

Some Genetic Traits in Solomon Island Populations

III. RELATIVE TOE LENGTH

CATHLEEN C. PAPADOPOULOS AND ALBERT DAMON
*Department of Anthropology, Harvard University, Cambridge,
Massachusetts 02138*

ABSTRACT Among 1,605 Solomon Islanders from four tribes, there was no sex difference in relative length of the first and second toes. In three of the tribes, longer first toes were slightly more frequent in persons over the age of 45. The percentages of longer first toes in the groups as a whole were 60.5% for Baegu, 66.4% for Nasioi, and 72.1% for Kwaio. These frequencies, resembling those reported for white Americans, Europeans, and single small samples of New Caledonians and Vietnamese, were much below those for Africans. The fourth tribe, the Lau, had only 37.1% with a longer first toe, the lowest percentage reported so far around the world. No simple mode of single-gene inheritance was apparent, and polygenic inheritance is proposed.

One of man's distinctive physical features, making possible his upright posture, is the foot. In the evolution of the human foot the hallux, or great toe, has become much longer relative to the other toes than it is among the other primates. In most persons the great toe is the longest, but populations differ in toe formula, for which a simple genetic basis has been claimed.

Toe formula refers to the relative length of the hallux or great toe as compared to the adjacent second toe. The third, fourth, and fifth toes are almost invariably shorter, in that order. When the first toe is longer, the formula is $1 > 2 > 3 > 4 > 5$; when the second toe is longer, $2 > 1 > 3 > 4 > 5$. Rarely, the first and second toes are of equal length, and very rarely the third toe is the longest.

The earliest studies of the human toe formula (Harrison, 1884; Grüning, 1886; Weissenberg, 1895) established population differences. Hawkes ('14) then demonstrated the anatomic basis for the trait. In the normal skeleton the second metatarsal is longer than the first, and the second metatarsal plus its three phalanges are longer than the first metatarsal plus its two phalanges. The soft tissue at the distal end of the hallux is always bulkier than that of the second toe, a difference which increases with age but according to Hawkes ('14) does not affect toe formula. The determinants of relative toe

length in the living, predominantly $1 > 2$, would therefore seem to be the size, shape, and angulation of the *tarsal* bones. Hawkes hypothesized that a single, irregularly dominant gene determines a longer first toe, and that expression is sex-influenced.

Kaplan ('63, '64) proposed a different mode of inheritance. Reporting on data from questionnaires filled out by 109 persons (relationship or family status unspecified) and from examination and questionnaires of 63 monozygotic and 44 dizygotic twin pairs, he concluded that "the normal anatomical trait involves two alleles and a single autosomal locus. The factor for relatively long hallux is recessive to the one for relatively long second toe. There is no evidence of sex influence. Penetrance is 100%. Expressivity is variable."

We report here data on relative toe length among 1,605 Solomon Islanders from four tribes, showing population differences but no simple, single-gene form of inheritance.

SUBJECTS AND METHODS

Toe size was observed by one of us (A.D.) among four Solomon Island population samples: 244 Nasioi on Bougainville Island and 441 Kwaio of Malaita Island in 1966, and 439 Lau and 481 Baegu on Malaita in 1968. All walked barefoot.

Toe formula was observed for the right

foot only. Persons old enough to stand were placed on a flat surface, wooden or metal; the feet of infants in arms were flattened by hand.

RESULTS AND COMMENT

Age and sex. Within each tribe, toe formula was independent of sex. There was a slight increase in the percentage of longer first toes among persons over 45 years of age in the Kwaio, Lau, and Baegu, as also found among the West African Dogon by Huizinga and DeVetten ('67), where longer first toes occurred in 225 persons out of 252 (89.3%) below age 45, and in 85 out of 86 (98.8%) older persons. In the three Solomon Island tribes just mentioned, the number and percentage of persons under 45 with longer first toes were as follows: Kwaio, 243/348 or 69.8%; Baegu, 237/397 or 59.7%; Lau, 126/356 or 35.4%. Corresponding figures for persons 45 years of age and over were: Kwaio, 75/93 or 80.6%; Baegu, 54/84 or 64.3%; Lau, 37/83 or 44.6%. The Nasioi showed no difference in the percentage of longer first toes between those under and over age 45. In view of the sizeable percentage of long second toes among older Solomon Island-

ers, it cannot be said of them, as Huizinga and DeVetten ('67: 108) could say of the Dogon, that "the long second toe appears to be rare phenomenon among older people."

Population differences. We have combined both sexes and all ages for population comparison. Table 1 shows the toe formulas for the four Solomon Island groups, as well as several previously reported series from around the world. The Nasioi, with 66.4% of longer first toes, did not differ from the Kwaio, with 72.1% ($p < 0.20$), or Baegu, with 60.5% ($p < 0.15$). The Kwaio and Baegu did differ significantly ($p < 0.001$), but by the small amount of 11.6%. These three groups of Solomon Islanders fell in the lower and middle part of the Caucasian range and were close to the 59.3% noted by Pales, Chippeaux and Pineau ('60) for Melanesians (32 New Caledonian soldiers). One Mongoloid sample of 75 Vietnamese soldiers had 58.6%, and three African series had 83.3 to 89.7% of longer first toes (Pales, Chippeaux and Pineau, '60).

