
Volume 85

Issue 1 *Special Issue on Revisiting the "Negrito"*

Article 13

Hypothesis

2013

Mountain Pygmies of Western New Guinea: A Morphological and Molecular Approach

M Tommaseo-Ponzetta

Department of Biology, University of Bari, Bari, Italy, mila.tommaseo@uniba.it

S Mona

Laboratoire Biologie intégrative des populations, Ecole Pratique des Hautes Etudes, Paris, France

F M. Calabrese

Department of Biochemistry and Molecular Biology, University of Bari, Bari, Italy

G Konrad

Deutsche Forschungsgemeinschaft, Research Program 1975, Papua/Indonesia

E Vacca

Department of Biology, University of Bari, Bari, Italy

M Attimonelli

Department of Biochemistry and Molecular Biology, University of Bari, Bari, Italy

Follow this and additional works at: <http://digitalcommons.wayne.edu/humbiol>

Recommended Citation

Tommaseo-Ponzetta, M; Mona, S; Calabrese, F M.; Konrad, G; Vacca, E; and Attimonelli, M (2013) "Mountain Pygmies of Western New Guinea: A Morphological and Molecular Approach," *Human Biology*: Vol. 85: Iss. 1, Article 13.

Available at: <http://digitalcommons.wayne.edu/humbiol/vol85/iss1/13>

Mountain Pygmies of Western New Guinea: A Morphological and Molecular Approach

Abstract

The presence of "pygmy" or pygmoid groups among New Guinea populations has been the object of scientific interest since the end of the nineteenth century. Morphological and molecular data are used here to study western New Guinea population variability, focusing in particular on two pygmoid groups living in the eastern fringe highlands of Papua: the Una and the Ketengban. Various kinds of anthropometric data are examined, as well as height, weight, and body mass index, to carry out comparisons with nearby ethnic groups living in the highland and lowland regions. The Ketengban data were also compared with other data recorded 20 years before. The results of previous research on the sequencing of the mitochondrial DNA hypervariable segment 1 region and nuclear DNA nonrecombining Y-chromosome polymorphisms are presented. Both morphological and molecular studies involve adult subjects of both genders, representative of the same ethnic groups and/ or geographic regions.

The pygmoid groups turn out to be significantly different from all other study groups, due to their small size, as confirmed by analysis of variance, although significant height and weight increments are observed with respect to those previously recorded. However, putative neutral genetic variation estimated from mitochondrial DNA and Y-chromosome markers support a recent shared common history between these pygmoid populations and the other central Papua groups (except for the Dani-Lani). These findings suggest that the short-stature phenotype is an independent secondary adaptation, possibly driven by an iodine-deficient environment, which leaves the potential for further investigations.

Keywords

New Guinea, Pygmies, Morphology, mtDNA, Hypervariable Segment 1, Nonrecombining Y Chromosome

Mountain Pygmies of Western New Guinea: A Morphological and Molecular Approach

M. TOMMASEO-PONZETTA,^{1*} S. MONA,^{2,3} F. M. CALABRESE,⁴ G. KONRAD,⁵ E. VACCA,¹
AND M. ATTIMONELLI⁴

Abstract The presence of “pygmy” or pygmoid groups among New Guinea populations has been the object of scientific interest since the end of the nineteenth century. Morphological and molecular data are used here to study western New Guinea population variability, focusing in particular on two pygmoid groups living in the eastern fringe highlands of Papua: the Una and the Ketengban. Various kinds of anthropometric data are examined, as well as height, weight, and body mass index, to carry out comparisons with nearby ethnic groups living in the highland and lowland regions. The Ketengban data were also compared with other data recorded 20 years before. The results of previous research on the sequencing of the mitochondrial DNA hypervariable segment 1 region and nuclear DNA nonrecombining Y-chromosome polymorphisms are presented. Both morphological and molecular studies involve adult subjects of both genders, representative of the same ethnic groups and/or geographic regions.

The pygmoid groups turn out to be significantly different from all other study groups, due to their small size, as confirmed by analysis of variance, although significant height and weight increments are observed with respect to those previously recorded. However, putative neutral genetic variation estimated from mitochondrial DNA and Y-chromosome markers support a recent shared common history between these pygmoid populations and the other central Papua groups (except for the Dani-Lani). These findings suggest that the short-stature phenotype is an independent secondary adaptation, possibly driven by an iodine-deficient environment, which leaves the potential for further investigations.

¹Department of Biology, University of Bari, Bari, Italy.

²Laboratoire Biologie intégrative des populations, Ecole Pratique des Hautes Etudes, Paris, France.

³CNRS UMR 7205, Muséum National d'Histoire Naturelle, Paris, France.

⁴Department of Biochemistry and Molecular Biology, University of Bari, Bari, Italy.

⁵Deutsche Forschungsgemeinschaft, Research Program 1975, Papua/Indonesia.

*Correspondence to: Mila Tommaseo-Ponzetta, Department of Biology, University of Bari “Aldo Moro,” Via Orabona, 4, 70125 Bari, Italy. E-mail: mila.tommaseo@uniba.it or mtommaseo@hotmail.com.

Human Biology, February–June 2013, v. 85, no. 1–3, pp. 285–308.

Copyright © 2013 Wayne State University Press, Detroit, Michigan 48201-1309

KEY WORDS: NEW GUINEA, PYGMIES, MORPHOLOGY, MTDNA, HYPERVARIABLE SEGMENT 1, NONRECOMBINING Y CHROMOSOME.

New Guinea (NG), together with Australia, was an early point of arrival of the first modern human expansion out of Africa, at least 50–40 kya (Groube et al. 1986; Summerhayes et al. 2010). Until 8 kya, the island was connected to Australia by low sea levels, forming the Sahul Shelf. Both the southwestern coastal lowlands and the northeastern coast—such as the Sepik-Ramu basin area—were then subjected to major geographic changes, due to sea level variation (Chappell 2005), a process that had important consequences on human distribution and internal migrations.

In the interior of the country, highland plateaus have offered humans favorable settlement opportunities; at the same time, mountain chains cut by steep slopes favored the isolation and ethnic fragmentation of the inhabitants, while protecting them until recently from undesirable western contacts. NG populations are therefore characterized by a high degree of cultural and linguistic variability, and their biological adaptations have attracted growing scientific attention (Attenborough and Alpers 1992; Pawley 2005; Pawley et al. 2005).

The NG “pygmies”—also known as “Oceanic negritos”—aroused the curiosity of the first explorers and have been the subject of great interest since early anthropological studies (Pöch 1904–1905; Luschan 1910; Haddon 1912; Wollaston 1912; Schlaginhaufen 1914; Van den Broek 1913, 1923; Bijlmer 1922, 1939; Wirz 1924; Kirschbaum 1927; Moyne and Haddon 1936; Speiser 1946; Vallois 1957; Ballard 2006). Much of the speculation on their possible origin was reduced when—on the basis of biochemical analyses carried out on pygmoid groups that had settled on the eastern half of the island—Graydon et al. (1958), Gates (1961), and Boyd (1963) concluded that the NG pygmies, as well as other pygmy groups from other regions of the world, were more similar to their neighbors than among themselves. It was therefore assumed that the NG pygmies could be regarded solely as a phenotypic variation of nearby mountain populations.

Speculation on the possible advantages of a small human body examined various environmental factors, such as limited quantities of food, promoting an “economic size,” and adaptation to a warm, humid tropical forest habitat (Collins 1990; O’Dea 1993). However, since pygmy populations are scattered in different ecological zones, there may be more than one explanation (Diamond 1991, 1992). Migliano et al. (2007) brilliantly suggested the advantages of interruption of early growth, favoring rapid reproductive maturation in conditions of early mortality, but this hypothesis cannot be extended to all the world populations of pygmies, since not all of them have short lives.

