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Craniodental Affinities of Southeast Asia's "Negritos" and the Concordance with Their Genetic Affinities

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Abstract

Genetic research into Southeast Asia's "negritos" has revealed their deep-rooted ancestry, with time depth comparable to that of Southwest Pacific populations. This finding is often interpreted as evidence that negritos, in contrast to other Southeast Asians, can trace much of their ancestry directly back to the early dispersal of *Homo sapiens* in the order of 70 kya from Africa to Pleistocene New Guinea and Australia. One view on negritos is to lump them and Southwest Pacific peoples into an "Australoid" race whose geographic distribution had included Southeast Asia prior to the Neolithic incursion of "Mongoloid" farmers. Studies into Semang osteology have revealed some hints of Southwest Pacific affinities in cranial shape, dental morphology, and dental metrical "shape." On the other hand, the Andamanese have been shown to resemble Africans in their craniometrics and South Asians in their dental morphology, while Philippine negritos resemble Mongoloid Southeast Asians in these respects and also in their dental metrics. This study expands the scope of negrito cranial comparisons by including Melayu Malays and additional coverage of South Asians. It highlights the distinction between the Mongoloid-like Philippine negritos and the Andamanese and Semang (and Senoi of Malaya) with their non-Mongoloid associations. It proposes that the early/mid-Holocene dispersal of the B4a1a mitochondrial DNA clade across Borneo, the Philippines, and Taiwan may be important for understanding the distinction between Philippine and other negritos.

Keywords

Negritos, Cranial Metrics, Cranial Morphology, Dental Metrics, Dental Morphology, Genetics.

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Abstract Genetic research into Southeast Asia's "negritos" has revealed their deep-rooted ancestry, with time depth comparable to that of Southwest Pacific populations. This finding is often interpreted as evidence that negritos, in contrast to other Southeast Asians, can trace much of their ancestry directly back to the early dispersal of *Homo sapiens* in the order of 70 kya from Africa to Pleistocene New Guinea and Australia. One view on negritos is to lump them and Southwest Pacific peoples into an "Australoid" race whose geographic distribution had included Southeast Asia prior to the Neolithic incursion of "Mongoloid" farmers. Studies into Semang osteology have revealed some hints of Southwest Pacific affinities in cranial shape, dental morphology, and dental metrical "shape." On the other hand, the Andamanese have been shown to resemble Africans in their craniometrics and South Asians in their dental morphology, while Philippine negritos resemble Mongoloid Southeast Asians in these respects and also in their dental metrics. This study expands the scope of negrito cranial comparisons by including Melayu Malays and additional coverage of South Asians. It highlights the distinction between the Mongoloid-like Philippine negritos and the Andamanese and Semang (and Senoi of Malaya) with their non-Mongoloid associations. It proposes that the early/mid-Holocene dispersal of the B4a1a mitochondrial DNA clade across Borneo, the Philippines, and Taiwan may be important for understanding the distinction between Philippine and other negritos.

The "negrito" populations of the Andaman Islands, Malay Peninsula, and the Philippines are defined by their modal possession of three phenotypic features: dark skin, spiraled to frizzy hair, and short stature (Coon 1962: 112). Skin color and hair morphology distinguish them fairly effectively from "Mongoloid" Southeast Asians northwest of Maluku and Nusa Tenggara [which constitute a transitional zone between the "Indo-Malay" phenotype that predominates across

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KEY WORDS: NEGRITOS, CRANIAL METRICS, CRANIAL MORPHOLOGY, DENTAL METRICS, DENTAL MORPHOLOGY, GENETICS.

Table 1. Skin Color, Hair Form, and Stature Where All Are Reported for Southeast Asian Populations (negritos shown in boldface)

POPULATION[a]	LOCATION	DOMINANT SKIN COLOR[b]
Vietnamese[1]	Vietnam	Saffron[c]
Moïs[1]	Vietnam	Light brown
Chams[1]	Vietnam	Light brown
Khmers[1]	Cambodia	Light brown to brown[c]
Saoch[2]	Cambodia	Brown to dark brown
Menriq Semang[3]	Malaya	Chocolate to dark chocolate
Jahai Semang[4]	Malaya	Light to dark chocolate
Ple/Temiar Senoi[4]	Malaya	Light brown to brown
Semai Senoi[5]	Malaya	Light brown to brown
Andaman Islanders[6]	Andaman Islands	"Black" (anecdotal)
Deli Malays[7]	Sumatra	Light brown
Aeta[8]	Luzon	"Dark brown" (anecdotal)
Igorot[9]	Luzon	"Saffron" to "dark brown" (anecdotal)
Tagalog[9]	Manila	As for Khmers[c]
Bagobo[10]	Mindanao	"Light reddish brown" (anecdotal)
Penan[10]	Borneo	Light brown to brown
Kayan[11]	Borneo	Brown
Iban[11]	Borneo	Brown
Land Dayak[11]	Borneo	Light brown
Kenyah[11]	Borneo	Brown
Bugis/ Makasar[12]	Sulawesi	Light brown
Javanese[11]	Java	Light brown
Tenggerese[11]	Java	Light brown

[a] Sources: 1, Olivier (1956). 2, Taillard (1942). 3, skin color, Schebesta and Lebzelter (1928); other traits, Wagenseil (1967). 4, Schebesta and Lebzelter (1928). 5, Kloss (1916). 6, stature, Dutta (1983); other traits, Flower (1880). 7, Sullivan (1918). 8, Barrows (1910), Glinka (1981), Sullivan (1918). 9, Barrows (1910). 10, Cole (1913: 56). 11, hair form, Glinka (1981); other traits, Sullivan (1918). 12, Sarasin (1906). Sarasin (1906) further reports the following data on the non-negrito Batak of Sumatra: predominantly light brown skin and straight hair (95%, with 5% having wavy hair) and an average male stature of 1,605 mm. The Sumatra Batak are not listed to avoid any possible confusion with the

Indo-Malaysia and the dark-skinned, frizzy-haired people of Melanesia (Bulbeck et al. 2006)]. Stature is not diagnostic, although negritos lie toward the lower end of the Southeast Asian range of variation. There are also Southeast Asian populations intermediate between the negrito and non-negrito categories, such as the Saoch of southern Cambodia (Table 1), and the Mamanwa of Mindanao, with their average male stature of 157 cm (Omoto 1985) and a variety of hair form and skin color (Stein 2007).

PROPORTION WITH HAIR TYPE			AVERAGE MALE STATURE
FRIZZY/SPIRALED	WAVY/CURLY	STRAIGHT	(mm; SAMPLE SIZE ≥ 20)
0%	32.5%	67.5%	1,542–1,611
0%	82%	8%	1,570–1,607
0%	60.5%	39.5%	1,590
0%	92.5%	7.5%	1,610–1,613
49%	45%	6%	1,528
61.5%	38.5%	0%	1,530
95%	5%	0%	1,536
0%	89%	11%	1,554
8%	92%	0%	1,520
100%	0%	0%	1,459–1,486
0%	100% (mainly straight)		1,622
89%	9%	2%	1,463
0%	100% (mainly straight)		1,546
0%	100% (mainly straight)		1,638
0%	100%	0%	1,586
5%	43%	52%	1,565
10%	60%	30%	1,563
6%	58%	36%	1,585
6%	65%	29%	1,577
7%	62%	31%	1,608
0%	10%	90%	1,622
0%	36%	64%	1,606
0%	33%	67%	1,600

Batak negritos of the Philippines, for whom quantitative data on skin color and hair morphology are unavailable (average male stature is reported as 1,531 mm by Eder 1987: 139).

[b] Except where qualified as anecdotal, the skin color data presented here follow the standard, common English equivalents for Von Luschan skin color recordings. See the references above for details.

[c] Jablonski and Chaplin (2000) report skin reflectance at 685 nm (red filter) for three Southeast Asian groups: Cambodians, 54.0; Manila Filipinos 54.1; Vietnamese, 55.0 and 56.8. The range recorded for southern and Tibetan Chinese is 54.5–59.9.

Culturally, negritos do not constitute a homogeneous group. The negritos of Malaya and the Philippines speak languages related to their neighbors' languages—Austroasiatic and Austronesian, respectively (Dunn et al. this issue; Reid this issue), whereas the two recorded languages on the Andaman Islands, Onge and Jarawa, may have a distant relationship with Proto-Austronesian (Blevins 2007). Foraging was the mode of subsistence traditionally practiced by most negritos, but the Ayta and the Batak of the Philippines are possible exceptions (Bellwood 2005: 33;

Novellino 2011). Further, there are non-negrito hunter-gatherers in Indo-Malaysia, such as the Austroasiatic-speaking Shompen of the Nicobar Islands and Semaq Beri of Malaya, and the Austronesian-speaking Penan of Borneo and Kubu of upland Jambi in Sumatra (Howells 1973a: 24; Dunn et al. this issue).

Do the negritos constitute a coherent group, biologically? In addressing that question, this study assumes that *Homo sapiens* dispersed from Africa to Asia and the Southwest Pacific after 95 kya (e.g., Bulbeck 2011a; Scally and Durbin 2012), with miniscule admixture of local presapient populations as witnessed in the nuclear genome (e.g., Reich et al. 2011; Oppenheimer 2012). From that perspective, negritos' dark skin and frizzy hair shared with sub-Saharan Africans would be most parsimoniously viewed as archaic retentions. Simplifying the representation of Asian and Southwest Pacific populations as independent lineages (Figure 1A), we would require only one "character change" from dark to light skin, and only three character changes from frizzy to nonfrizzy hair, to account for the geographic distribution of skin color and hair morphology as recorded in physical anthropology textbooks (e.g., Coon and Hunt 1965).

