al. 1973
27	Czechs in Canada	Canada	49	N	0.18	adults	17	Leichter 1972
28	Poles in Canada	Canada			0.29	adults	21	Leichter 1972
29	Punjabis	Canada	31	N	0.33	adults	9	Murthy and Haworth 1970
30	Jews, Canadian and American	Canada	49.2		0.69	adults	32	Leichter 1971
31	Indians in Canada	Canada			0.93	adults	15	Murthy and Haworth 1970
32	Indians	Canada, w.coast	52	N	0.63	adoles.	30	Leichter and Lee 1971
33	China–Kazakh	China	43.5	N	0.76	16–28	195	Yongfa et al. 1984
34	China–Mongols	China	40.5	N	0.88	17–46	198	Yongfa et al. 1984
35	Han (chinese) - general	China	39.5	N	0.92	17–35	248	Yongfa et al. 1984
36	Chami Indians	Columbia	5	N	1	adults	24	Alzate et al. 1969
37	Tussi in Congo	Congo	1	S	0	adults	15	Elliott et al. 1973
38	Caucasian in Congo			Congo	0.2	adults	10	Elliott et al. 1973
39	Danes	Denmark	55.4	N	0.02	adults	670	Gudmand-Huyer et al. 1969
40	Danes	Denmark	56.2	N	0.03	adults	91	Busk et al. 1975

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
41	North Sinai Egyptians (Nomadic)	Egypt	30	N	0.11		72	Hussein and Ezzilarab 1994
42	New Valley Egyptians	Egypt	24	N	0.51		100	Hussein and Ezzilarab 1994
43	Egypt–South Nile	Egypt	26.1	N	0.6	14–34	85	Hussein et al. 1982
44	Egypt–Urban	Egypt	30	N	0.67	14–34	67	Hussein et al. 1982
45	Egypt–suez canal	Egypt	30	N	0.69	14–34	16	Hussein et al. 1982
46	Egypt–Nile	Delta	Egypt	30.6	N	0.73	1 4 – 34	291 Hussein et al. 1982
47	Egypt–North Nile	Egypt	29.2	N	0.85	14–34	111	Hussein et al. 1982
48	Egyptian fellahin	Egypt	30	N	0.93	16–75	14	Halsted et al. 1969
49	Ethiopian infants	Ethiopia	9	N	0.61	<1 yr	26	Habte et al. 1973
50	Ethiopians/ Eritreans	Ethiopia	9	N	0.9	7–13	58	Habte and Hjalmarsson 1973
51	Ethiopian children	Ethiopia	9	N	0.9	7–13	157	Habte et al. 1973
52	Fijians	Fiji	18.1	S	1	adults	12	Masarei et al. 1972
53	Finns	Finland	60.2	N	0.06	7–15	129	Launiala et al. 1971; Sahi et al. 1972
54	Swedes in Finland	Finland	59.2	N	0.08	adults	91	Sahi 1974
55	Finns	Finland	60.2	N	0.17	adults	159	Jussila et al. 1970
56	Finns	Finland	60	N	0.18	50–70	134	Jussila 1969
57	French	France	48.5	N	0.07	adults	14	Gouin et al. 1972
58	French–north	France	48.5	N	0.23	18–21	62	Cuddenec et al. 1982
59	French–South	France	43.4	N	0.42	20–75	55	O'Morain et al. 1978
60	French–south	France	43.4	N	0.5	18–21	16	Cuddenec et al. 1982