In the African pygmies studied by Cavalli-Sforza (1986), the evidence of low levels of expression of genes encoding for growth hormone receptors and insulin-like growth factor-1 was cited as a possible cause of reduced growth (Merimée et al. 1981, 1987; Merimée and Rimoin 1986; Baumann et al. 1989), but these fell within normal ranges in other NG pygmy populations (Schwartz et al. 1987; Baumann et al. 1991), suggesting that other factors were responsible for their short stature (Rosenfeld 2003; Perry and Dominy 2009; Ramirez-Rozzi and Sardi 2010). Recently, a large study of the Human Genome Diversity Panel discovered two genes involved in the thyroid hormone pathway (*TRIP4* in Mbuti

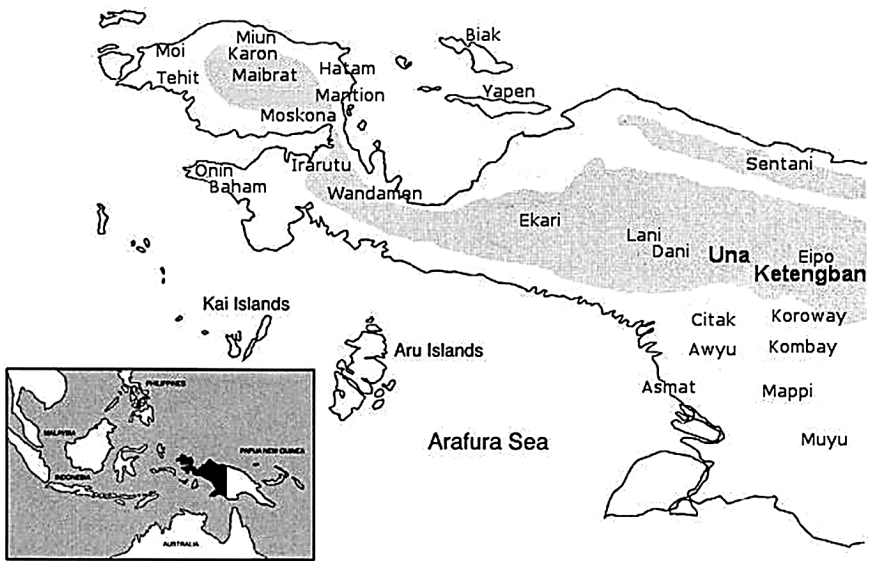


Figure 1. Location of Una and Ketengban study groups and of the other groups considered in this work. The populations reported are listed in Table 1. The locations of the Una and Ketengban pygmy groups are shown in bold. The gray areas in the map represent interior mountain regions. The Aru and Kai Islands and the Arafura Sea location are shown. In the bottom (left), the location of Western New Guinea is shown within the Indonesian region.

pygmies and *IYD* in Biaka pygmies) showing signs of selection that may be related to their short stature (Lopez Herráez et al. 2009). Pygmies living in different habitats—from tropical humid African forest to the NG highlands—suffer from iodine-deficient diets. Alterations in the thyroid hormone pathway may therefore be among the causes of pygmies' short stature, arising as an indirect consequence of selection in response to an iodine-deficient environment. Jarvis et al. (2012), searching for evidence of short-stature selection in African pygmies, considered the possibility that genes with regulatory effects on different functions—such as metabolism or immunity—could have pleiotropic effects and be an indirect cause of pygmies' short stature.

This research focused on two short-stature groups (alternatively defined as pygmy or pygmoid), living in the fringe highlands area of Western New Guinea: the Una (or Uniang), settled in the Langda district (2,000 m), and the Ketengban, who live the Bime Valley, in Turwe (1,350 m) and Calap (1,890 m) villages. Both morphological and molecular data, collected in 1995, are taken into account. For comparisons, other West Papua groups of normal stature are considered: Wamena (Dani), living in the West Papua Central Highlands; Senngo and Piramanak (Awyu, Citak, Mappi, Muyu), along the lowland plains; and Ewer and Basim (Asmat), in coastal areas (Table 1, Figure 1), all of which have been the subject of previous

Table 1. The Study Populations

LANGUAGE	GEOGRAPHIC LOCATION	POPULATION
<i>Northwestern Papua</i>		
West Papuan	Central area	Baham (<i>bdw</i>)
		Karon (<i>kgw</i>)
		Mai Brat (<i>ayz</i>)
	West and southwest areas	Miun (<i>kgw</i>)
		Moi (<i>mxn</i>)
East Bird's Head	Eastern area	Tehit (<i>kps</i>)
	Eastern area	Hatam (<i>had</i>)
	Southeast area	Mantion (<i>mxn</i>)
	Southeast area	Moskona (<i>mtj</i>)
Malayo Polynesian	East Bomberai Peninsula	Irarutu (<i>irh</i>)
	Northwest Bomberai Peninsula	Onin (<i>oni</i>)
	West Cenderawasih Bay	Wandamen (<i>wad</i>)
	Biak and Numfor islands	Biak (<i>bhw</i>)
	Yapen island	Yapen (*)
<i>Eastern Papua</i>		
Trans-New Guinea	Western and Central Highlands	Dani (<i>dna</i>)
		Eipo (<i>eip</i>)
		Ekari (<i>ekg</i>)
		Ketengban (<i>xte</i>)
		Una (<i>mtg</i>)
		Yali (<i>yac</i>)
	Lowland riverine southwest areas	Awyu (<i>awu</i>)
		Kombay (<i>tyu</i>) + Yakay (<i>jaq</i>)
		Korowai (<i>khe</i>)
		Asmat (<i>cns</i>)
		Citak (<i>txt</i>)
Coastal southwest areas	Mappi (*)	
	Muyu (<i>kts</i>)	
	Sentani (<i>set</i>)	

Study populations are subdivided according to language family and geographic location. Population names are reported as indicated by the research subjects. The geographic locations of the listed populations are displayed in Figure 1. M and F = male and female anthropometric study; mtDNA = HVS1 study; Y = Y-chromosome study. Trans-New Guinea, West Papuan, and East Bird's Head are Papuan

ANTHROPOMETRIC DATA		MOLECULAR DATA	
M	F	mtDNA	Y CHROMOSOME
		27	24
		27	22
		43	24
		5	
		22	8
		15	5
		13	12
		14	11
		9	10
		9	5
		6	2
		11	10
		19	10
		9	
32	31	26	24
		1	
		36	19
90	63	25	19
53	45	50	46
		4	5
		15	10
		5	13
35	16	10	
80	49	26	20
		39	28
70	41	19	10
		9	8
		1	

languages. Malayo Polynesian is an Austronesian language. Language codes (in parentheses) are reported following *Ethnologue*, 17th edition (Lewis et al. 2013). (*) Mappi (Mappi Regency) and Yapen (Yapen Island) indicate mere geographic origin, not language. Note that Yakay is also spelled Yaqay (*jaq*); Manton is an alternate name for Manikion (*mnx*); Miun is an alternate name for Karon (*kgw*).

research (Cortivo et al. 1987; Re et al. 1989; Tommaseo et al. 1989, 1990, 1992; Tommaseo and Lucchetti 1992).

To evaluate the possible height and weight trends of the short-stature study groups considered here, Ketengban anthropometric data are compared with other data concerning the same population, collected by G. Konrad in 1975 and kindly made available for this research. The diagnosis of a possible stature increase of these pygmoid populations in the time span of 20 years (1975–1995) will be an interesting indicator of the causal factors of the body size: whether (or how much) this is determined by a genetic background and/or consequent to an environmental factor, such as diet or medical assistance.

Lastly, for a genetic perspective of the relationships of the Una and Ketengban with their “normal-stature” neighbors, the results of previous molecular studies of West Papua populations based on the mitochondrial DNA (mtDNA) hypervariable segment 1 (HVS1) (Tommaseo-Ponzetta et al. 2002, 2007) and nonrecombining Y-chromosome polymorphisms (Kayser et al. 2003; Mona et al. 2007) are here presented and discussed. In the latter research, populations living in the Bird’s Head area and nearby regions—including two additional “short-stature” mountain groups, the Ekkari and the Yali—were also considered.

Here, we address by means of both morphology and molecular markers three main topics: (1) we provide a description of the morphological variation of Western New Guinea pygmoid groups and compare them with their neighbors, in order to have a complete picture of the diversity in the area; (2) we investigated the existence of a possible secular trend in one of the two pygmoid groups, the Ketengban, by using height data collected in 1975 in the course of a medical research (Konrad and Seiler 1980; Fleckenstein 1981); and (3) we used neutral genetic variation data from many Western New Guinea populations—some of which have been the object of previous studies—to understand whether the short stature phenotype occurred in the island as a secondary adaptation (and, if so, to which specific factor).

Materials and Methods

Personal and cultural data, anthropometric measurements, and biological samples of Una and Ketengban populations (adult men and women) were collected by M.T.-P. during field research in 1995, promoted by the University of Bari, the Ligabue Study and Research Centre of Venice (Italy), and the University of Bandung (Indonesia). The populations were informed by means of a local interpreter on the scope of our research, and anthropometric data collection was performed after the subjects gave an appropriately informed consent. Anthropometric measurements were carried out following the International Biological Program (Weiner and Lourie 1981).

Data Analysis

Morphological Data. We first computed basic descriptive statistics in the two pygmy populations relative to body and head dimensions, as well as several

anthropometric indices. Data were compared with those previously recorded among the Ketengban in 1975. Next, we extended the study to other groups living in the nearby highland, lowland, and coastal regions, whose measurements had previously been collected in west Papua by M.T.-P. in 1985 (Tommaseo and Lucchetti 1991, 1992; Tommaseo and Viviani 1991) (see Table 1).

All statistical analyses (*t*-tests, analyses of variance) and graphical representations (box plots, scatter plots) were performed using R (R Development Core Team 2011).

Molecular Data

- *mtDNA*. The data reported here are relative to a molecular study consisting of the amplification and sequencing of the entire HVS1 of the D-loop, the main regulatory region of the mitochondrial genome. mtDNA was extracted from hair roots, and the HVS1 region was directly amplified from rCRS (revised Cambridge reference sequence) positions 16024–16374 (Andrews et al. 1999).