Even this simplistic approach would fail in any attempt to interpret negritos' small stature as an archaic retention. Two obvious objections are the demonstrated plasticity of stature in response to health and nutrition status (e.g., World Health Organization 1995) and the lack of evidence that the dispersal of *Homo sapiens* from Africa involved short-statured people (but see Bulbeck and O'Connor 2011; Détroit et al. this issue). Further, the skeletal record from the Malay Peninsula points to a circa 10% reduction in stature between the early Holocene and ethnohistorical times, affecting non-negrito Orang Asli ("Senoi" and "Aboriginal Malays"), as well as the Semang negritos (Bulbeck 2011a). Thus, the short stature of the Semang would appear too recent in derivation to qualify as a retention shared with Andaman Islanders and Philippine negritos. Additionally, short stature would fail as a negrito marker because it also characterizes non-negrito Orang Asli. Hence, negritos' typical short stature would appear to be independently derived for each negrito lineage (Migliano et al. this issue), as well as any non-negrito populations with similarly short stature (Figure 1A). Nonetheless, negritos' small body size is an important characteristic to consider when interpreting craniodental comparisons between negritos and other populations.

Figure 1A is too simplistic to square with the evidence from genetic studies undertaken on populations in Indo-Malaysia (briefly reviewed below). Both negrito and non-negrito populations contain deeply rooted components in their gene pool and others that reflect Holocene genetic interaction. The "two-layer hypothesis" (Bronson 1977) accommodates this reality while retaining the Figure 1A lineages as the "essence" for understanding population history in Indo-Malaysia (Figure 1B). Gene flow (marital exchanges between neighbors and small-scale population dispersal) would have been an ongoing process since *Homo sapiens*' colonization of the region, as represented by thin gray lines. However, this would not have obliterated the dichotomy between predominantly dark-skinned, frizzy-hair populations in Southeast Asia and lighter-skinned, straighter-haired populations in Northeast Asia.

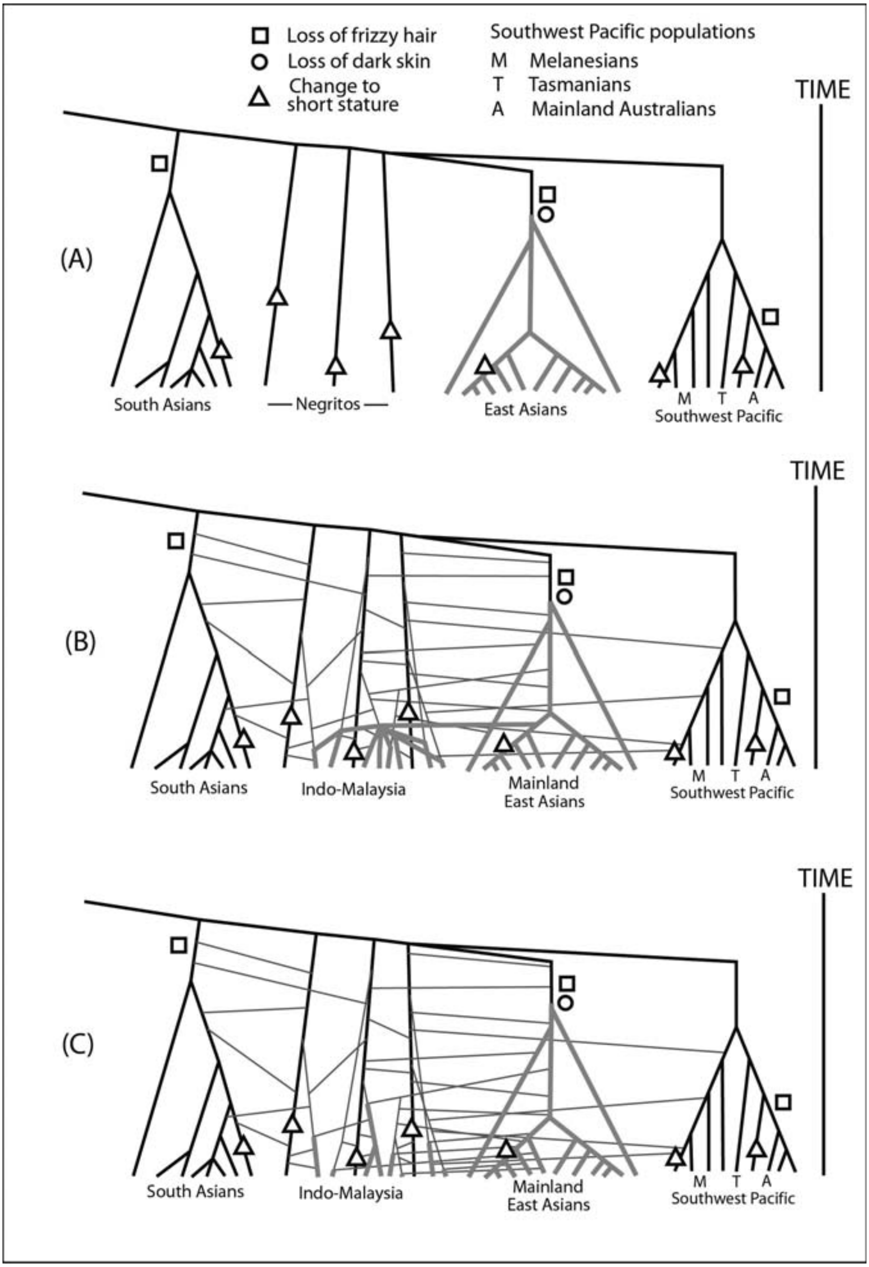


Figure 1. Out of Africa hypotheses to explain negrito human biology. (A) Out-of-Africa "negrito" hypothesis: simplified lineage representation. (B) Out-of-Africa two-layer hypothesis: gene flow and immigration affecting Indo-Malaysia. (C) Out-of-Africa regional diversification hypothesis: gene dispersal involving Indo-Malaysia.

Instead, the latter phenotype spread across Southeast Asia (barring relict pockets of negritos) through Holocene migration (thick gray lines). The best known version of the two-layer hypothesis invokes a mid-Holocene demic diffusion of "Mongoloid" farmers from south China, introducing the Austroasiatic and Austronesian languages spoken across Southeast Asia (e.g., Bellwood 1997, 2005; Higham this issue).

However, the claim for two colonization events (late Pleistocene and mid-Holocene) relevant to understanding Indo-Malaysian population history has not gone unchallenged (e.g., Bulbeck 1981, 2000; Turner 1983; Turner and Eder 2006; Hill et al. 2007). An alternative hypothesis, referred to here as the regional diversification hypothesis, would view gene dispersal both within Indo-Malaysia and between Indo-Malaysia and neighboring regions as an ongoing process of sufficient magnitude to explain biological variability in Indo-Malaysia (Figure 1C). For instance, lighter skin color and nonfrizzy hair may have been variably present in Southeast Asia long before any presumed introduction by mid-Holocene farmers from China (as in the two-layer hypothesis). The difference between negritos and Indo-Malays in this regard would reflect some combination of assortment based on physical looks and relative genetic isolation of negrito lineages.

According to the two-layer hypothesis, negritos should stand apart from other Southeast Asians in having derived most of their ancestry from pre-Neolithic Southeast Asians. The latter have historically been characterized as "Australoid" (Coon 1962), "Old Melanesians" (Howells 1973a), or "Australo-Melanesian" (Bellwood 1997) by proponents of the two-layer hypothesis, but this is not a necessary expectation. If Southeast Asia was the source for the colonizing thrusts by ancestral *H. sapiens* into Northeast Asia, as well as the Southwest Pacific (Oppenheimer 2012), the negritos' ancestors should have been related more or less equally closely to the ancestral colonists of both of these latter regions. Nonetheless, under the two-layer hypothesis, negritos and Indo-Malays should show marked biological differences, whether or not negritos resemble Southwest Pacific populations (Figure 1B).

Under the regional diversification hypothesis, genetic interchange across East Asia and within Indo-Malaysia would have been a continuous process before, during, and after the Neolithic (Figure 1C). Therefore, the populations biologically most similar to negritos should be their Indo-Malay neighbors.

The two-layer and regional diversification hypotheses respectively predict marked and modest biological differences between negritos and their Indo-Malay neighbors. This study tests between these opposing expectations with reference to the genetic, dental, and cranial data. The genetic and dental data are addressed through a review of other studies, whereas the cranial data are addressed mainly through new analyses presented here.

Materials and Methods

Table 2 presents basic information on the negrito and main non-negrito groups included in the comparisons covered by this contribution. Numerous Malaysian

Borneo and Indonesian populations have also been covered in these comparisons, but they are not listed in Table 2 for reasons of space. Where the Table 2 groups were included specifically in the dental morphology comparisons, their geographic location is presented in Figure 2, in the context of the major dental morphology "complexes" recognized by C. G. Turner II and his students (Turner 1983; Scott and Turner 1997; Hawkey 1998).