The Lau, however, with only 37.1% of longer first toes, differed markedly from all other groups reported to date. Wells ('31: 241) stated, unfortunately without

TABLE 1
Relative toe length in four groups of Solomon Islanders and other populations

Population	Author	Date	Toe formula, by per cent			
			N	1 > 2	2 > 1	1 = 2
Caucasians						
English	Harrison	1884	68	75.0	20.6	4.4
English males	Hawkes	1914	1,461	90.2	9.7	0.1
English females	Hawkes	1914	840	83.5	16.3	0.2
Lithuanians	Grüning	1886	100	69.0	30.0	1.0
German Jews	Weissenberg	1895	1,009	64.1	30.2	5.7
French	Pales et al.	1960	55	88.2	8.2	3.6
Americans	Kaplan	1963	109	64.2	33.9	
American MZ twins	Kaplan	1964	126	76.2	23.8	1.8
American DZ twins	Kaplan	1964	88	76.1	23.9	
Africans						
W. Afr. Dogon	Huizinga, de Vetten	1967	338	87.7	12.3	
W. Afr. Negroes	Pales et al.	1960	93	83.3	11.3	5.4
Malagasy	Pales et al.	1960	107	89.7	7.5	2.8
Asians						
Vietnamese	Pales et al.	1960	75	58.7	31.3	9.3
Melanesians						0.7
New Caledonians	Pales et al.	1960	32	59.4	26.6	14.1
Nasioi	Present		224	66.4	27.5	6.1
Kwaio	Present		441	72.1	21.3	6.6
Baegu	Present		481	60.5	36.6	2.9
Lau	Present		439	37.1	56.5	6.4

data, that the longer first toe was "practically never" found in the Bantu, who "most commonly" had the longer second toe. Otherwise, the Lau seem to stand alone.

This aberrant value for the Lau is puzzling. Their genetic relationship to the Baegu, who live a few miles inland from the Lau Lagoon, is not wholly settled, but it appears to be close. The two tribes have formal economic relations, but there has been little or no known intermarriage for several generations. Some Lau customs, linguistic traits, and legends, absent

among the Baegu, suggest Polynesian influence. The genetic evidence summarized in the first paper of this series show that of 15 genetic traits studied so far, the Lau differed from the Baegu in three — namely, ABO secretion, Gm phenogroup, and Australia antigen pattern. In brief, we cannot explain the anomalously high percentage of longer second toes among the Lau and may have to fall back on genetic drift or the founder effect.

Inheritance. Table 2 shows the number of matings in each of the four possible categories, and the number and percent-

TABLE 2
Relative toe length¹ in four Solomon Island populations: assortative mating and family patterns

Parents		Offspring		
Mating type Fa × Mo	N ²	N	N with toe formula 1 > 2	Per cent with toe formula 1 > 2
Nasioi				
1 × 1	19	29	21	72.4
1 × 2	12	16	11	68.8
2 × 1	11	32	22	68.8
2 × 2	4	11	6	54.5
Totals	46	88	60	68.2
X ²	0.22		1.99	
d.f.	1		3	
p ≤	0.70		0.70	
Kwaio				
1 × 1	26	68	50	73.5
1 × 2	5	7	4	57.1
2 × 1	7	11	8	72.7
2 × 2	2	8	5	62.5
Totals	40	94	67	71.3
X ²	0.01		2.40	
d.f.	1		3	
p ≤	0.95		0.50	
Baegu				
1 × 1	28	63	44	69.8
1 × 2	13	31	23	74.2
2 × 1	11	22	17	77.3
2 × 2	10	22	9	40.9
Totals	62	138	93	67.4
X ²	1.19		9.26	
d.f.	1		3	
p ≤	0.30		0.05	
Lau				
1 × 1	9	28	22	78.6
1 × 2	7	23	6	26.1
2 × 1	7	23	11	47.8
2 × 2	19	79	26	32.9
Totals	42	153	65	42.5
X ²	2.48		20.89	
d.f.	1		3	
p ≤	0.20		0.001	

¹ Configurations other than 1 > 2 and 2 > 1 are disregarded in this table.

² Total number of matings, including those without offspring.

age of offspring with longer first toe born to each parental combination. For these analyses, persons with first and second toes equal in length were disregarded. There was no assortative mating for relative toe length in any of the four tribes or when Nasioi, Kwaio, and Baegu were combined. The Lau were kept separate because of their distinctive preponderance of longer second toes.

In all four tribes, the offspring of parents with the same toe formula tended to follow their parents' pattern, the tendency reaching statistical significance among the Baegu ($p < 0.05$), the combined Nasioi-Kwaio-Baegu ($p < 0.05$), and the Lau ($p < 0.001$). No mating combination produced exclusively one type of offspring.