The sequences obtained were analyzed with the “fragment classifier tool” available through the Human Mitochondrial DataBase (Attimonelli et al. 2005; Rubino et al. 2012), where genomes are annotated with specific information and are analyzed; the tool can detect polymorphic sites, and haplogroup assignment is based on PhyloTree, a phylogenetic tree of global human mtDNA variation (van Oven and Kayser 2009). The results of previous studies (Tommaseo-Ponzetta et al. 2002, 2007) were revised and partially integrated with data concerning the Bird’s Head region and the surrounding northwestern populations. A matrix of F_{ST} distances between all the populations was computed using Arlequin, version 3.5 (Excoffier and Lischer 2010). Data were displayed by means of a multidimensional scaling (MDS) computed with the isoMDS function implemented in the library MASS available in R (R Development Core Team 2011).

- *Y Chromosome*. To enable comparisons of Una and Ketengban maternal and paternal lineages, in the context of the surrounding populations, we report here the results of a Y-chromosome study conducted on the same southwestern and central west NG population samples considered in the HVS1 study. This research concerned a combined Y-chromosome analysis of 26 binary markers and 7 short tandem repeat (STR) loci (Kayser et al. 2003).

For a wider perspective, this Y-chromosome overview was then extended to the results of a second research, focused on the Bird’s Head region and the surrounding northwestern areas (Mona et al. 2007), the mtDNA HVS1 male study subjects of which had previously been sequenced (Tommaseo-Ponzetta et al. 2007). The computation and plot of the genetic distances between populations were performed as above using both haplogroup frequencies (F_{ST}) and STR loci (R_{ST}).

Results

Morphological Study. Summary statistics of the dimensions and indexes of the Una and Ketengban are given in Tables 2–5. Our interest focuses in particular on height. The males of both groups present identical mean heights, 150.1 ± 6.4 cm (Una) and 150.1 ± 6.2 cm (Ketengban), which places them at the limit of what Schmidt (1905), quoted in Martin (1988), considered a pygmy size (150.0 cm). Minimal height values were found in the Ketengban (136.5 cm), but some Una were also small (138.0 cm); the Ketengban, a larger population sample, displayed greater variability, reaching a greater maximum (167.0 cm) than the Una (162.0 cm). Una females had a mean height slightly lower than that of the Ketengban (142.2 and 143.0 cm, respectively). Minimum values were quite low in both groups: 127.5 and 130.0 cm; the maximum values did not exceed 153.0 and 154.0 cm, respectively.

The body mass index (BMI) of both men and women was within normal ranges, slightly higher in the Una, in both genders. Although there were some very slender individuals, overweight was also recorded among the Una (maximum of 29.9). Both populations appeared robust, with legs of medium length in relation to the trunk. Men's shoulders were medium-large, varying from 35.3 cm (Una) to 34.1 cm (Ketengban), with biacromial/height indexes of 23.5 in the former and 22.7 in the latter group. Women's shoulders showed medium breadth values. In both men and women, the pelvis breadth was medium-low (according to Brugsch, qtd. in Facchini 1988). Both groups were brachicephalous, with values of 82.1 (Una) and 82.9 (Ketengban) for the men and 81.9 and 81.1 for the women.

When the Una and Ketengban are compared with other NG pygmy/pygmoid groups reported in the literature (Table 6), their height falls within their range of variation, which is not far from the short statures recorded among mountain Papua inhabitants by the first researchers. The brachycephality of our groups, while distinguishing them from the majority of NG populations, confirms their similarity to the Goliath pygmies of the Nassau Range, described by Van den Broek (1913)—belonging to the same Mek language family—to which they have often been assimilated, and to a lesser degree to their mountain neighbors, the Eipo (Büchi 1981). For wider comparisons, the heights and weights of other West Papua groups, recorded in 1985 by M.T.-P., are listed in Table 7. Table 8 presents ANOVA multiple comparison values and shows that the Una and Ketengban differ significantly from all other populations in both height and weight, particularly compared with the coastal Asmat and the nearby mountain Dani. Figures 2 and 3 show how the Una and Ketengban are set apart from the Asmat and other groups of the lowland riverine regions, on account of their height, cephalic index, and weight, the lowest height values being matched by the higher cephalic indexes.

Table 9 lists the Ketengban (Bime) dimensions recorded in 1975 and made available for this research. When compared with 1995 data, we can see how the height of the male and female population has increased significantly in the last

Table 2. Una Population, Males: Anthropometric Dimensions and Indexes (n = 53)

MEASURE	MEAN \pm SD	RANGE
Height (cm)	150.1 \pm 6.4	138.0–162.0
Sitting height (cm)	78.1 \pm 3.0	71.5–83.5
Weight (kg)	49.8 \pm 6.5	34.0–64.0
<i>Diameter (cm)</i>		
Biacromial	35.3 \pm 1.8	32.0–38.7
Bicristal	25.4 \pm 1.4	22.4–28.5
<i>Head (cm)</i>		
Length	18.1 \pm 0.7	16.6–19.4
Breadth	14.8 \pm 0.4	13.8–15.8
Skeletal index	52.0 \pm 1.7	48.1–57.1
Body mass index	22.1 \pm 2.2	16.2–29.9
<i>Height index</i>		
Biacromial	23.5 \pm 0.8	21.8–25.4
Bicristal	16.9 \pm 0.7	15.6–18.4
Cephalic index	82.1 \pm 3.5	74.6–91.3

Table 3. Ketengban Population, Males: Anthropometric Dimensions and Indexes (n = 90)

MEASURE	MEAN \pm SD	RANGE
Height (cm)	150.1 \pm 6.2	136.5–167.0
Sitting height (cm)	77.5 \pm 2.8	69.0–84.0
Weight (kg)	47.3 \pm 5.7	34.0–61.0
<i>Diameter (cm)</i>		
Biacromial	34.1 \pm 1.3	30.6–37.2
Bicristal	24.6 \pm 1.3	20.9–28.9
<i>Head (cm)</i>		
Length	18.0 \pm 0.5	16.6–19.4
Breadth	14.9 \pm 0.5	13.7–16.9
Skeletal index	51.6 \pm 1.5	46.1–55.9
Body mass index	21.0 \pm 2.0	15.2–26.2
<i>Height index</i>		
Biacromial	22.7 \pm 0.9	20.1–24.7
Bicristal	16.4 \pm 0.8	14.6–18.2
Cephalic index	82.9 \pm 3.2	74.1–91.8

20 years (+3.9 cm for males and +3.4 for females). Weight also increased (+3.9 kg males, +3.6 kg females), perhaps owing to the presence of some westerners in the area and to their occasional help in overcoming health problems and food shortages due to recurrent environmental crises. The BMI also shows a positive difference: +0.8 (males) and +0.7 (females) (Figure 4). When height variation is considered according to age class (Figure 5), a positive trend is more evident in the younger subjects.

Table 4. Una Population, Females: Anthropometric Dimensions and Indexes (n = 45)

MEASURE	MEAN ± SD	RANGE
Height (cm)	142.2 ± 4.5	127.5–153.0
Sitting height (cm)	73.8 ± 3.5	65.5–82.5
Weight (kg)	44.6 ± 5.5	31.5–59.0
<i>Diameter (cm)</i>		
Biacromial	31.6 ± 1.4	28.9–34.5
Bicristal	24.7 ± 1.4	22.0–28.4
<i>Head (cm)</i>		
Length	17.4 ± 0.6	16.0–18.6
Breadth	14.3 ± 0.3	13.4–15.0
Skeletal index	51.9 ± 1.5	49.1–56.0
Body mass index	22.0 ± 1.9	18.9–27.9
<i>Height index</i>		
Biacromial	22.2 ± 0.7	20.7–23.8
Bicristal	17.3 ± 1.0	14.5–21.0
Cephalic index	81.9 ± 3.1	75.5–90.2

Table 5. Ketengban Population, Females: Anthropometric Dimensions and Indexes (n = 63)

MEASURE	MEAN ± SD	RANGE
Height (cm)	143.0 ± 5.5	130.0–154.0
Sitting height (cm)	74.3 ± 2.7	69.5–80.5
Weight (kg)	42.7 ± 6.1	27.0–58.0
<i>Diameter (cm)</i>		
Biacromial	31.0 ± 1.7	26.5–37.6
Bicristal	25.1 ± 1.2	22.0–28.9
<i>Head (cm)</i>		
Length	17.5 ± 0.5	15.9–18.7
Breadth	14.2 ± 0.5	13.2–15.7
Skeletal index	52.0 ± 1.8	48.2–57.6
Body mass index	20.8 ± 2.4	13.8–29.6
<i>Height index</i>		
Biacromial	21.7 ± 1.0	19.7–25.8
Bicristal	17.6 ± 0.7	14.7–19.5
Cephalic index	81.1 ± 3.2	73.5–90.8