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
61	Bantu	Gabon	0.4	N	0.6	adults	20	Gendrel et al. 1989
62	Germany–North	Germany	53.3	N	0.06	adults	100	Flatz et al. 1982
63	Germany–NW	Germany	51.2	N	0.088	adults	341	Flatz et al. 1982
64	Germany–south	Germany	48.1	N	0.136	adults	221	Flatz et al. 1982
65	Germany–west	Germany	52.2	N	0.137	adults	182	Flatz et al. 1982
66	Germans from cent. Europe	Germany	50.4	N	0.15	adults	55	Rotthauwe et al. 1972
67	Germany–East	Germany	52.3	N	0.224	adults	246	Flatz et al. 1982
68	Germany–SW	Germany	49	N	0.235	adults	136	Flatz et al. 1982
69	Arabs from Jordan,Syria, Saudi Arabia, Egypt,Iraq, Tunisia	Germany	50.4	N	0.81	adults	26	Rotthauwe et al. 1971
70	Children	Ghana	5.3	N	0.73	children	100	White and Latham 1973
71	Greeks,	mainland	Greece 37.6	N	0.38	adults	16	Spanidou and Petrakis 1972
72	Greeks, mainland	Greece	37.6	N	0.45	adults	600	Kanaghinis et.el. 1974
73	Greeks	Greece	37.6	N	0.54	7–13	24	Doxiadis and Papageorgiadis 197
74	Greek Cretans	Greece	35.2	N	0.56	adults	50	Kanaghinis et el. 1974
75	Greek Cypriots	Greece	35.1	N	0.67	adults	50	Kanaghinis et.el. 1974
76	Greeks	Greece	37.6	N	0.67	7–13	82	Kattamis et al. 1973
77	Greenland Eskimos/nw eur.mixed	Greenland	64.1	N	0.14	adults	7	Gudmand-Hoyer and Jarnum 1969

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
78	Greenland Eskimos/nw eur.mixed	Greenland	64.1	N	0.5	adults	4	Asp et al. 1975
79	Eskimos	Greenland	69.2	N	0.84		81	Gudmand-Hoyer et al. 1973
80	Eskimos	Greenland	64.1	N	0.85	adults	13	Asp et al. 1975
81	Eskimos	Greenland	64.1	N	0.88	adults	25	Gudmand-Huyer et al. 1973
82	Eskimos, greenland	Greenland	64.1	N	0.94	18–60	19	Asp et al. 1975
83	Hungarians–west	Hungary	47.3	N	0.28	17–39	100	Czeizel et al. 1983
84	Hungarians–east	Hungary	47.3	N	0.29	17–39	70	Czeizel et al. 1983
85	Hungary–Matyo	Hungary	47.5	N	0.37	16–54	172	Czeizel et al. 1983
86	Hungarians–mixed	Hungary	47.3	N	0.41	17–39	262	Czeizel et al. 1983
87	Hungarians–NE	Hungary	47.3	N	0.42	17–39	103	Czeizel et al. 1983
88	Hungary–Romai (Gypsies)	Hungary	47.6	N	0.56	16–47	113	Czeizel et al. 1983
89	"Mohajirs" (mixed pkastani/ dravidians)	India	24.5	N	0.2	adults	15	Rab and Baseer 1976
90	Indians in Bombay	India	18.6	N	0.24	adults	17	Desai et al. 1967
91	Indians in Hyderabad (Deccan)	India	17.2	N	0.61	adults	18	Reddy and Pershad 1972
92	Indians in Bombay	India	18.6	N	0.64	adults	100	Desai et al. 1970
93	Iranians	Iran	35.4	N	0.86	20–25	21	Sadre and Karbasi 1979
94	Iraqi Jews	Iraq	15	N	0.84	17–65	38	Gilat et al. 1970
95	Irish	Ireland	53.2	N	0.04	16–68	50	Fielding et al. 1981

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
96	Jews in Israel	Israel	32	N	0.54	8–46	50	Gilat et al. 1974
97	Jews in Israel	Israel	32	N	0.6	adults	58	Gilat et al. 1973
98	Jews in Israel	Israel	31.5	N	0.61	adults	93	Rozen and Shafrir 1968
99	Jews in israel, summary of following:	Israel	32	N	0.71	17–70	215	Gilat et al. 1970
100	Sephardi, other	Israel	32	N	0.72	17–69	36	Gilat et al. 1970
101	Ashkenazi	Israel	32	N	0.79	20–70	53	Gilat et al. 1970
102	Arab villagers in Israel	Israel	32	N	0.81	adults	67	Gilat et al. 1971
103	Jews, other orientals	Israel	33	N	0.85	24–64	20	Gilat et.al 1970
104	Sicilians	Italy	37.3	N	0.29	adults	100	Burgio et al. 1984
105	Italians–northern	Italy	45.4	N	0.49	adults	208	Burgio et al. 1984
106	Italians	Italy	45.3	N	0.8	adults	20	Zuccato et al. 1983
107	Sardinians–mts	Italy	40.3	N	0.81	20–51	38	Meloni et al. 1998
108	Italians, Neapolitans	Italy	40.5	N	0.84	27–70	37	Rinaldi et al. 1984
109	Sardinians–lowlands	Italy	39.4	N	0.85	20–55	47	Meloni et al. 1998
110	Sardinians–north	Italy	40.4	N	0.86	adults	50	Meloni et al. 2001
111	Sardinians–mts	Italy	40.1	N	0.88	19–59	53	Meloni et al. 1998
112	Italians in Naples	Italy	40.5	N	1	adults	9	De Ritis et al. 1970
113	Japanese	Japan	40.34	N	0.73	adults	40	Yoshida et al. 1975
114	Jordanians–bedouins	Jordan	?	?	0.24	17–46	162	Hijazi et al. 1983
115	Jordanians–urban	Jordan	31.4	N	0.75	18–33	148	Hijazi et al. 1983