The relationships between the groups compared for their genetic affinities were obtained through a variety of statistical techniques, as detailed in the original sources (Table 2). The most frequent techniques were cluster (hierarchical dendrogram) and multidimensional scaling (MDSCAL) plots to summarize intergroup genetic distances, principal component analysis (PCA) of the compared individuals' genetic data, and (in the case of sex-specific genetic data) maximum parsimony reconstruction of common ancestors and their descendent branches.

The dental morphological distances in the studies reviewed here were calculated using the Smith's or mean measure of divergence (MMD) distance. These intergroup distances were summarized using hierarchical dendrograms, MDSCAL plots, and/or minimum spanning trees.

In the studies on dental metrics covered here, tooth measurements were analyzed for both their overall "size" and their "shape" (relative size of the measurements to each other). This was achieved either by using Penrose's size and shape statistic (Bulbeck et al. 2005), or by calculating summed tooth area for size and applying factor analysis to tooth-size *z*-scores for shape (Matsumura and Hudson 2004).

This study's analysis of negrito craniometric affinities approached the Andamanese, Philippine negritos, and Semang in quite different ways, to accommodate the differences in how well their crania are documented. The Andamanese are the best documented, thanks to their inclusion in Howells's (1973b, 1989) study of worldwide human craniometrics and publication of Howells's original measurements on the web (Howells 1973–1995). Accordingly, the Andamanese are available for inclusion in every analysis presented here. Philippine negritos are the second best documented, thanks to Tsunehiko Hanihara's (personal communication) measurement of a substantial sample of Philippine negritos for many of the same variables as recorded by Howells, and von Bonin's (1931: 74) measurement of a different, well-documented museum collection of "Aeta" for many of the Howells variables. Hanihara's and von Bonin's data are analyzed separately because some of the Howells variables recorded by Hanihara were not recorded by von Bonin and *vice versa*. Finally, Semang crania are the poorest documented negrito crania, as the sample size is small and the available measurements, most of them taken from the literature, differ among specimens. Accordingly, the Semang are analyzed here as individual specimens rather than as a group, as described in due course.

Three craniometric analyses are presented here that include negrito groups. These analyses focus on male crania because Howells measured a sample of male Philippine crania but no sample of female Philippine crania. Further, my analyses

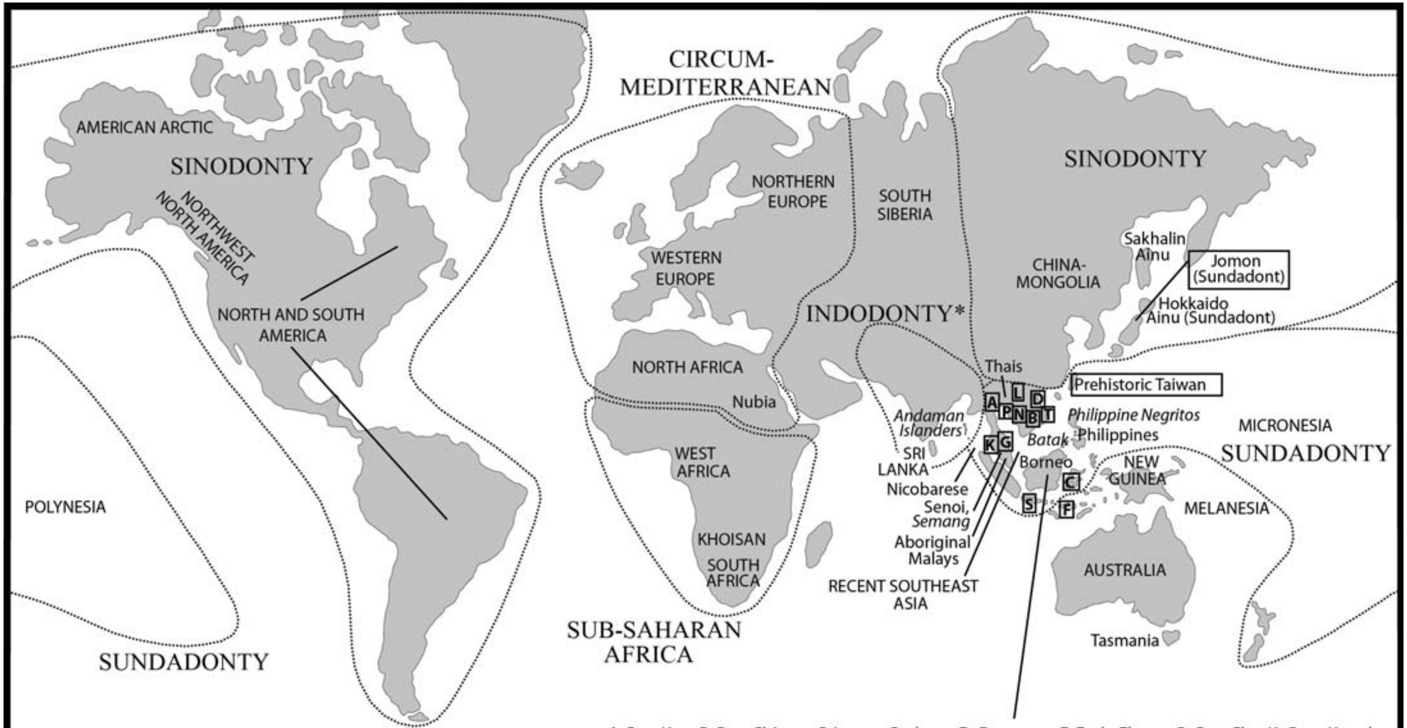
Table 2. Negrito (boldface) and Main Non-Negrito Groups Included in the Biological Comparisons Covered in This Study

LOCATION/GROUP	ANALYSIS PERFORMED	REFERENCE
Malaya		
Semang	Nuclear DNA markers	Lie-Injo 1976
	Single-nucleotide polymorphism (SNP) data	Hatin et al. 2011; Chaubey and Endicott this issue
	mtDNA	Hill et al. 2006
	Dental morphology	Rayner and Bulbeck 2001
	Dental metrics	Bulbeck et al. 2005
	Cranial metrics	Bulbeck 2011a
	Cranial morphology	This study
Senoi, Aboriginal Malays, Melayu Malays	Nuclear DNA markers	Lie-Injo 1976; Tan 2001
	mtDNA	Hill et al. 2006, 2007
	Dental metrics	Bulbeck et al. 2005; Matsumura and Hudson 2004
Senoi, Aboriginal Malays	Dental morphology	Rayner and Bulbeck 2001
	Cranial metrics	Bulbeck 2011a
Senoi	Cranial morphology	Bulbeck 1981
Aboriginal Malays	SNP data	Hatin et al. 2011
Melayu Malays	SNP data	Hatin et al. 2011; Chaubey and Endicott this issue
	Cranial metrics	Bulbeck et al. 2006
	Cranial morphology (included in "Indo-Malays")	Bulbeck and Adi 2005
Nicobar Islands		
Nicobarese	Dental morphology	Hawkey 1998
	Cranial morphology (included in "Indo-Malays")	Bulbeck 1981
Andaman Islands		
Great Andamanese	SNP data	Chaubey and Endicott this issue
Onge	SNP data	Chaubey and Endicott this issue
Andamanese[a]	SNP data, mtDNA	Rasmussen et al. 2011; Barik et al. 2008
	Dental morphology	Hawkey 1998; Matsumura and Hudson 2004
	Dental metrics	Matsumura and Hudson 2004
	Cranial metrics	Howells 1989
	Cranial morphology	This study
Taiwan		
Atayal, Bunun, Paiwan	Nuclear DNA markers	Tan 2001
Ami, Atayal	SNP data	Chaubey and Endicott this issue

LOCATION/GROUP	ANALYSIS PERFORMED	REFERENCE
Taiwan Aborigines	mtDNA and Y-chromosomes	Scholes et al. 2011; Heyer et al. this issue
Prehistoric Taiwan	Dental morphology	Turner and Eder 2006
Atayal	Cranial metrics	Howells 1989
Luzon		
Aeta	Nuclear DNA markers	Omoto 1985
	SNP data	Rasmussen et al. 2011
	Y-chromosomes	Scholes et al. 2011
	Cranial metrics	von Bonin 1931
Aeta, **Agta**	mtDNA and Y-chromosomes	Heyer et al. this issue
Luzon, Panay		
Agta, **Ati**, **Dumagat**	Nuclear DNA markers	Omoto 1985
Agta, **Ati**	SNP data	Chaubey and Endicott this issue
	Y-chromosomes	Scholes et al. 2011
Luzon, Cebu		
Tagalog, Visayas, Ifugao	Nuclear DNA markers	Omoto 1985; Tan 2001
Palawan		
Batak	Nuclear DNA markers	Omoto 1985
	mtDNA and Y-chromosomes	Scholes et al. 2011
	Dental morphology	Turner and Eder 2006
Palawan non-negritos	mtDNA and Y-chromosomes	Scholes et al. 2011
Mindanao		
Mamanwa[b]	Nuclear DNA markers	Omoto 1985
	SNP data	Chaubey and Endicott this issue
	mtDNA and Y-chromosomes	Heyer et al. this issue
	Y-chromosomes	Scholes et al. 2011
Manobo	SNP data and Y-chromosomes	Chaubey and Endicott this issue
Philippines		
Philippine negritos[a]	Dental morphology	Matsumura and Hudson 2004
	Dental metrics	Matsumura and Hudson 2004
	Cranial metrics	Uytterschaut 1983
Philippine non-negritos	mtDNA and Y-chromosomes	Scholes et al. 2011; Heyer et al. this issue

[a] The "Andamanese" group covers all negritos from the Andaman Islands, whether Great Andamanese, Onge or Jarawa. "Philippine negritos" covers generalized groupings of negritos from the Philippines.