Table 6. Historical Data of Pygmies: Anthropometric Dimensions, Males (cm)

PYGMIES	N	HEIGHT	CEPHALIC INDEX	BIZYGOMATIC DIAMETER	NOSE HEIGHT	NOSE WIDTH	REFERENCE
Tapiro	49	148.9	78.9	13.7	4.9	4.3	Bijlmer 1939
Pesechem	44	152.5		12.4	4.9	4.0	Van den Broek 1923
Goliath	12	149.2	83.4	12.7	5.0	4.2	Van den Broek 1923
Ayome	137	144.8	76.4	13.2	5.2	4.2	Gusinde 1961
Eipo	56	146.2	81.6	13.4	5.2	4.5	Büchi 1981

Table 7. Height and Weight of Western New Guinea Groups

POPULATION	MALES			FEMALES		
	N	MEAN ± SD	RANGE	N	MEAN ± SD	RANGE
<i>Height (cm)</i>						
Dani	32	163.6 ± 4.7	152.0–172.0	31	157.5 ± 4.4	150.0–169.0
Lowland riverine ^a	35	161.5 ± 5.6	147.2–174.0	16	151.8 ± 3.5	146.0–158.5
Coastal riverine ^b	70	160.8 ± 5.4	147.0–175.0	41	152.9 ± 5.3	142.3–167.0
Asmat	80	164.5 ± 5.8	150.0–178.0	49	155.3 ± 5.7	144.5–172.0
<i>Weight (kg)</i>						
Dani	32	57.8 ± 8.0	40.0–74.0	31	51.5 ± 5.5	43.0–66.0
Lowland riverine ^a	35	53.3 ± 4.6	35.0–63.0	16	44.5 ± 4.3	37.0–50.5
Coastal riverine ^b	70	54.2 ± 6.1	43.0–71.5	41	46.8 ± 7.9	34.0–69.0
Asmat	80	58.0 ± 6.7	44.5–77.0	49	47.1 ± 7.6	36.0–63.0

^aLowland riverine: Awyu, Koroway, Kombay, Yakai. ^bCoastal riverine: Muyu, Mappi, Citak.

Table 8. Analysis of Variance for Height and Weight

	DANI	UNA	KETENGBAN	LOWLAND RIVERINE ^a	COASTAL RIVERINE ^b	ASMAT
<i>Height</i>						
Dani	—	—	—	—	—	—
Una	13.54*	—	—	—	—	—
Ketengban	13.51*	-3.02	—	—	—	—
Lowland riverine ^a	2.15	-11.39*	-11.36*	—	—	—
Coastal riverine ^b	2.66	-10.87*	-10.84*	0.518	—	—
Asmat	-0.87	-14.41*	-14.38*	-3.02	-3.54*	—
<i>Weight</i>						
Dani	—	—	—	—	—	—
Una	8.01*	—	—	—	—	—
Ketengban	10.55*	2.54	—	—	—	—
Lowland riverine ^a	4.56	-3.46	-5.99*	—	—	—
Coastal riverine ^b	3.87	-4.14*	-6.68*	-0.69	—	—
Asmat	-0.29	-8.30*	-10.84*	-4.85*	-4.16*	—

^aLowland riverine: Awyu, Koroway, Kombay, Yakai. ^bCoastal riverine: Muyu, Mappi, Citak.

**p*<0.05.

Table 9. Ketengban Male and Female Dimensions Recorded in 1975 (G. Konrad)

MEASURE	MALES (N = 102)			FEMALES (N = 63)		
	MEAN ± SD	RANGE	COEFFICIENT OF VARIATION	MEAN ± SD	RANGE	COEFFICIENT OF VARIATION
Height (cm)	146.2 ± 5.8	134.0–161.0	0.040	139.6 ± 4.1	133.0–151.5	0.029
Weight (kg)	43.4 ± 5.4	29.0–57.0	0.124	39.1 ± 4.5	22.0–47.0	0.114
Body mass index	20.2 ± 0.07	16.2–22.7	0.069	20.1 ± 2.1	12.7–24.7	0.102

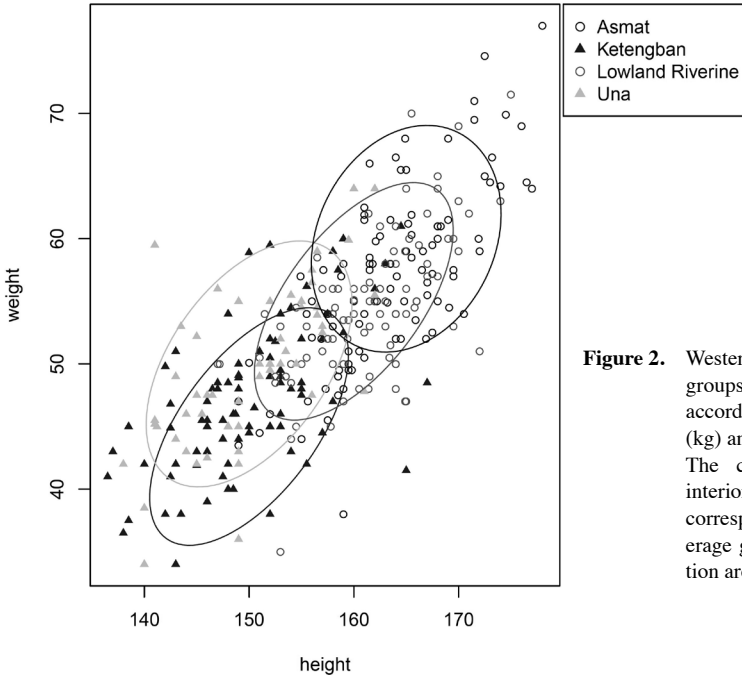


Figure 2. Western New Guinea groups distribution according to weight (kg) and height (cm). The circles at the interior of the plot correspond to the average group distribution area.

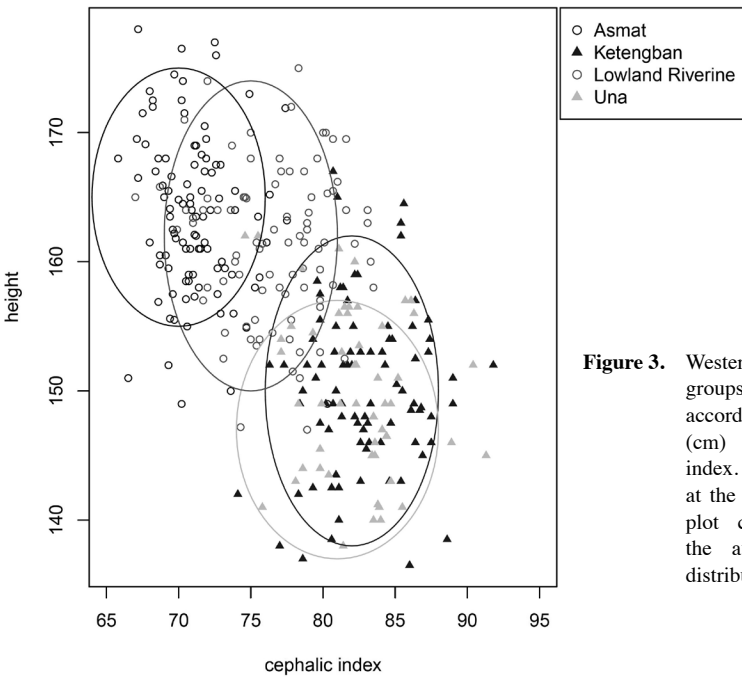


Figure 3. Western New Guinea groups distribution according to height (cm) and cephalic index. The circles at the interior of the plot correspond to the average group distribution area.