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
116	Jordanian Arabs	Jordan	31.4	N	0.77	adults	56	Snook et al. 1976
117	Kenyans (bantu agricultural tribes)	Kenya	1.17	S	0.73	5–15	71	Pieters and Van Rens 1973
118	Lebanese	Lebanon	33.5	N	0.78	17–43	74	Nasrallah 1979
119	Niger–nomads (Tuareg valley)	Mali	?	?	0.127	adults	118	Flatz et al. 1986b
120	Mexican Mestizos	Mexico	19.2	N	0.74	18–72	100	Lisker et al. 1974
121	N. African Sephardi	Morocco	32	N	0.63	19–65	32	Gilat et al. 1970
122	!Kung Bushmen	Namibia	19.6	S	0.92	adults	40	Jenkins et al. 1974
123	Herero	Namibia	?	?	0.978	≥11	46	Currie et al. 1978
124	New guineans	New Guinea	3.5	S	0.75	adults	32	Arnhold et al. 1981
125	Massim(NW Guinea)	New Guinea	10.2	S	0.83	adults?	35	Gibney et al. 1981
126	Anglo–saxons in Nigeria	Nigeria	?		0.13	adults	8	Kretchmer et al. 1971
127	Europeans in Nigeria	Nigeria	?		0.22	≥3	9	Ransome-Kuti et al. 1975
128	Yoruba/ European	Nigeria	6.3	N	0.44	≥3	43	Ransome-Kuti et al. 1975
129	Hausa/Fulani	Nigeria	7.2	N	0.6	adults	15	Olatunboson and Adadevoh 1971
130	Fulani (fulani/ hausa), urban	Nigeria	10.5	N	0.71	adults	24	Kretchmer et al. 1971
131	Hausa	Nigeria	12	N	0.76	ad.+ child	17	Kretchmer et al. 1971
132	Ibo	Nigeria	7.2	N	0.82	adults	11	Olatunboson and Adadevoh 1971
133	Yoruba	Nigeria	7.22	N	0.84	adults	48	Olatunboson and Adadevoh 1971
134	Yoruba	Nigeria	6.3	N	0.98	≥4	41	Kretchmer et al. 1971

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
135	S. Nigerians (mostly)	Nigeria	7.2	N	1	adults	9	Olatunboson and Adadevoh 1971
136	Yoruba	Nigeria	6.3	N	1	≥3	11	Ransome-Kuti et al. 1975
137	Punjabis	Pakistan	24.5	N	0	adults	9	Rab and Baseer 1976
138	Sindhis	Pakistan	24.5	N	0	adults	12	Rab and Baseer 1976
139	Baloochis	Pakistan	24.5	N	0	adults	4	Rab and Baseer 1976
140	Pathans	Pakistan	24.5	N	0	adults	15	Rab and Baseer 1976
141	Pakistani	Pakistan	33.4	N	0.516	adults	66	Abbas 1984
142	Pakistani–Sindh	Pakistan	25.2	N	0.58	18–48	33	Ahmad and Flatz 1984
143	Pakastani–punjab	Pakistan	31	N	0.59	18–48	322	Ahmad and Flatz 1984
144	Pakistani–Baluchistan	Pakistan	28	N	0.62	18–48	32	Ahmad and Flatz 1984
145	Kashmir (pakistan)	Pakistan	34	N	0.7	18–48	27	Ahmad and Flatz 1984
146	Peruvian students	Peru	12	S	0.63	21–29	44	Calderon-Viacava et al. 1971
147	Peruvian Mestizos	Peru	12	S	0.8	adults	50	Figueroa et al. 1971
148	Polish–mixed	Poland	52.1	N	0.36	16–59	85	Socha and Ksiazyk 1984
149	Polish–east	Poland	51.3	N	0.37	16–59	35	Socha and Ksiazyk 1984
150	Polish–central	Poland	51.5	N	0.37	16–59	92	Socha and Ksiazyk 1984
151	Polish–south	Poland	50	N	0.38	16–59	29	Socha and Ksiazyk 1984
152	Polish–northeast	Poland	53	N	0.41	16–59	34	Socha and Ksiazyk 1984
153	Tussi in Rwanda	Rwanda	2	S	0.08	adults	27	Cox and Elliot 1974
154	Hutu/Tussi mixed	Rwanda	2	S	0.55	adults	11	Cox and Elliot 1974