[b] The Mamanwa are treated as negritos in the genetic studies referenced here.



*Indodonty covers Burma, Sri Lanka and mainland South Asia. Sri Lanka groups include Sinhalese, Tamils, Veddas and Late Pleistocene to mid-Holocene samples.

A: Ban Kao; B: Ban Chiang; C: Leang Codong; D: Dongson; F: Early Flores; G: Gua Cha; K: Guar Kepah; L: Tam Hang/Prehistoric Laos; N: Non Nok Tha; P: Khok Phanom Di; S: Sampung; T: Early Vietnam. Early Mainland Southeast Asia: A, L, N, T (+ Don Klang & Ban Na Di). Early Malay Archipelago: C, F, G, K, S. Mid-Holocene Thailand: A, N, P. Early Holocene Vietnam/Laos: L, T. Early Flores/Malaya: F, G.

complement the Howells craniometric database with data from seven populations not measured by Howells—six from India measured by Pathmanathan Raghavan (Raghavan et al. 2013), and the Melayu Malays measured by Daniel Rayner (Bulbeck et al. 2006). The six Indian populations are Punjabis, Haryanavis and Uttar Pradesh Hindis from northern India, and the Telugu, Kannada, and Tamils from southern India. Some of the Howells variables are excluded: his radii, which Raghavan and Rayner did not measure; his cranial fractions, whose excessive variability indicates difficulties in accurate mensuration (Raghavan et al. 2013); bimaxillary breadth and zygomaxillary subtense, because Rayner (personal communication) incorrectly located the zygomaxillary anatomical point; and mastoid breadth, because univariate comparisons indicate that Hanihara and Rayner took a systematically larger measurement than Howells did. As a result, 39 measurements are available for the first analysis, in which Andamanese are the only negrito group included, and 21 and 16 measurements are available for the second and third analyses, which respectively include Hanihara's and von Bonin's Philippine negrito samples. Intergroup metrical distances were calculated using the Mahalanobis D^2 statistic using XLSTAT software, converted into Euclidean distances by taking their square roots.

The intergroup metrical affinities indicated by the three craniometric analyses described above are presented though seriated hierarchical dendrograms, a technique developed by the author (e.g., Bulbeck 1996, 2000, 2011a). Seriated hierarchical dendrograms retain the clustering structure of the original dendrogram but add supplementary information on the secondary affinities that would otherwise be sacrificed in generating the dendrogram. They do this by positioning the groups that are most distant from each other at the poles of the seriation and then sorting the other groups in sequence between the two extremes. Excel worksheets with the calculations used in generating the seriated dendrograms presented here are available from the author on request.

Because the generation of a hierarchical dendrogram involves reducing the original intergroup distances to progressively smaller half-matrices of intergroup/cluster distances, these same half-matrices can be employed in reverse order of their generation to seriate all of the groups. For instance, if the final clustering steps involved A joining a cluster made up of B and C, then A would take up one pole of the seriation and B or C would take up the other pole of the seriation, depending on which was more distant from A. Also, if, say, A consisted of two subclusters, then the subcluster more distant from B and C would be positioned at the extreme, and the other subcluster would be positioned between the extreme subcluster and B/C. To further elaborate on this example, if, say, B was the intermediate cluster, and it consisted of two subclusters, the subcluster that on balance was less distant from A would be positioned toward the A pole, and the subcluster that on balance was less distant from C would be positioned toward the C pole. This process of

Figure 2 (*opposite*). Prehistoric (boxed) and recent samples (generalized samples in capital letters) in the dental morphology comparisons referred to in this study.

positioning subclusters and groups along the seriated order continues until we have retraced our steps to the first two groups that clustered, and we seriate these two groups based on all of their original distances.

How successful the seriated order is in positioning the groups along a unilinear sequence can be calculated as follows. The original distances are sorted according to the order of groups. If the seriated order were perfectly successful, then starting at any place in the sorted half-matrix of distances, the distances would increase or at least stay the same as we move from any closer group to any more distant group (retaining the sense of the seriated order). For instance, take two adjacent groups x and y that respectively seriate toward the A and C poles of the seriation. In a perfect seriation, x would be less distant than y (or equally distant) from every group lying closer toward the A pole, but more distant (or equally distant) than y from every group lying closer toward the C pole. Accordingly, the sorted distances are transposed until a perfect seriation is obtained with as few transpositions as appear necessary. The sorted distances, and their counterparts in the closest found perfect seriation, are extracted and regressed against each other. The resulting coefficient of variation (the square of Pearson's *r*) explains the variance of a perfect seriation as captured by the seriated order actually obtained. The ~70–80% coefficients of variation achieved for the seriated dendrograms presented here (Figures 3–6) could be described as a "fair" result.

As noted above, a different approach was taken for the Semang (and other Orang Asli) crania. Linear discriminant function analysis (using the canonical variate analysis option) was performed (using XLSTAT) for each Orang Asli cranium comparing it with the Howells, Indian, and Melayu Malay populations of the same sex. Orang Asli crania were analyzed as long as a minimum of three variables (see Bulbeck 2011b) defined identically to the Howells variables were available. The Orang Asli crania include two Semang recorded by the author, three Semang recorded by Schebesta and Lebzelter (1926), and 22 Semang, Senoi, and Aboriginal Malays whose published measurements are tabulated by Martin (1905). The posterior probabilities of membership with the comparative populations were pasted into an Excel spreadsheet and the "PERCENTILE 0.7" was function applied, to summarize overall affinities. This summarization of the individually obtained results is superior to simply counting up the number of "classifications" (i.e., which population is closest) for two reasons (Bulbeck 2011b). First, counting up classifications makes no allowance for how strong the statistical support is for each obtained classification. Second, the 70th percentile scores are unaffected by "absent" results, which were obtained whenever female Orang Asli crania were analyzed (in relation to Philippine and Anyang Chinese crania, which are represented only by male samples). In contrast, if we relied on counting up classifications, we would be confronted with a systematic bias against obtaining Philippine and Anyang Chinese classifications.

The same approach was taken for Philippine negrito crania, to expand on the results obtained from Mahalanobis D^2 analysis. This way, female as well as male Philippine negritos could be incorporated in the same overall perspective, as could the male Philippine negrito crania excluded from the Mahalanobis D^2 analysis on the basis of missing variables. Also, an overall perspective on Philippine negrito craniometric affinities was obtained, whether measured with Hanihara's or von Bonin's variables. In sum, 93 Philippine negrito crania (31 from Hanihara and 62 from von Bonin) measured on 5–21 Howells variables were included.

The final analysis in this contribution considers cranial morphology in terms of the 22 "race discrimination characters" defined by Larnach and Macintosh (1966, 1970). The reference groups are recent Indo-Malays, Melanesians, Australians (Bulbeck and Adi 2005: Table 16.11), and South Asians (predominantly from Sri Lanka and South India). Unfortunately, comparable data have not been collected for other populations. To determine which characters appear to have strong interobserver agreement, the author recorded 24 coastal Papua New Guinea crania previously recorded by Larnach (Stanley Larnach Papers, South Australian Museum, Adelaide, Australia) and by Green (1990). Although I knew which crania to record, the test was "blind" as I took my observations without reference to Larnach's or Green's observations. Only the 17 characters with modal 90% or better agreement between observers were retained for analysis. To obtain this level of agreement, it was also necessary to collapse the three grades of expression originally defined by Larnach and Macintosh into two grades—either because the 24 Papua New Guinea crania were limited in their range of expression to just two of the three grades, or because two of the grades showed low interobserver agreement and so needed to be collapsed (Bulbeck 2012).

Collapsing Larnach's grades of expression into two also simplified analysis because the characters are now dichotomous—either "true" or "false" (when not missing) for every specimen. Crania frequently miss at least one character, which implies either imputation of missing values or use of an analytical technique that successfully accommodates missing values. The latter approach was adopted, through the construction of Boolean expressions. In Boolean logic, an OR expression is true as long as any of the components is true, whereas an AND expression is false as long as any of the components is false. Therefore, Boolean expressions can be evaluated notwithstanding certain missing observations. Also, the OR and AND operators allow the construction of logically opposite expressions; for instance, the logical opposite of "a OR b" is "NOT a AND NOT b." So if we find two characters a and b for which all Indo-Malays have either but Melanesians (for example) have neither, we would achieve 100% classification of Indo-Malays and Melanesians (in this hypothetical example).

Accordingly, I analyzed my database to find Boolean formulas that distinguished Indo-Malays from Australians, from Melanesians, and from South Asians. Application of these formulas to Andaman Islander and Orang Asli crania tests would then allow their classification as Indo-Malay or with another group (observations on Philippine negritos were unavailable). Only males were considered because the Andaman Islander and Orang Asli crania for which I have data are male. Only those characters with a significantly different expression between Indo-Malaysians and the other group being compared (as tested with the difference of proportions test at the conventional $p < 0.05$ confidence level) were considered for inclusion in the Boolean formulas.