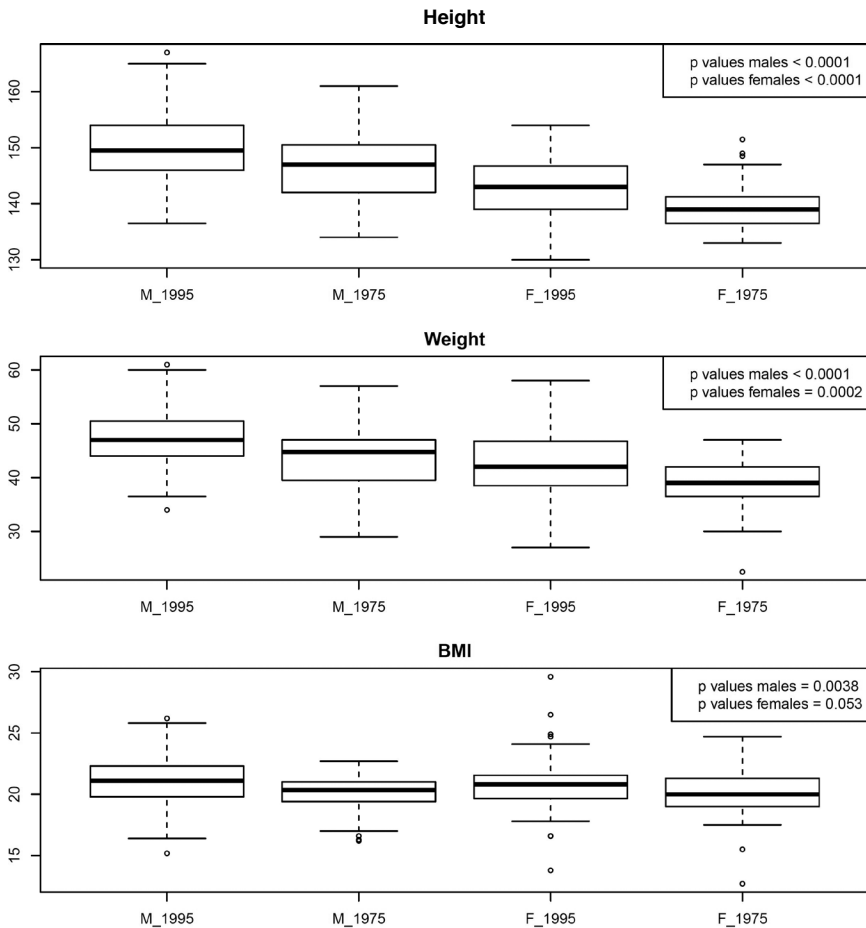


Figure 4. Ketengban height (cm), weight (kg), and body mass index variation over 20 years (*t*-test). M, males, F, females, 1995–1975.

Medical Data. Medical research (Jüptner 1981), carried out among the Eipo pygmies—Ketengbans’ closest neighbors—reports thyroid hormone values well below the average in both men and women (Table 10). For a wider comparison, the coastal Asmat values are also reported (Tommaseo et al. 1989).

Similar hormone data were not available for the Ketengban population (Konrad and Seiler 1980). However, in his analytic evaluation of the results of the x-ray skull and whole-body research of the Ketengbans carried out by Konrad, Fleckenstein (1981) observes that when both male and female pygmoids were compared with Europeans of the same age (Ketengban age was determined on the basis of x-ray examination), these NG subjects “appeared physiognomically older

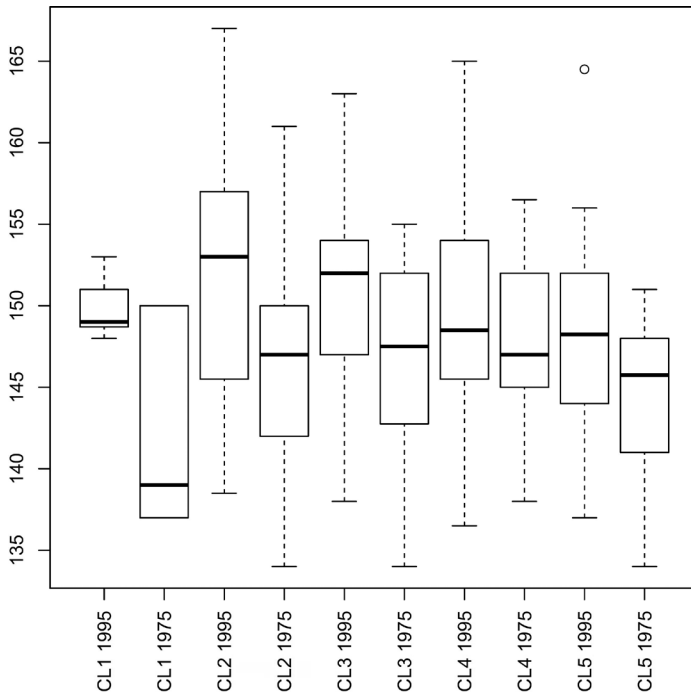


Figure 5. Ketengban height increase (cm) according to age classes. CL1, 17–19 years; CL2, 20–29 years; CL3, 30–39 years; CL4, 40–49 years; CL5, 50+ years.

than their biological skeletal age, and thus older than their true age.” Also according to Fleckenstein, among the most common diseases registered in this group were goiter, osteomyelitis, enlarged thyroid glands, bone cysts, and osteoporosis.

Molecular Study

mtDNA. Application of SiteVar software (Pesole and Saccone 2001) to the mtDNA HVS1 sequences of 467 subjects (202 from the southwestern region; 267 from the Bird’s Head Peninsula and northwestern area) identified 83 variant sites out of 351 nucleotides. Application of CLEANUP software (Grillo et al. 2005) defined 158 haplotypes, 88 unique and 70 shared. While the haplogroup variability of the Bird’s Head Peninsula and surrounding islands is high and includes haplogroups of Austronesian origin shared by populations of the nearby Southeast Asian and insular Indonesian regions, the interior of NG conserves its mtDNA specificity, characterized by P and Q haplogroups (Figure 6). These haplogroups are both

Table 10. Thyroid Hormone Values in the Eipo and Asmat Populations

POPULATION	TT ₄ ^a	TT ₃ ^b
<i>Eipo [mean (range)] (Jüptner 1981)</i>		
Males	42.0 (10–108)	2.5 (1.4–3.8)
Females	57.1 (10–113)	—
<i>Asmat (mean ± SD) (Tommaseo et al. 1989)</i>		
Males	60.0 ± 13.9	1.3 ± 0.2
Females	56.3 ± 14.3	1.2 ± 0.2

^aTT₄, total thyroxine; normal range: 45–110 ng/ml.

^bTT₃, total triiodothyronine; normal range: 0.5–2 ng/ml.

very ancient and typical of Papua populations (Tommaseo-Ponzetta et al. 2002, 2007; Friedlaender et al. 2005, 2007). P frequency is highest in the Ketengban, reaching 76%. P is also present among the Una (26%), but this group has a higher Q frequency (Q1, 62%; Q2b, 8%), comparable to that of other populations nearby. The high frequency of P found among the Mappi (36%), who live in the lowland region south of the Ketengban, may suggest possible wife exchange with the latter, along southward-trending river valleys.

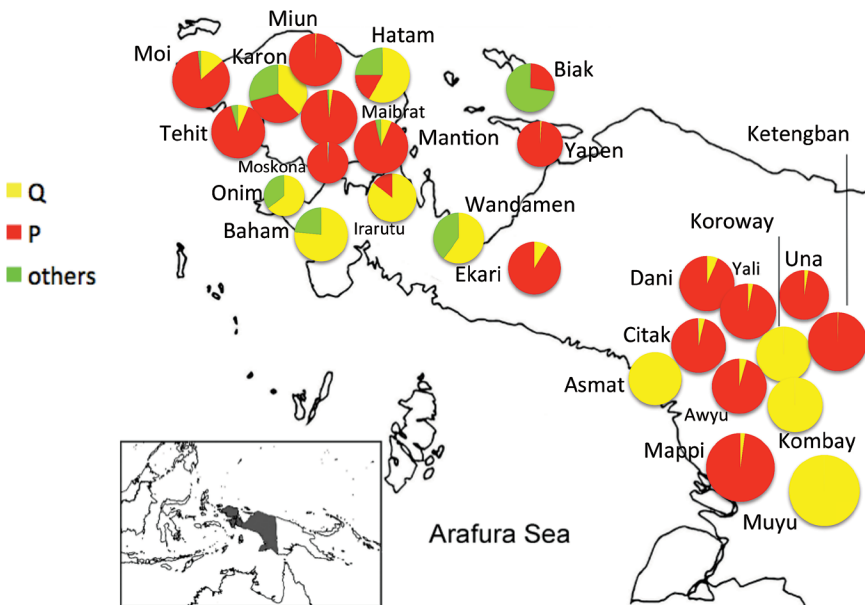


Figure 6. Mitochondrial DNA (mtDNA) hypervariable segment 1 (HVS1) haplogroup frequency distribution in Western New Guinea study groups.