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
155	Hutu	Rwanda	2	S	0.58	adults	36	Cox and 7 Elliot 1974
156	Twa	Rwanda	2	S	0.77	adults	22	Cox and Elliot 1974
157	Shi, Bantu of Lake Kivu area	Rwanda	2	S	0.96	adults	28	Cox and Elliot 1974
158	Arabs(Saudi), urban	Saudi Arabia	24.41	N	0.13	adults	8	Cook and Al-Torki 1975
159	Arabs, bedouins	Saudi Arabia			0.14	adults	14	Cook and Al-Torki 1975
160	Yemen Arabs	Saudi Arabia	24.4	N	0.25	16–40	8	Cook and Al-Torki 1975
161	"Khadiry" (mixed african/ arab)	Saudi Arabia	24.41	N	0.78	14–60	9	Cook and Al-Torki 1975
162	Khants(west. Siberia)	Siberia	61.1	N	0.869	14–57	61	Lember et al. 1995
163	Indians in Singapore	Singapore	1.17	N	0.8	3–10	5	Chua and Seah 1973
164	Chinese	Singapore	1.17	N	0.9	3–16	10	Chua and Seah 1973
165	Chinese, Malays,Indians	Singapore	1.17	N	1	adults	22	Bolin et al. 1970a
166	Sotho	South	Africa	26.2	S	0.65	23	Segal et al. 1983
167	Zulu	South Africa	26.2	S	0.81		32	Segal et al. 1983
168	Xhosa	South Africa	26.2	S	0.82		17	Segal et al. 1983
169	Tswana	South Africa	26.2	S	0.83		24	Segal et al. 1983
170	Swazi	South Africa	26.2	S	0.86		12	Segal et al. 1983
171	Bantu of South Africa	South Africa	26.1	S	0.9	N/A	31	Jersky and Kinsley 1967
172	Spaniards	Spain	40.2	N	0.15	adults	265	Pena-Yanez et al. 1971
173	Ceylonese	Sri Lanka	7	N	0.73	adults	200	Senewiratne et al. 1977
174	Bedja	Sudan	15	N	0.111	adults	9	Bayoumi et al. 1981

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
175	Beja	Sudan	19	N	0.17		303	Bayoumi et al. 1982
176	Gomocia	Sudan	15	N	0.323	adults	31	Bayoumi et al. 1981
177	Kahli	Sudan	15	N	0.381	adults	21	Bayoumi et al. 1981
178	Jaali	Sudan	15	N	0.469	adults	113	Bayoumi et al. 1981
179	Baggara (sudan)	Sudan	11	N	0.49	adults	53	Bayoumi et al. 1981
180	Sudanese, central	Sudan	15	N	0.5	adults	56	Bayoumi et al. 1981
181	Habbani	Sudan	14.5	N	0.526	adults	19	Bayoumi et al. 1981
182	Sudanese, North Nile	Sudan	16.5	N	0.542	adults	24	Bayoumi et al. 1981
183	Sudanese, northern nomadic	Sudan	15	N	0.565	adults	23	Bayoumi et al. 1981
184	Sydanese, southern	Sudan	5.5	N	0.857	adults	13	Bayoumi et al. 1981
185	Misseri	Sudan	14.5	N	0.6	adults	20	Bayoumi et al. 1981
186	Shaygi	Sudan	16.5	N	0.619	adults	42	Bayoumi et al. 1981
187	Nilotic (Sudan)	Sudan	5.5	N	0.667	adults	18	Bayoumi et al. 1981
188	Nubians	Sudan	16.5	N	0.667	adults	21	Bayoumi et al. 1981
189	sudanese (central), aboriginal negroid	Sudan	14	N	0.692	adults	26	Bayoumi et al. 1981
190	Nilotes (Dinka)	Sudan	6.5	N	0.745		282	Bayoumi et al. 1982
191	Nuba	Sudan	14	N	0.793	adults	20	Bayoumi et al. 1981
192	Dongolawi	Sudan	16.5	N	0.813	adults	16	Bayoumi et al. 1981
193	Bush negroes	Surinam	4	N	1	adults	29	Luyken et al. 1970