Results

Review of Nuclear DNA Studies on Negritos. Early studies by human geneticists on blood groups and other nuclear DNA markers extended to the Semang and Philippine negritos. Lie-Injo (1976) presented genetic distances between the Orang Asli, other Asians, and Australian Aborigines. Bulbeck's (1996) seriated hierarchical dendrograms of these distances placed the Semang, Senoi, and Aboriginal Malays intermediate between South Asians and Thais/Melayu Malays, with the Semang closest to South Asians and Aboriginal Malays closest to Thais/Melayu Malays. In one study, Omoto (1985) found a primary split between the Mamanwa and other Philippine populations, both negrito and Indo-Malay. In the final study of his data, Omoto (1995) found a primary link between the Mamanwa and Aeta and a secondary link between them and Indo-Malays to the exclusion of mainland East Asians and Pacific groups. Subsequently, Tan (2001) found that the Aeta and Senoi clustered together and then clustered loosely with South Asians, to the exclusion of other East Asians (including Aboriginal Malays and Philippine non-negritos). In summary, to the degree that negritos (along with the Senoi) could be distinguished from other Southeast Asians based on their nuclear DNA markers, it would be in terms of a loose South Asian affinity.

More recently, comparative studies of nuclear (autosomal) DNA have made use of an extensive database of single-nucleotide polymorphism (SNP) data on populations across the world (unfortunately, excluding the Senoi). Rasmussen et al. (2011) found that a partially sequenced Australian Aboriginal genome was most closely approached by Melanesian genomes and then by Munda (South Asian), Southeast Asian (especially Aeta), and Kusunda (South Asian) genomes. Andaman Islander genomes clustered with (non-Munda non-Kusunda) South Asian genomes, a finding consistent with the genomic relatedness between the Onge (Andaman Islanders) and South Asians noted by Reich et al. (2009). On the other hand, Aeta genomes sat closest to Mongoloid Southeast Asian genomes (although this point was not emphasized by Rasmussen et al. 2011).

Further, statistical analysis of 54,000 SNPs documented for Indo-Malaysian, Yunnan, and Indian populations (Hatin et al. 2011) found the following. The 10 Yunnan and Indo-Malay populations (which included one Aboriginal Malay population) formed a coherent cluster. The two sampled Semang populations clustered together and were closer to the 10 comparative Mongoloid populations than to the two comparative Indian populations.

Several articles in this special issue also address autosomal SNP relatedness of negritos to neighboring populations. In their analysis of 28 autosomal short tandem repeats, Heyer et al. (this issue) identify two distinct Philippine negrito lineages, both very distant from each other and from any of the East Asian, Southwest Pacific, or African populations included in the analysis. On the other hand, Chaubey and

Endicott (this issue, their Figure 2) present a PCA plot with a "negrito space" characterized by scores of around 0 on PC1 and scores between 0.02 and –0.14 on PC2. The Semang and, to a lesser degree, the Onge were the most distinct from South Asians and Mongoloid East Asians. Philippine negritos and Austronesian-speaking Indo-Malays overlapped, while the affinities of the Great Andamanese ranged widely and included Austroasiatic-speaking South Asians, the Onge, and Austronesian speakers (both negrito and non-negrito). Overall, the findings of Chaubey and Endicott are consistent with a scenario of negritos' deep genetic roots and subsequent admixture with neighboring populations (both between negrito lineages and with non-negrito lineages), but not with a scenario in which negrito groups descended from a unique common ancestry. While the genetic evidence would appear consistent with continuous settlement of the Andamans from at least the terminal Pleistocene, Holocene genetic additions would be expected, given the evidence for Holocene contacts in the form of pottery manufacture, outrigger canoes, and feral pigs on the Andamans (Cooper 2002).

Review of Negritos' mtDNA and Y-Chromosome Sequences. The majority of Andaman Islanders' mitochondrial DNA (mtDNA) lineages belong to two lineages unique to the Andamans: M31a1, estimated to have diverged from the M31a2 lineage found in India at 24 ± 9 kya; and M32, estimated to have diverged from M31 at 45 ± 12 kya (Barik et al. 2008). However, the time depth of differentiation of the lineages restricted to the Andaman Islands is less ancient: around 10 kya for M32 and 1.5 kya for M31a1.

Orang Asli mtDNA has been analyzed in the context of an extensive coverage of mtDNA across Southeast Asia (Hill et al. 2007). My own interpretation of the data ascribes ~50–95% of the Semang lineages back to *Homo sapiens*' Africa–Australia dispersal, and virtually the remainder to early Holocene dispersals into Malaya from Sumatra and Vietnam. The Temiar Senoi, Aboriginal Malays, and Melayu Malays sequentially trace a decreasing proportion of their mtDNA lineages to these ancient dispersals and an increasing proportion to middle and late Holocene population incursions (Bulbeck 2011a). Oppenheimer's (2011) interpretation of the same basic database differs in detail, especially in terms of ascribing a larger proportion of Orang Asli and Melayu mtDNA lineages to *in situ* population diversification.

A study of the Batak negritos found their mtDNA haplogroup frequencies placed them relatively close to Chinese and Mongoloid Southeast Asians, notably Palawan Indo-Malays, and very distant from the Semang and Senoi (who clustered together) and Andaman Islanders (who were the most isolated). Further, Y-chromosome haplogroup frequencies placed the Batak in a Philippine (negrito and non-negrito) cluster to the exclusion of other Southeast Asians and Chinese (Scholes et al. 2011). While the authors interpreted their results in the light of the two-layer hypothesis, they conform to the expectations of the regional diversification hypothesis.

A similar assessment may apply to the analysis presented by Heyer et al. (this issue). Their multidimensional scaling analysis of mtDNA genetic distances found that the Agta and Aeta negritos of Luzon cluster together. However, they are also located adjacent to Mongoloid populations, especially those in the Philippines—closer to them than the Mamanwa (who, however, also abut the Mongoloid cluster) or negrito groups from Palawan, Malaya, or the Andamans (who all take up isolated positions in the plot). Similarly, multidimensional scaling plots of the Y-chromosome genetic distances cluster the Agta with the Mamanwa and Indo-Malay populations, albeit with the Agta tending toward the Aeta, who take up an isolated position in these plots.

Review of Dental Morphology Studies on Negritos. The dental morphological variants focused on by dental anthropologists are those under strongest apparent genetic control (Scott and Turner 1997). Five geographically discrete complexes have been identified (Figure 2). Sinodonty involves high expressions of shoveled incisors, supernumerary molar cusps, and various other elaborations. Sundadonty involves intermediate expressions of these elaborations (see also Matsumura and Hudson 2004), whereas Indodonty (Hawkey 1998) and the "Circum-Mediterranean" ("Western Eurasia," in Scott and Turner 1997) and sub-Saharan African complexes (Irish 1997) are each marked by their specific traits. As described below, the statistically inferred population affinities as calculated from dental morphology and from nuclear DNA markers resemble each other in the following respect: populations that we already know to be closely related prove to be so under analysis, but the more distant relationships (those of anthropological interest) are portrayed differently depending on which populations and which traits are compared.

In her study of Indodonty, Hawkey (1998) found that the complex includes Andamanese but excludes Nicobarese. Rayner (2008) confirmed Hawkey's finding for the Andamanese. He also found that the Semang are non-Indodont and instead join up with New Guinea and European groups (as also noted by Rayner and Bulbeck 2001). They also clustered with Batak negritos in some but not all of the analyses where they were compared. Aboriginal Malays, for their part, are convincingly Sundadont in most of Rayner's comparisons. Finally, while the Senoi generally plot reasonably close to the Semang on two-dimensional graphs, a Semang-Senoi clustering never emerged. Instead, the Senoi cluster with Southeast Asians, especially the Semelai Aboriginal Malays, along with Australian Aborigines in several of the graphs. Previously, Rayner and Bulbeck (2001) had found that the Senoi cluster with "Melanesia," a grouping that excludes New Guinea (Figure 2), but also have subsidiary affinities with Sundadont groups from Polynesia, Southeast Asia, and Micronesia. Notwithstanding the ambiguous associations of the Senoi, Hawkey's and Rayner's results overall provide mixed support for the two-layer hypothesis.

Turner and Eder (2006: Figure 7.1) presented an average-linkage hierarchical dendrogram intended to display the dental morphology affinities of the Batak negritos. However, their published MMD distances would definitely join their Melanesia and Sri Lanka samples into a binary cluster (Figure 3), unrecognized in Turner and Eder's dendrogram. On the other hand, seriation of the dendrogram

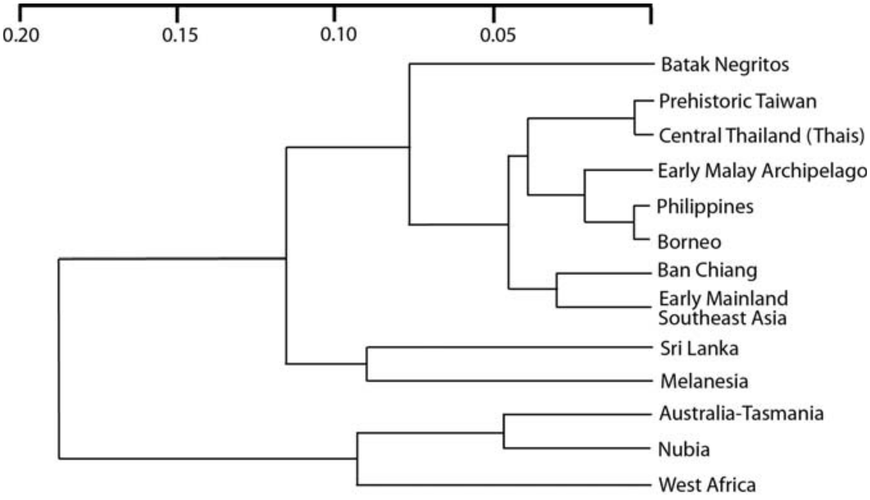


Figure 3. Seriated average-linkage dendrogram: Batak negrito: dental morphology mean measure of divergences, amended from Turner and Eder (2006). Coefficient of variation with a perfect seriation, 76.9%.

produces virtually the same ordering of the analyzed samples as obtained by the rank ordering of their MMD distances from the Batak (Turner and Eder 2006: Table 7.4). In addition, seriation indicates that North Africans (Nubians) and Southwest Pacific groups are closer to sub-Saharan Africans than are Southeast Asians, as also found by Irish and Guatelli-Steinberg (2003: Figure 3). [As a technical point, note that the "Early Mainland Southeast Asia" and "Early Malay Archipelago" samples of Turner and Eder are chronologically wide-ranging and include Neolithic and Metal Age as well as early to mid-Holocene specimens (see Scott and Turner 1997: 320; Bulbeck 2000).]