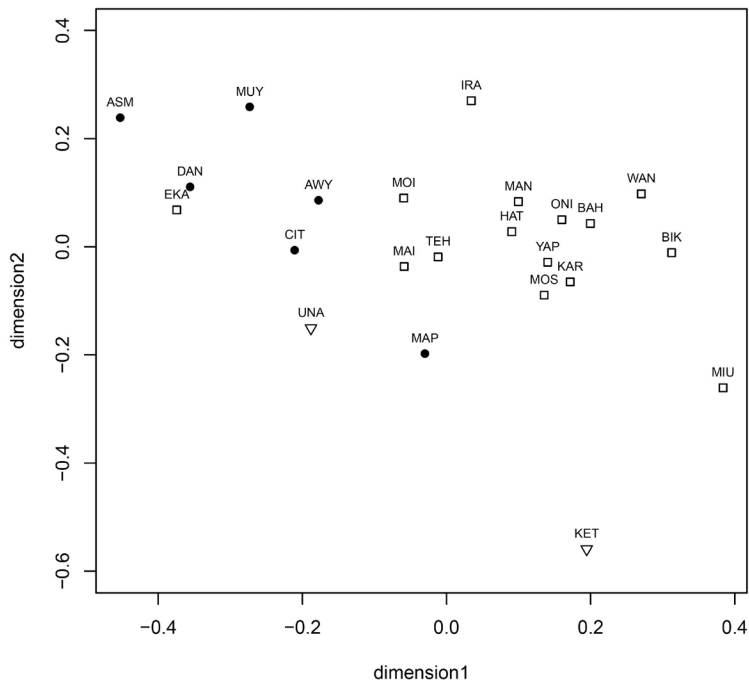


Figure 7. Multidimensional scaling (MDS) of the F_{ST} pairwise distance matrix computed from mtDNA. MDS stress value, 8.8%. Populations reported in the plot are labeled as follows: ASM, Asmat; AWY, Auyu; BAH, Baham; BIK, Biak; CIT, Citak; DAN, Dani; EKA, Ekkari; HAT, Hatam; IRA, Iraputu; KAR, Karon; KET, Ketengban; MAI, Maibrat; MAN, Manton; MAP, Mappi; MIU, Miun; MOI, Moi; MOS, Moskona; MUY, Muyu; ONI, Onin; THE, Tehit; UNA, Una; WAN, Wandamen; YAP, Yapen.

When compared with the Bird's Head, the central and southwestern Papua regions confirm their relative isolation—especially the internal highland territories. Conversely, the northwestern peninsula, favoring contacts with Southeast Asian and north and central Indonesian archipelagos, was the point of arrival of various migration waves, as indicated by the presence of several Austronesian-speaking populations.

Y Chromosome. Most of the males analyzed from Western New Guinea (77.5% from lowlands/coast and 74.5% from the highlands) carried M-P34, a haplogroup of Melanesian origin (Kayser et al. 2006), with the exception of the Dani-Lani group, which stands apart due to the highest frequency of C-M208. In the Una and Ketengban populations, as well as in the Yali highland pygmoid group and the Auyu lowland population, M-P34 frequency reached 100%. The same haplogroup is the most frequent in NG (average frequency 46.8%). Coalescence analyses indicate that M-P34 arose around 7,356 years ago in the eastern part of NG, from where it

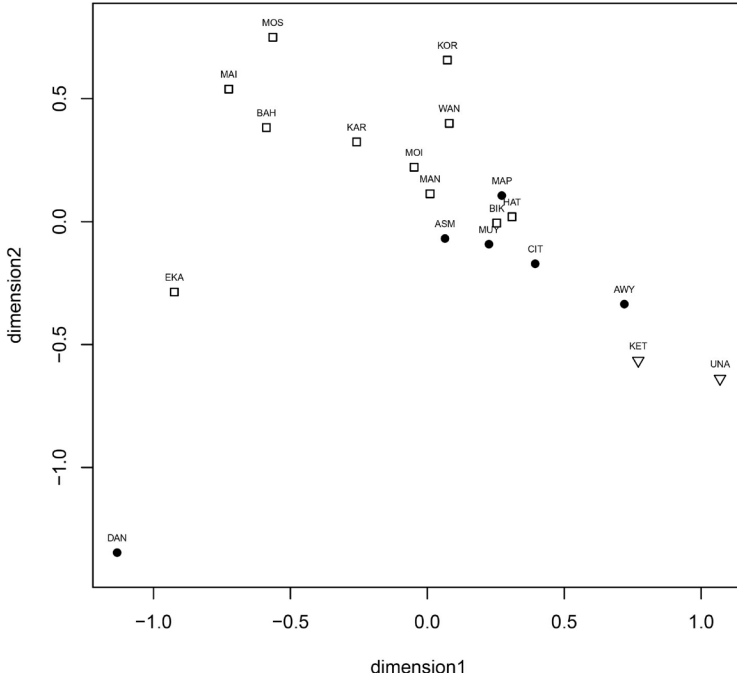


Figure 8. Multidimensional scaling (MDS) of the F_{ST} pairwise distance matrix computed from the frequency distribution of Y-chromosome haplogroups. MDS stress value, 10%. Populations reported in the plot are labeled as follows: ASM, Asmat; AWY, Awyu; BAH, Baham; BIK, Biak; CIT, Citak; DAN, Dani; EKA, Ekkari; HAT, Hatam; KAR, Karon; KET, Ketengban; KMB, Kombay; KOR, Koroway; MAI, Maibrat; MAN, Manton; MAP, Mappi; MOI, Moi; MOS, Moskona; MUY, Muyu; UNA, Una; WAN, Wandamen.

spread westward to the southwestern and central part of the island, reaching the Bird’s Head Peninsula, Eastern Indonesia, and the nearby Melanesian archipelagos (Mona et al. 2007). Mona et al. (2007) connect M-P34 diffusion from the eastern to the western part of NG to the expansion of the Trans-New Guinea languages, driven by the spread of agriculture (Pawley 1998; Pawley et al. 2005). Following this picture, it appears that most of the male variability in both Una and Ketengban arose relatively recently. This supports the view that pygmies are tightly related to the surrounding populations and have been involved in the same migrations that have shaped the genetic background of the whole island. This is confirmed by the MDS plot based on Y-chromosome genetic distances (Figures 7–9), where the Dani rather than the pygmies is the outlier population. Nonetheless, Una and Ketengban show higher affinities compared with the other populations, suggesting that they may have a more recent common origin (i.e., probably they started to diverge after having acquired the short stature phenotype).

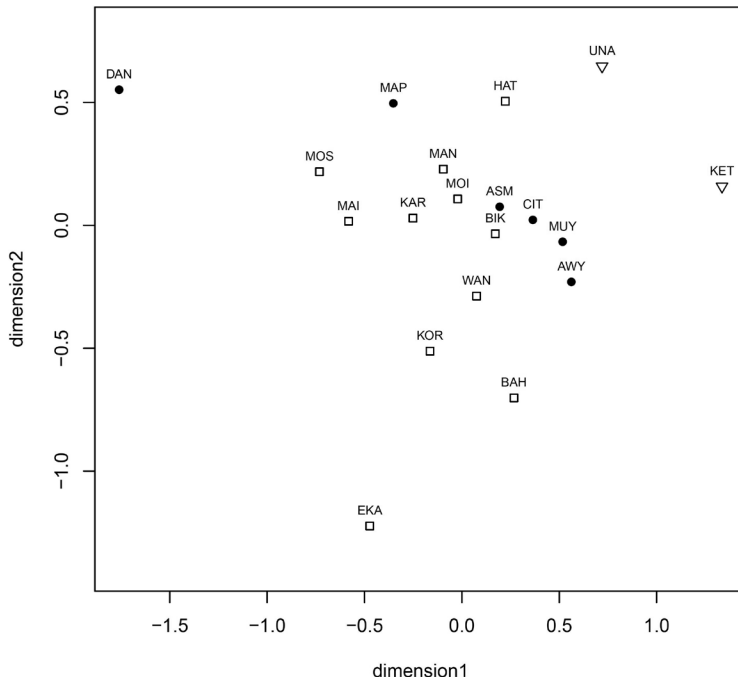


Figure 9. Multidimensional scaling (MDS) of the R_{ST} pairwise distance matrix computed from the Y-chromosome STR loci. MDS stress value, 13.3%. Populations reported in the plot are labeled as in Figure 8.

Conclusions

The dimensions of the Una and Ketengban are almost identical, with the exception of shoulder breadth, body weight, and BMI, which are slightly larger in the Una. When the Ketengban secular trend is considered, their dimensions are significantly different with respect to those recorded 20 years previously. Their nutritional status has improved in recent years and may have contributed to their increased height, more evident in individuals younger than 30 years of age, whose early growth exploited the advantages of better nutrition and basic medical assistance. The same may be stated when the Una and Ketengban 1995 anthropometric data are pooled and compared with the 1975 group. This height increment seems to match the results of previous studies concerning secular trends in NG populations (Ulijaszek 1993), although the observation of altered growth patterns in the Ok pygmoid group over 25 years recorded growth acceleration but no significant increase in final adult height (Adhikari et al. 2011).

However, when the Una and Ketengban are considered in the wider context of Western New Guinea human morphological variability, they still stand apart

for both their low body dimensions and head morphology. The possible allometric relationship between short stature and head shape and/or dimensions deserves further attention, since brachycephaly may also be associated to hypothyroidism (Wilkins and Fleischman 1941; Aufderheide and Rodríguez-Martín 1998).