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
194	Indians in Surinam	Surinam		0.66			27	Luyken et al. 1970
195	Surinam creole adults	Surinam		0.71			31	Luyken et al. 1970
196	Swedes in Sweden	Sweden	59.2	N	0.01	adults	400	Dahlqvist and Linquist 1971
197	Chinese in Taiwan	Taiwan	?		1	adults	71	Sung et al. 1972
198	Thai/nw europ.	Thailand	18.47	N	0.5	adults	6	Flatz and Rotthauwe 1971
199	Thai	Thailand	13.45	N	0.96	adults	100	Flatz and Saengudom 1969
200	Thai	Thailand	13.45	N	0.97	adults	140	Keusch et al. 1969
201	Thai	Thailand	18.47	N	0.99	adults	75	Flatz et al. 1969
202	Thai	Thailand	18.47	N	1	ad + child	9	Flatz and Rotthauwe 1971
203	Thai	Thailand	18.47	N	1	4–12	24	Flatz et al. 1969
204	Thai	Thailand	13.45	N	1	adults	39	Troncale et al. 1967
205	Thai	Thailand	13.45	N	1	2–4	16	Varavithya et al. 1976
206	Indians from trinidad	Trinidad	?		0.6	adults	25	Bartholomew and Young Pong 1976
207	Tunisians	Tunisia	34	N	0.83	adults	43	Filali et al. 1987
208	Turkish	Turkey	39.5	N	0.71	18–28	480	Flatz et al. 1986a
209	American whites	U.S.	44.6	N	0.06	adults	100	Newcomer et al. 1967
210	American whites	U.S.	37.5	N	0.08	adults	12	Calloway et al. 1969
211	American whites	U.S.	29.2	N	0.09	2–14	17	Woteki et al. 1976

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
212	American whites	U.S.	39.2	N	0.1	18–54	20	Bayless and Rosensweig 1966
213	Non–Jewish American whites	U.S.	41.4	N	0.11	adults	53	Tandon et al. 1971
214	American whites	U.S.	29.2	N	0.13	19–57	8	Dill et al. 1972
215	Anglo–american whites	U.S.			0.15	18–82	142	Woteki et al. 1977
216	American whites	U.S.	39.2	N	0.16	adults	19	Cuatrecasas et al. 1965
217	American whites	U.S.	31	N	0.17	adults	18	Knudsen et al. 1968
218	American whites	U.S.			0.19		93	Marenco et al. 1970
219	American whites	U.S.	35.3	N	0.19	3–80	145	Welsh and Rohrer 1967
220	American blacks	U.S.	39.2	N	0.24	children	25	Paige et al. 1977
221	American whites	U.S.	61.1	N	0.25	adults	16	Duncan and Scott 1972
222	American whites	U.S.	42	N	0.25	>5 yrs	65	Lebenthal et al. 1975
223	Chippewa/nw europ.mixed	U.S.	47.5	N	0.36	5–73	39	Newcomer et al. 1977b
224	American blacks	U.S.	39.2	N	0.45	children	31	Paige et al. 1971
225	Mexican Americans	U.S.	35.3	N	0.47	adults	17	Sowers and Winterfeldt 1975
226	Mexican Americans	U.S.	29.2	N	0.53	18–94	277	Woteki et al. 1977
227	American blacks	U.S.	39.2	N	0.54	6–13	89	Paige et al. 1975
228	Mexican Americans	U.S.	29.2	N	0.55	18–57	11	Dill et al. 1972
229	Mexican Americans	U.S.	29.2	N	0.56	2–14	75	Woteki et al. 1976