In addition, we examined pedigrees to test several possible modes of inheritance: autosomal, with longer great toe dominant or recessive to longer second toe; X-linked, with longer great toe dominant or reces-

sive; and Y-linked. No pedigree was found to support Y-linked inheritance. Autosomal or X-linked recessivity for longer great toe or longer second toe was ruled out by several pedigrees (fig. 1: A,B,C), in which both parents had formula 1 or 2 but produced offspring with the opposite formula. X-linked dominance for either formula was ruled out by the same pedigrees, in which two parents with the same formula produced sons of the opposite formula. Disregarding possible incomplete penetrance and variable expressivity, there seems to be no simple, single-gene inheritance at work, autosomal or X-linked.

Both the distribution of offspring by parental mating type (table 2) and the pedigree analysis suggest a polygenic rather than a monogenic basis for relative toe length. Actual measurement of toe length might disclose a normal distribution of the difference between first and second toes, as found by Legay and

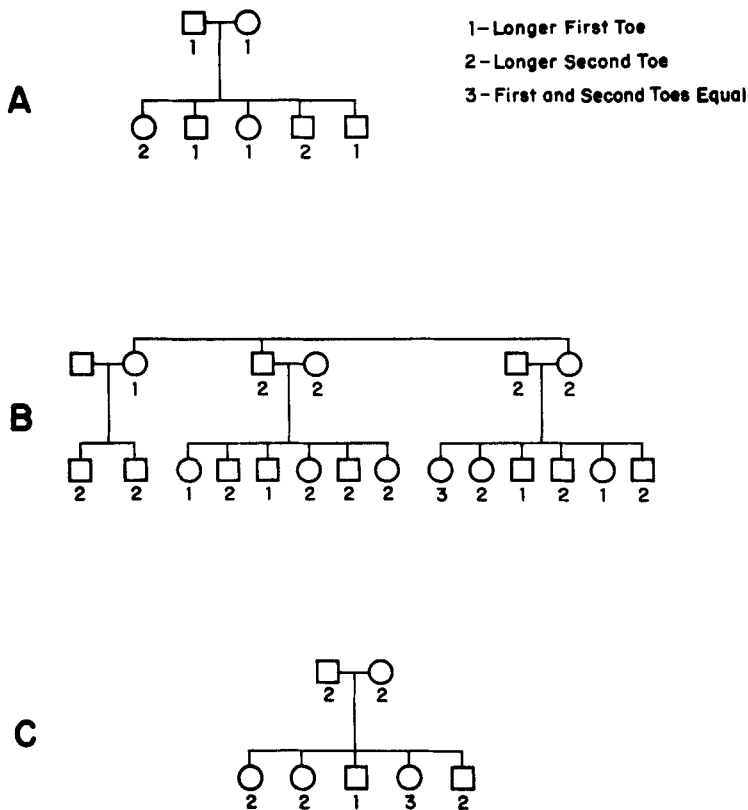


Fig. 1 Relative toe length among Solomon Islanders — sample pedigrees.

Heizmann ('67) for fourth-finger minus index-finger length. Polygenic determination could explain the sometimes puzzling results obtained by treating a continuous distribution as discontinuous, as if one should classify height as tall, medium, or short.

LITERATURE CITED

- Grüning, J. 1886 Über die Länge der Finger und Zehen bei einigen Völkerstämmen. *Arch. f. Anthrop.*, 16: 511-518.
- Harrison, J. P. 1884 On the relative length of the first three toes of the human foot. *J. Anthrop. Inst. Gt. Brit. Ireland*, 13: 258-269.
- Hawkes, O. A. M. 1914 On the relative lengths of the first and second toes of the human foot, from the point of view of occurrence, anatomy and heredity. *J. Genetics*, 3: 249-274.
- Huizinga, J., and A. L. de Vetten 1967 Preliminary study of the foot of the Dogon. *Proc. Kon. Ned. Akad. v. Wetensch., Series C*, 70: 97-109.
- Kaplan, A. R. 1963 Inheritance of relative digit size in the human foot. *J. Hered.*, 54: 35-37.
- 1964 Genetics of relative toe lengths. *Ann. Gemell. Med. Genet.*, 13: 295-304.
- Legay, J. M., and A. Heizmann 1967 Dissymétrie et liaison avec le sexe dans la longueur relative des doigts de la main chez l'Homme (différence annulaire-index). *C. R. Acad. Sci. Paris*, 265: 1199-1201.
- Pales, L., C. Chippeaux and H. Pineau 1960 Le pied dans les races humaines. *J. Soc. des Océanistes*, 16: 45-90.
- Weissenberg, R. 1895 Die Formen der Hand und des Fusses. *Z. f. Ethnologie*, 27: 82-111.
- Wells, L. H. 1931 The foot of the South African native. *Am. J. Phys. Anthrop.*, 15: 185-289.