The Una and Ketengban share the same mtDNA and Y-chromosome polymorphisms that dominate the human population landscape of the interior of the island, where the uniformity of our groups are indicative of ancient isolation and genetic drift, if not of the crude effect of bottlenecks, especially regarding the Ketengban. If their genetic roots are ancient and similar to those of their neighbors, with whom they share most “neutral” genetic markers, it would seem reasonable that their ancestors acquired a smaller body size after the peopling of the island, as a secondary effect of selection, favoring their survival in peripheral, difficult environments. The Una and Ketengban both live in highland regions, where human pathologies caused by iodine deficiencies have been extensively documented (Garruto et al. 1974; Gajdusek et al. 1974; Gajdusek and Garruto 1975). The medical research (Jüptner 1981) carried out among the Eipo pygmies—who are Ketengbans’ neighbors—reports thyroid hormone values well below the average in both men and women, and also lower than the same data reported for the Asmat (Tommaseo et al. 1989). Thyroid hormone dysfunctions—such as goiter and thyroid gland enlargement—were also reported (Fleckenstein 1981). Since short stature and large heads may be associated with genetic alterations in the thyroid hormone pathway, the reduced size and the brachycephaly of these mountain groups may have arisen as an indirect consequence of selection in response to an iodine-deficient environment (Dormitzer et al. 1989; Lopez Herráez et al. 2009; Jarvis et al. 2012).

On the other hand, the higher stature of central highland populations—such as the Dani—or of the coastal Asmat settled in Ewer, appears associated to favorable habitats, promoting the development of agriculture and pig raising in the former and of coastal fishing/sago gathering in the latter. This opens the way to an alternative explanation, which posits the first immigrants in the island as short-stature groups who would have increased their body size with the improvement of survival in the more favorable environments. Both these interesting hypotheses encourage further research.

Acknowledgments We are deeply grateful to the Una and Ketengban communities for their participation in this research. We thank Achmad Saifuddin Noer (Bandung University) and Sangkot Marzuki, Herawati Sudoyo, and Helena Syukriani (Eijkmann Institute for Molecular Biology in Jakarta) for their support and fruitful collaboration. Thanks are due to Leonisio Doglioni and Hubert Schindler for their useful suggestions. M.T.-P. is particularly grateful to Giancarlo Ligabue (Ligabue Study and Research Center of Venice) and Desmond Clark for inspiring this study.

Received 14 October 2012; revision accepted for publication 6 May 2013.

Literature Cited

- Adhikari, A., A. Sen, R. C. Brumbaugh et al. 2011. Altered growth patterns of a mountain Ok population of Papua New Guinea over 25 years of change. *Am. J. Hum. Biol.* 23:325–332.
- Andrews, R. M., I. Kubacka, P. F. Chinnery et al. 1999. Reanalysis and revision of the Cambridge reference sequence for human mitochondrial DNA. *Nat. Genet.* 23:147.
- Attenborough, R. D., and M. P. Alpers, eds. 1992. *Human Biology in Papua New Guinea*. Oxford: Clarendon Press.
- Attimonelli, M., M. Accetturo, M. Santamaria et al. 2005. HmtDB, a human mitochondrial genomic resource based on variability studies supporting population genetics and biomedical research. *BMC Bioinformatics* 6:S4.
- Aufderheide, A. C., and C. Rodríguez-Martín. 1998. *The Cambridge Encyclopedia of Human Paleopathology*. Cambridge: University Press.
- Ballard, C. 2006. Strange alliance: Pygmies in the colonial imaginary. *World Archaeol.* 38:133–155.
- Baumann, G., M. A. Shaw, R. C. Brumbaugh et al. 1991. Short stature and decreased serum growth hormone-binding protein in the Mountain Ok people of Papua New Guinea. *J. Clin. Endocrinol. Metab.* 72:1346–1349.
- Baumann, G., M. A. Shaw, and T. J. Merimée. 1989. Low levels of high-affinity growth hormone-binding protein in African pygmies. *N. Engl. J. Med.* 320:1,705–1,709.
- Bijlmer, H. J. T. 1922. Anthropological results of the Dutch Scientific Central New Guinea Expedition A° 1920, followed by an essay on the anthropology of the Papuans. *Nova Guinea, Leiden*, no. 7:355–448.
- Bijlmer, H. J. T. 1939. Tapiro pygmies and Pania Mountain Papuans. Results of the Anthropological Mimika expedition in New Guinea 1935–36. *Nova Guinea, NW* 3:113–184.
- Boyd, W. C. 1963. Four achievements of the genetical method in physical anthropology. *Am. Anthropol.* 65:243–252.
- Büchi, E. C. 1981. *Physische Anthropologie der Eipo im Zentralen Bergland von Irian Jaya (West-Neuguinea), Indonesien*. Berlin: Dietrich Reimer.
- Cavalli-Sforza, L. L., ed. 1986. *African Pygmies*. Orlando, FL: Academic Press.
- Chappell, J., 2005. Geographic changes of coastal lowlands in the Papuan past. In *Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples*, A. Pawley, R. Attenborough, J. Golson et al., eds. Canberra: Pacific Linguistics, 525–540.
- Collins, D., ed. 1990. *The Last Rainforests*. London: Mitchell Beazley.
- Cortivo, P., M. Tommaseo, L. Caenazzo et al. 1987. Genetic studies on the Asmat population (Irian Jaya, Indonesia). *Anthropol. Anz.* 45:323–329.
- Diamond, J. M. 1991. Anthropology. Why are pygmies small? *Nature* 354:111–112.
- Diamond, J. M. 1992. A question of size. *Discover* May: 70–77.
- Dormitzer, P. R., P. T. Ellison, and H. H. Bode. 1989. Anomalously low endemic goiter prevalence among Efe pygmies. *Am. J. Phys. Anthropol.* 78:527–531.
- Excoffier, L., and H. E. L. Lischer. 2010. Arlequin suite ver. 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Res.* 10:564–567.
- Facchini, F. 1988. *Evoluzione, Uomo e Ambiente: Lineamenti di Antropologia*. Torino: Utet.
- Fleckenstein, P. 1981. Analyse röntgenologischer Untersuchungen bei den Bime, einem Stamm aus West-Irian auf Neu-Guinea. Ph.D. diss., Universität Heidelberg.
- Friedlaender, J. S., F. Gentz, F. Friedlaender et al. 2005. Mitochondrial genetic diversity and its determinants in Island Melanesia. In *Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples*, A. Pawley, R. Attenborough, J. Golson et al., eds. Canberra: Pacific Linguistics, 693–716.
- Friedlaender, S., F. R. Friedlaender, J. A. Hodgson et al. 2007. Mitochondrial DNA variation in Northern Island Melanesia. In *Genes, Languages, and Culture History in the Southwest Pacific*. J. S. Friedlaender, ed. New York: Oxford University Press, 61–79.

- Gajdusek, D. C., and R. M. Garruto. 1975. The focus of hyperendemic goiter, cretinism and associated deaf-mutism in Western New Guinea. In *Biosocial Interrelations in Population Adaptation*, E. Watts, F. E. Johnston, and G. W. Lasker, eds. The Hague: Mouton, 267–285.
- Gajdusek, D. C., R. M. Garruto, and R. Dedecker. 1974. Congenital defects of the central nervous system associated with hyperendemic goiter in a Neolithic highland society of Netherlands New Guinea. V. A note on birth weights and infantile growth rates in the Mulia population. *Hum. Biol.* 46:339–344.
- Garruto, R. M., D. C. Gajdusek, and J. ten Brink. 1974. Congenital defects of the central nervous system associated with hyperendemic goiter in a Neolithic highland society of Netherlands New Guinea. III: Serum and urinary iodine levels in goitrous and adjacent populations. *Hum. Biol.* 46:311–329.
- Gates, R. R. 1961. The Melanesian dwarf tribe of Aiome, New Guinea. *Acta Genet. Med. Gemellol. X*: 277–311.
- Graydon, J. J., N. M. Semple, R. T. Simmons et al. 1958. Blood groups in pygmies of the Wissellakes in Netherlands New Guinea. With anthropological notes by H. J. T. Bijlmer. *Am. J. Phys. Anthropol.* 16:149–171.
- Grillo, G., M. Attimonelli, S. Liuni et al. 1996. CLEANUP: A fast computer program for removing redundancies from nucleotide sequence databases. *Comput. Appl. Biosci.* 12:1–8.
- Groube, L. M., J. Chappell, J. Muke et al. 1986. A 40,000-year-old occupation site at Huon Peninsula, Papua New Guinea. *Nature* 324:453–455.
- Gusinde, M. 1961. Somatology of the Ayom pygmies of New Guinea. *Proc. Am. Philos. Soc.* 105:394–411.
- Haddon, A. C. 1912. Appendix B: The pygmy question. In *Pygmies and Papuans*, A. F. R. Wollaston, ed. London: Smith Elder, 303–312.
- Jarvis, J. P., L. B. Scheinfeldt, S. Soi et al. 2012. Patterns of ancestry, signatures of natural selection, and genetic association with stature in Western African pygmies. *PLoS Genet.* 8:e1002641.
- Jüptner, H. 1981. *Tropenmedizinische Untersuchung der Eipo im Zentralen Bergland von Irian Jaya (West-Neuguinea), Indonesien*. Berlin: Dietrich Reimer.
- Kayser, M., S. Brauer, G. Weiss et al. 2003. Reduced Y-chromosome, but not mitochondrial DNA, diversity in human populations from West New Guinea. *Am. J. Hum. Genet.* 72:281–302.
- Kayser, M., S. Brauer, R. Cordaux et al. 2006. Melanesian and Asian origins of Polynesians: mtDNA and Y chromosome gradients across the Pacific. *Mol. Biol. Evol.* 23:2,234–2,244.
- Kirschbaum, P. F. 1927. Ein neuentdeckter Zwergstamm auf Neu-Guinea. *Anthropos* 22:202–215.
- Konrad, G., and D. Seiler. 1980. Klinisch-chemische Untersuchung bei den Bime. In *Allgemeinmedizinische Untersuchungen bei den Bime im Zentralen Bergland von Irian Jaya (West-Neuguinea), Indonesien*, G. Konrad, D. Seiler, and W. Fiehn, eds. Teil 1. Berlin: Dietrich Reimer, 4–20.
- Lewis, M. P., G. F. Simons, and C. D. Fennig, eds. 2013. *Ethnologue: Languages of the World*. 17th ed. Dallas, TX: SIL International. www.ethnologue.com.
- Lopez Herráez, D., M. Bauchet, K. Tang et al. 2009. Genetic variation and recent positive selection in worldwide human populations: Evidence from nearly 1 million SNPs. *PLoS One* 4:e7888.
- Luschan, F. V. 1910. Über Pygmaen in Melanesien. *Zeit. Ethnol.* 42:939–945.
- Martin, R. 1988. *Anthropologie. Handbuch der Vergleichenden Biologie des Menschen*. New York: Fisher.
- Merimée, T. J., and D. L. Rimoin. 1986. Growth hormone and insulin-like growth factors in the western pygmy. In *African Pygmies*, L. L. Cavalli-Sforza ed., Orlando, FL: Academic Press, 166–177.
- Merimée, T. J., J. Zaff, and E. R. Froesch. 1981. Dwarfism in the pygmy. *N. Engl. J. Med.* 305:965–968.
- Merimée, T. J., B. Hewlett, L. L. Cavalli-Sforza et al. 1987. The riddle of pygmy stature. *N. Engl. J. Med.* 317:709–710.
- Migliano, A. B., L. Vinicius, and M. Mirazon Lahr. 2007. Life history trade-offs explain the evolution of human pygmies. *Proc. Natl. Acad. Sci. USA* 104:20,216–20,219.