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
230	American blacks	U.S.	39.2	N	0.59	adoles.	32	Mitchell et al. 1975
231	American Indian/anglo mixed	U.S.	33.3	N	0.61	≥4	41	Johnson et al. 1977
232	American indians mixed	U.S	35.3	N	0.63	3mo–57	16	Bose and Welsh 1973
233	Orientals in US (chinese and filipino)	U.S.			0.65	adults	20	Hua and Bayless 1968
234	American Jews	U.S.	41.4	N	0.71	adults	41	Tandon et al. 1971
235	American blacks	U.S.	39.2	N	0.73	adults	41	Cuatrecasas et al. 1965
236	American blacks	U.S.	39.2	N	0.75	18–52	20	Bayless and Rosensweig 1966
237	American blacks	U.S.	41.5	N	0.75	adults	24	Littman et al. 1968
238	American blacks	U.S.	44.6	N	0.75	adults	8	Knudsen et al. 1968
239	American blacks	U.S.	35.3	N	0.77	3–82	22	Welsh and Rohrer 1967
240	Indians in US	U.S.			0.83	adults	18	Mehta and Latham 1977
241	Chippewa, Minnesota	U.S.	47.5	N	0.93	5–73	15	Newcomer et al. 1977b
242	Popago	U.S.	33.27	N	0.93	adults	14	Johnson et al. 1978
243	Pima	U.S.	33.27	N	0.95	≥4	62	Johnson et al. 1977
244	Indians, Oklahoma	U.S.	35.3	N	0.95	adults	20	Bose and Welsh 1973
245	Orientals in US	U.S.			1	adults	11	Chung and McGill 1968
246	Pima	U.S.	33.27	N	1	adults	4	Johnson et al. 1978
247	Hopi	U.S.	33.27	N	1	adults	21	Johnson et al. 1978
248	Apache	U.S.	33.27	N	1	adults	22	Johnson et al. 1978

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
249	Chinese in US	U.S.	39.5	N	1	adults	6	Calloway et al. 1969
250	Vietnamese in US	U.S.	16	N	1	adults	31	Anh et al. 1977
251	Tussi	Uganda	0.2	N	0	adults	5	Cook and Dahlqvist 1968
252	Hima Pastoralists	Uganda	0.4	S	0.09	adults	11	Cook and Kajubi 1966
253	Tussi Pastoralists in Uganda	Uganda	0.2	N	0.17	adults	12	Cook and Kajubi 1966
254	Iru (mixed Bantu/Hamitic)	Uganda	0.2	N	0.39		13	Cook and Dahlqvist 1968
255	Nilotes, nilo–hamites in Uganda	Uganda	0.2	N	0.44	adults	9	Cook and Kajubi 1966
256	Ganda	Uganda	0.2	N	0.67	5–12	6	Cook et al. 1967
257	Uganda (agricultural Bantu, I.e. Ganda)	Uganda	0.2	N	0.96	adults	52	Cook and Kajubi 1966
258	Ganda and others in Uganda	Uganda	0.2	N	1	adults	12	Cook and Dahlqvist 1968
259	Yemen Jews	Yemen	32.1	N	0.44	20–70	36	Gilat et al. 1970
260	Ibo	Zaire	4.2	S	0.75	adults	4	Elliott et al. 1973
261	Bantu of various types	Zaire	4.2	S	0.95	adults	52	Elliott et al. 1973
262	Bantu of Zambia	Zambia	15.28	S	1	adults	26	Cook et al. 1973
263	canadian whites	?			0.06		16	Cox and Elliot 1974
264	Indians from trinidad	?			0.2		5	Murthy and Haworth 1970
265	Fulani, nomadic	?	10.5	N	0.22	≥4	9	Kretchmer et al. 1971

Index	Population	Country	Lat.	N/S	LM	Ages	#subj.	Reference
266	Hutu (mixed Bantu/Hamitic)	?	0	N/S	0.33		15	Cook and Dahlqvist 1968
267	Greenland Eskimos/nw eur.mixed	?	69.2	N	0.39	1–30	97	Gouin et al. 1972
268	American Indian/anglo mixed	?			0.5		6	Gilat et al. 1974
269	Africans–north (Maghreb)	?			0.78	20–70	55	O'Morain et al. 1978
270	Dinka	?			1		5	Elliott et al. 1973

Complete data of all populations for which LM frequencies are available. ? = information could not be determined.

Appendix A. References

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