As Figure 3 shows, Batak negritos not only cluster with other Southeast Asians in their dental morphology (Turner and Eder 2006: 178) but in fact appear "super" Sundadont. With reference to Figure 1, Batak negritos would represent a lineage that has diverged in its dental morphology farther from the ancestral African phenotype than have other Melanesians, Australians (see Irish and Guatelli-Steinberg 2003: 136), Southeast Asians, or South Asians. The reason that these other Southeast Asians appear intermediate between Melanesians/South Asians and the Batak (in terms of their divergence from the ancestral African phenotype) could be admixture with the ancestors of the Batak, in accord with the regional diversification hypothesis.

However, different implications emerge when Northeast Asians are introduced into the comparisons and Africans and South Asians are excluded (Matsumura and Hudson 2004). One main cluster is Sinodont, and it includes "Mongoloid"

Northeast Asians, along with Sakhalin Ainu, and the Iron Age Southeast Asian samples from Dong Son and Leang Codong (see Figure 2). The other main cluster includes recent Southeast Asians, mid-Holocene Thailand, the Hokkaido Ainu, the prehistoric Jomon of Japan, early to mid-Holocene Southeast Asian samples (early Holocene Vietnam/Laos and early Flores/Malaya in Figure 2), and Southwest Pacific groups. Andaman Islanders (forming a subcluster with the early to mid-Holocene Southeast Asian samples) are particularly distant from Mongoloid Northeast Asians. Philippine negritos (who form a subcluster with Hokkaido Ainu and the Jomon) also tend toward the Andaman Islander subcluster, well removed from Mongoloid Northeast Asians (Bulbeck 2011a: Figure 3). This result is broadly compatible with the two-layer hypothesis, except that it would not date any Mongoloid incursion across Southeast Asia any earlier than the Iron Age (Bulbeck 2011a).

In summary, if the results of Hawkey (1998) are combined with those of Matsumura and Hudson (2004; see Bulbeck 2011a), the inference would be that early to mid-Holocene Southeast Asians had a broadly Indodont dental morphology, retained by Andamanese and, to a lesser degree, at least some Philippine negritos. No indications have emerged that this Andamanese-like dental morphology is shown by any Southwest Pacific groups. (For their part, Southwest Pacific groups exhibit such a motley range of similarities, variably with Circum-Mediterranean, African, Sri Lanka, and Southeast Asian "Mongoloid" groups, that there is no justification for recognizing an Australoid dental morphology complex. Just how wide-ranging the dental morphological resemblances of Southwest Pacific groups can be is further exemplified by their sporadic similarities with the Semang and Senoi.) While the dental morphology of the Batak negritos and Semang clearly diverges from Indodonty, it is also distinct from the dental morphology of other recent (and late prehistoric) Southeast Asians.

Notwithstanding the ambiguities in the results, they would be consistent with a version of the two-layer hypothesis that involved an Iron Age Mongoloid incursion across Southeast Asia, or a version of the regional diversification hypothesis that involved a predominantly north-to-south flow of genes from China into Southeast Asia as of the Neolithic.

Review of Dental Metrical Studies on Negritos. Family studies on tooth sizes have found these to have a high hereditary component (Hillson 1996: 79–80). Although these studies have addressed the hereditability of individual tooth dimensions and not the relative size of different tooth dimensions (viz., dental metrical shape), negritos have been compared with surrounding populations for both their tooth size and shape.

Negritos, unlike most Southwest Pacific populations, have small teeth, consistent with their small body size. Philippine negritos resemble the Ainu in having among the smallest teeth in East Asia/Pacific, while Andaman Islander tooth size resembles that of Chinese and Japanese (Matsumura and Hudson 2004: Figure 3). Semang tooth size is similar to that of other Orang Asli, as well as Melayu Malays (Bulbeck et al. 2005).

Analysis of dental metrical shape points to variable negrito affinities. The Andamanese were found to cluster with Southwest Pacific groups, the Ainu, and early to mid-Holocene Southeast Asians, whereas Philippine negritos clearly clustered with Mongoloid East Asians (Matsumura and Hudson 2004; Bulbeck 2011a). The Semang resemble Australian Aborigines and New Guinea Highlanders, whereas the Senoi more resemble Aboriginal Malays (Bulbeck et al. 2005). These results are consistent with the two-layer hypothesis for the Semang and Andamanese but with the regional diversification hypothesis for Philippine negritos.

Negrito Craniometrics. Our first craniometric analysis presents the most reliable results for Andamanese because it is based on all 39 variables available for study. The comparative population with the smallest Mahalanobis *D* distance from Andamanese is the Philippines (3.77), followed by Hainan Chinese, and the West African Dogon (both 4.06). However, the Philippine and Hainan populations are closer to other East Asians (except for the Buriats of Siberia) than to the Andamanese, and these East Asians cluster with Micronesians and Polynesians, which are quite distant from Andamanese. Accordingly, Andamanese cluster with sub-Saharan Africans (Teita, Zulu and Dogon, and Kalahari Bushmen at a greater remove). Further, the secondary affinity of Andamanese as detectable from seriation (Figure 4) lies with European (Norse, Zalavar, Berg) and Egyptian populations. In this analysis, Andamanese appear clearly distinct from Southwest Pacific populations (Australians, Tasmanians, and the New Britain Tolai) and from Indians.

Our second craniometric analysis includes the 21 Howells-compatible variables measured by Hanihara for Philippine negritos (sample size for this analysis = 21). The resulting clusters and seriated order (Figure 5) are similar to those in the first analysis, except that the Amerindians (Santa Cruz, Peru, and Arikara) now cluster with East Asians rather than Europeans/Egyptians. Andamanese and Philippine negritos are closer to each other (Mahalanobis *D* distance = 2.26) than to any comparative population and so cluster together. The next closest Andamanese affinities are with the Dogon (2.90), whereas Philippine negrito affinities are with East Asians (2.44 with Philippines, 2.49 with Atayal). Together, Andamanese and Philippine negritos cluster with sub-Saharan Africans (here excluding Kalahari Bushmen) and now seriate adjacently to the Indian cluster (Figure 5). As in the first analysis, negrito and Southwest Pacific crania are distant from each other.

Our third craniometric analysis includes the 16 Howells-compatible variables measured by von Bonin for Philippine negritos (sample size for this analysis = 18). The resulting clusters are very similar to those in the second analysis, but the seriated order differs in that the cluster of three Southwest Pacific populations is now located adjacently to the sub-Saharan African cluster (Figure 6). Philippine negritos and Malays are closer to each other (Mahalanobis *D* distance = 1.80) than either is to any other population, and together they cluster with other East Asians. The Andamanese have variable affinities (e.g., 2.63 with the Dogon, and