- Mona, S., M. Tommaseo-Ponzetta, S. Brauer et al. 2007. Patterns of Y-chromosome diversity intersect with the Trans-New Guinea hypothesis. *Mol. Biol. Evol.* 24:2,546–2,555.
- Moynes, W. G., and K. Haddon. 1936. The pygmies of the Aiome mountains, mandated territory of New Guinea. *J. R. Anthropol. Inst.* 66:269–290.
- O’Dea, J. D. 1993. Possible contribution of low ultraviolet light under the rainforest canopy to the small stature of pygmies and negritos. *Homo* 44:284–287.
- Pawley, A. 1998. The Trans-New Guinea phylum hypothesis: A reassessment. In *Perspectives on the Bird’s Head of Irian Jaya, Indonesia*. J. Miedema, C. Odé, and R. A. C. Dam, eds. Amsterdam: Editions Rodopi, 655–689.
- Pawley, A. 2005. The chequered career of the Trans-New Guinea hypothesis: Recent research and its implications. In *Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples*, A. Pawley, R. Attenborough, J. Golson et al., eds. Canberra: Pacific Linguistics, 67–107.
- Pawley, A., R. Attenborough, J. Golson et al., eds. 2005. *Papuan Pasts: Cultural, Linguistic and Biological Histories of Papuan-Speaking Peoples*. Canberra: Pacific Linguistics.
- Perry, G. H., and N. J. Dominy. 2009. Evolution of the human pygmy phenotype. *Trends Ecol. Evol.* 24:218–225.
- Pesole, G., and C. Saccone. 2001. A novel method for estimating substitution rate variation among sites in a large dataset of homologous DNA sequences. *Genetics* 157:859–865.
- Pöch, R. 1904–1905. Falle von Zwergwuchs unter den Kai (Deutsch NG). *Sitzungsber. Anthropol. Ges. Wien* 35:40–42.
- Ramirez-Rozzi, F. V., and M. L. Sardi. 2010. Diversity among African pygmies. *PLoS One* 5:e13620.
- R Development Core Team. 2011. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Re, M. C., M. Tommaseo, G. Furlini et al. 1989. High prevalence of serum antibody against human T cell leukemia virus type I (HTLV-I) among the Bisman Asmat population (Indonesian New Guinea). *AIDS Res. Hum. Retrovir.* 5:551–554.
- Rosenfeld, R. G. 2003. Insulin-like growth factors and the basis of growth. *N. Engl. J. Med.* 349:2,184–2,186.
- Rubino, F., R. Piredda, F. M. Calabrese et al. 2012. HmtDB, a genomic resource for mitochondrial-based human variability studies. *Nucl. Acids Res.* 40:D1150–D1159.
- Schlaginhaufen, O. 1914. Pygmaen in Melanesien. *Arch. Suisses Anthropol. Gen.* 1(1–2):37–42.
- Schmidt, E. 1905. Die Grösse der Zwerge und die sogenannten Zwergvölker. *Globus* 87:121–125.
- Schwartz, J., R. C. Brumbaugh, and M. Chiu. 1987. Short stature, growth hormone, insulin-like growth factors, and serum proteins in the Mountain Ok people of Papua New Guinea. *J. Clin. Endocrinol. Metab.* 65:901–905.
- Speiser, F. 1946. Die Pygmaenfrage. *Experientia II* 8:1–16.
- Summerhayes, G. R., M. Leavesley, A. Fairbairn et al. 2010. Human adaptation and plant use in highland New Guinea 49,000 to 44,000 years ago. *Science* 330:78–81.
- Tommaseo, M., A. G. Baroni, and G. Altinier. 1990. Asymptomatic hepatitis among the Asmat. *Int. J. Anthropol.* 5:35–44.
- Tommaseo, M., L. Doglioni, and G. Alciati. 1989. Haematochemical data of the Asmat population. *Homo* 3–4:117–133.
- Tommaseo, M., and E. Lucchetti. 1991. Gli Asmat della Nuova Guinea: Analisi antropometrica. *Antropol. Cont.* 14:191–207.
- Tommaseo, M., and E. Lucchetti, 1992. Anthropometrical study of the Asmat. *Anthropol. Anz.* 50:217–234.
- Tommaseo, M., E. Lucchetti, G. Alciati et al. 1992. Contribution to study of Asmat genetic variability. *Int. J. Anthropol.* 7:59–67.
- Tommaseo-Ponzetta, M., I. Cascione, M. Attimonelli et al. 2007. Mitochondrial DNA M and N haplogroups in West New Guinea populations. In *Recent Advances on Southeast Asian Paleoanthropology and Archaeology*, Ety Indriati, ed. Yogyakarta: Gadjah Mada University, 207–215.

- Tommaseo-Ponzetta, M., M. De Robertis, F. Tanzariello et al. 2002. Mitochondrial DNA variability in West Papua populations. *Am. J. Phys. Anthropol.* 117:49–67.
- Tommaseo, M., and F. Viviani. 1991. Il somatotipo degli Asmat (Irian Jaya, Indonesia). *Quad. Anat. Prat.* 47: 139–148.
- Ulijaszek, S. J. 1993. Evidence for a secular trend in heights and weights of adults in Papua New Guinea. *Ann. Hum. Biol.* 20:345–355.
- Vallois, H. V. 1957. Pygmées de la Nouvelle-Guinée. *L'Anthropologie* 61:375–376.
- Van den Broek, A. J. P. 1913. Über Pygmäen in Niederländisch Süd-Neu-Guinea. *Zeit. Ethnol.* 45:23–44.
- Van den Broek, A. J. P. 1923. Zur Anthropologie des Bergstammes Pěšěchěm im Innern von Niederländisch-Neu-Guinea. *Nova Guinea* 7:233–276.
- van Oven, M., and M. Kayser. 2009. Updated comprehensive phylogenetic tree of global human mitochondrial DNA variation. *Hum. Mutat.* 30:E386–E394.
- Weiner, J., and J. A. Lourie. 1981. *Practical Human Biology*. London: Academic Press.
- Wilkins, L., and W. Fleischman. 1941. The diagnosis of hypothyroidism in children. *JAMA* 1116:2,459–2,465.
- Wirz, P. 1924. *Anthropologische und ethnologische Ergebnisse der Zentral-Neuguinea-Expedition 1921/22*. Nova Guinea 16, no. 1. Leiden: Brill.
- Wollaston, A. F. R. 1912. *Pygmies and Papuans*. London: Smith and Elder.