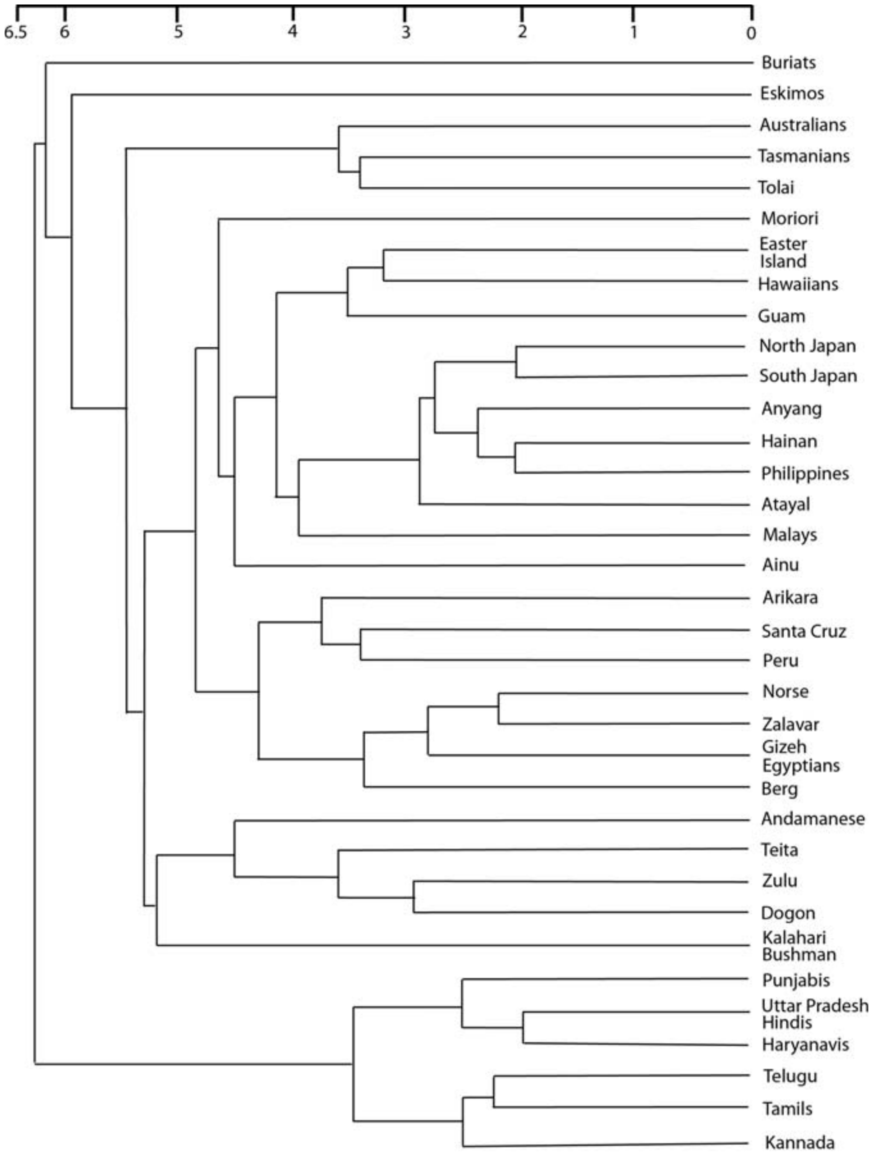


Figure 4. Seriated average-linkage dendrogram: Mahalanobis *D* distances for 35 male populations, using 39 cranial variables. Coefficient of variation with a perfect seriation, 78.2%.

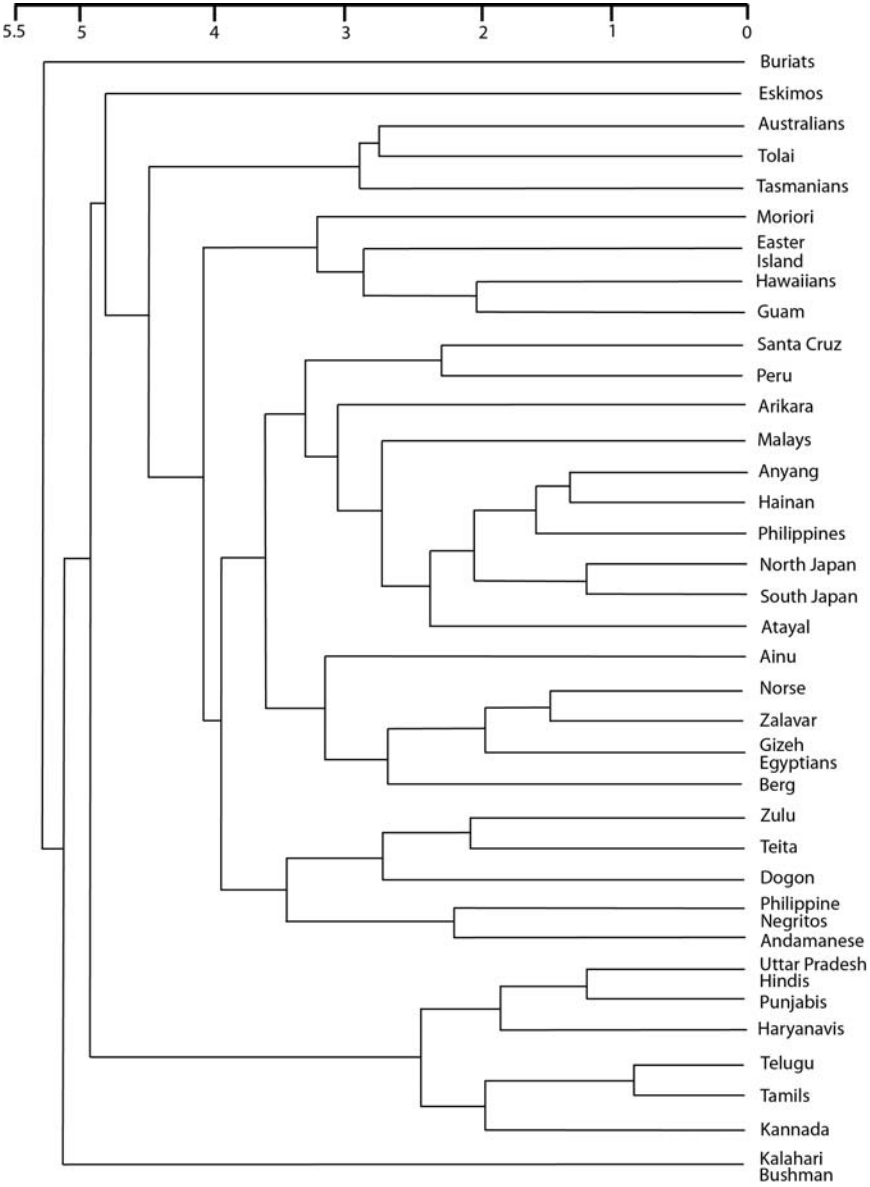


Figure 5. Seriated average-linkage dendrogram: Mahalanobis *D* distances for 36 male populations, using 21 cranial variables. Coefficient of variation with a perfect seriation, 70.0%.

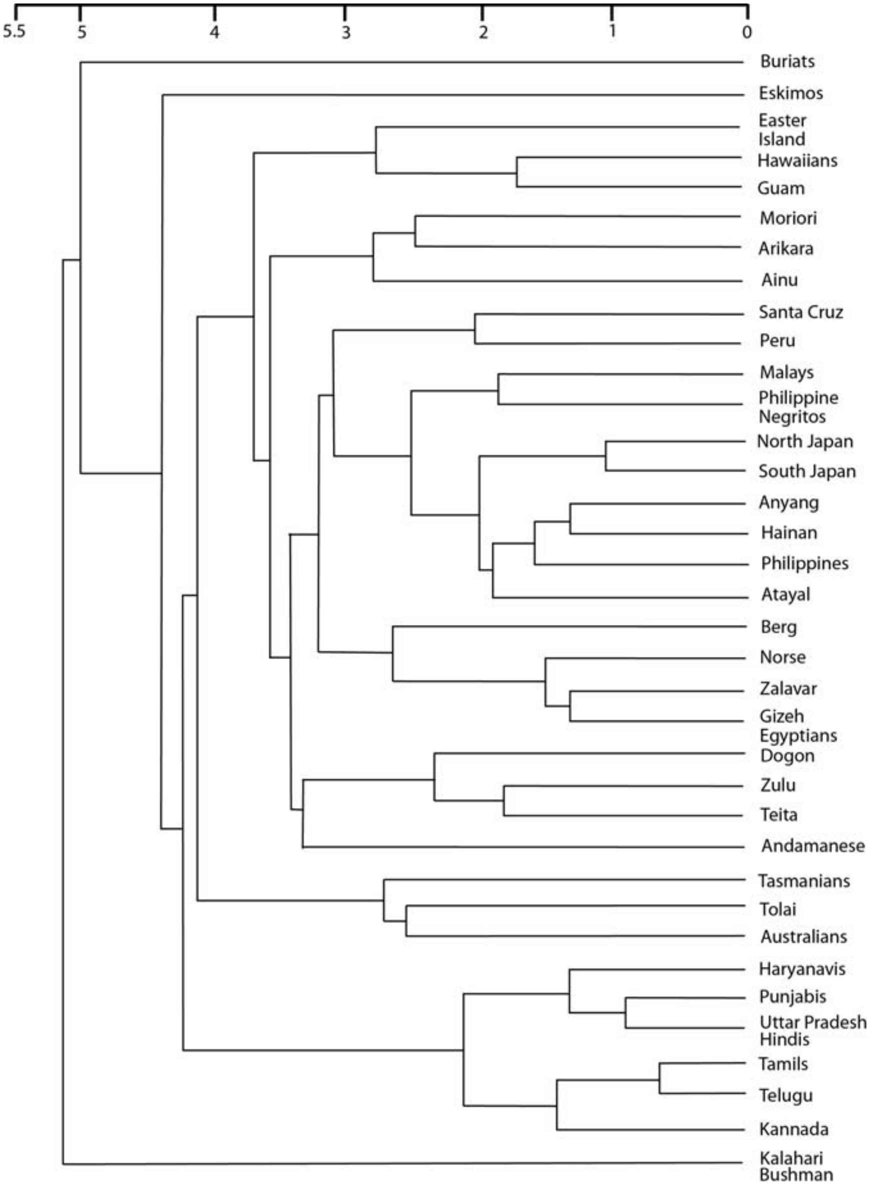


Figure 6. Seriated average-linkage dendrogram: Mahalanobis *D* distances for 36 male populations, using 16 cranial variables. Coefficient of variation with a perfect seriation, 69.1%.

2.76 with Atayal and with Punjabis, vs. 3.10 with Philippine negritos). As in the two previous analyses, Andamanese cluster with sub-Saharan Africans. However, they now seriate next to Southwest Pacific populations.

Linear discriminant function classification of the Philippine negrito crania, analyzed as individual specimens, echoes the results described above. The negritos measured by Hanihara have their highest probability of membership (70th percentile posterior probability) with the Andamanese, whereas the negritos measured by von Bonin have their highest probability of membership with the Malays (Table 3). Considering all 93 Philippine negrito crania together, we see that the highest probability of membership lies with Malays, but this reflects the larger number measured by von Bonin (62) than by Hanihara (31). If there is any common ground between Hanihara's and von Bonin's Philippine negrito samples, it is that both are moderately similar to the Philippine crania measured by Howells. The 70th percentile score for Philippine negritos' membership with Howells's Philippine crania is ~0.12, regardless of which set or subset of crania is considered (Table 3). This similarity did not register in the graphical representations of the Mahalanobis *D* distances (Figures 4–6), because Howells's Philippine crania, while similar to Philippine negritos, are even more similar to other populations often dissimilar from Philippine negritos. Finally, note the total dissimilarity of Philippine negritos from Howells's Southwest Pacific populations—zero classifications, and 70th percentile scores that never rise above 0.0011 (Table 3).

Linear discriminant function classification was also undertaken for the Orang Asli crania. The individual results are presented in Table 4, arranged in descending order of the number of variables available for analysis. To simplify the presentation, these individual results are presented only for the six comparative populations with the highest 70th percentile posterior probability scores. The Orang Asli classifications ranged widely beyond these six populations (Table 4, last column), to include southern Indian, Polynesian, New World, and Northeast Asian populations. However, even these sporadic similarities did not extend to Southwest Pacific populations, Melayu Malays, or Howells's Philippine sample.

In our attempt to understand Orang Asli craniometric affinities, we may focus just on the six most similar comparative populations. These include three sub-Saharan African populations (Dogon, Teita, and Zulu) and the Andamanese (Table 4). The Dogon and Andamanese essentially tie for being closest to the Orang Asli, with four and six classifications, respectively, and a 70th percentile score of ~0.1. From the available results, there is no reason to distinguish between the Semang and the Senoi in their craniometric affinities; for instance, of the eight Orang Asli classifications with sub-Saharan African populations, four involve the Semang and four involve the Senoi. Orang Asli crania also show some similarities with Punjabi and Hainan Chinese crania. However, the results overall suggest a broad affinity with sub-Saharan African and Andamanese crania.

The three main conclusions to take from the current analysis of negrito crania are as follows. First, Andamanese show a loose affinity with sub-Saharan Africans. Second, the Semang (and the Senoi) are similar to both Andamanese

Table 3. Results from Discriminant Function Analysis of Philippine Negrito Crania (highest score shown in boldface)

POPULATION	NUMBER OF CLASSIFICATIONS	70TH PERCENTILE SCORE			
		HANIHARA—ALL VARIABLES[a]	VON BONIN—ALL VARIABLES[b]	OTHER CRANIA, INCOMPLETE[c]	ALL 93 CRANIA
Malays	23	0.019	**0.238**	**0.464**	**0.204**
Philippines	7[d]	0.119	0.118	0.121	0.119
Hainan	11	0.027	0.116	0.075	0.080
Andamans	11	**0.337**	0.034	0.018	0.068
Atayal	6	0.120	0.019	0.039	0.039
Dogon	4	0.053	0.027	0.011	0.037
Anyang	1[d]	0.008	0.079	0.030	0.028
North Japan	0	0.0079	0.054	0.029	0.027
South Japan	1	0.011	0.050	0.037	0.026
Arikara	4	0.0038	0.0070	0.028	0.013
Peru	4	0.0096	0.0079	0.033	0.011
Berg	4	0.0072	0.0026	0.013	0.0074
Zalavar	0	0.0057	0.014	0.0042	0.0060
Hawaiians	3	0.100	0.015	0.0052	0.0050
Guam	2	0.0002	0.033	0.0053	0.0033
Egyptians	1	0.0040	0.0034	0.0019	0.0024
Punjabis	1	0.0067	0.0004	0.0020	0.0024
Zulu	0	0.0044	0.0013	0.0010	0.0023
Santa Cruz	2	0.0007	0.0014	0.0028	0.0013
Buriats	0	0.00007	0.0030	0.0017	0.0013
Uttar Pradesh	0	0.0059	0.0003	0.0010	0.0012
Ainu	1	0.0006	0.0013	0.0014	0.0008
Norse	0	0.0021	0.0009	0.0008	0.0008
Moriori	0	0.00001	0.0012	0.0010	0.0006
Teita	3	0.0014	0.0002	0.0003	0.0004
Haryanavis	0	0.0008	0.0001	0.0004	0.0004
Tasmanians	0	0.0011	0.0001	0.0002	0.0003
Telugu	0	0.0002	0	0.0013	0.0003
Bushman	3	0.0081	0	0.00008	0.0002
Kannada	1	0.0002	0.0001	0.0005	0.0002
Tolai	0	0.0001	0.00004	0.0002	0.0001
Tamils	0	0.0001	0	0.0003	0.0001
Easter Island	0	0.0000001	0.0002	0.00003	0.00004
Eskimos	0	0	0	0.00001	0.000001
Australians	0	0.000001	0	0.000006	0.000001

[a] Results are based on 21 male and 7 female Philippine negritos.

[b] Results are based on 18 male and 2 female Philippine negritos.

[c] Results are based on 24 male and 21 female Philippine negritos.

[d] Number of classifications relates only to the 65 male Philippine negrito crania.

Table 4. Posterior Probabilities of Orang Asli Crania Membership (classifications in boldface)

SPECIMEN[a]	GROUP[b]	NV[c]	DOGON	ANDAMANS	TEITA	PUNJABIS	HAINAN	ZULU	OTHER[d]
Pangan ♂	SM	39	**0.65**	0.06	0.06	<0.01	<0.01	0.22	—
Pekan ♂	SM	39	0.04	0.03	<0.01	0.11	0.01	<0.01	**HI (0.40)**
B. Labu ♂	SN	24	<0.01	<0.01	<0.01	0.40	<0.01	<0.01	**HA (0.40)**
B. Labu ♀	SN	24	0.12	<0.01	0.06	0.07	0.01	0.02	**KA (0.24)**
S. Piah ♂	SM	22	0.05	**0.93**	0	<0.01	0	<0.01	—
B. Padang ♀	SN	22	0.02	0	0.06	0.10	<0.01	**0.49**	—
Jahai ♂	SM	21	0.085	<0.01	<0.01	0.03	0.07	0.10	**NJ (0.33)**
Kensiu ♂	SM	21	**0.19**	0.09	0.07	0.03	0.02	0.02	—
Menriq ♂	SM	21	**0.57**	<0.01	<0.01	0	0.01	<0.01	—
Kinta ♂	SN	19	<0.01	**0.56**	<0.01	0.18	<0.01	<0.01	—
Pangan ♂	SM	14	<0.01	<0.01	0.03	**0.42**	<0.01	0.03	—
Jahai 5 ♂	SM	14	<0.01	0.01	<0.01	0	**0.28**	<0.01	—
Mani 3 ♀	SM	14	0.18	<0.01	0.03	0.05	0.02	<0.01	**KA (0.54)**
M.D. 9 ♀	SN	14	0.12	<0.01	**0.51**	0	<0.01	0.01	—
Jahai 6 ♂	SM	13	0.04	<0.01	0.11	<0.01	<0.01	0.04	**AI (0.39)**
Gerik ♀	SM	13	**0.20**	0.13	0.16	<0.01	0.05	<0.01	—
Kampar ♂	SN	13	<0.01	**0.51**	<0.01	0.12	<0.01	<0.01	—
M.D. 8 ♂	SN	13	<0.01	<0.01	0.07	0.05	0.02	0.05	**EI (0.19)**
Jahai 4 ♀	SM	12	0.01	<0.01	0.01	0.01	0.03	<0.01	**AI (0.26)**
Jahai 7 ♀	SM	12	<0.01	<0.01	<0.01	<0.01	0.03	<0.01	**SC (0.26)**
Bk. Sapi ♂	SM	10	<0.01	0.44	<0.01	<0.01	<0.01	<0.01	—
Ulu Pahang 10 ♂	SN	10	0.01	0.04	<0.01	<0.01	0.18	<0.01	—
Berlin ♀	SN	10	0.03	<0.01	0.01	0.05	0.09	0.20	—
Jakun 15 ♂	AM	10	0.07	0.54	0.04	0.02	<0.01	0.04	—
Pangan ♂	SM	9	<0.01	0.05	<0.01	<0.01	0.01	<0.01	**PE (0.35)**
M.D. 10 ♀	SN	6	0.11	0.03	0.28	0.01	0.03	0.01	—
Mani 2 ♂	SM	4	0.11	0.24	0.05	0.02	0.07	<0.01	—
70th percentile	Orang Asli	—	*0.11*	*0.10*	*0.06*	*0.05*	*0.03*	*0.02*	—

[a] B., Batang; Bk., Bukit; M.D., Mai Darat; S., Sungei.

[b] SM stands for Semang, SN for Senoi, and AM for Aboriginal Malay.

[c] Number of variables available for analysis.

[d] AI, Ainu; EI, Easter Island; HA, Haryanavis; HI, Hawaiians; KA, Kannada; NJ, North Japan; PE, Peru; SC, Santa Cruz.

and sub-Saharan Africans. Third, this characterization also partly applies to the Philippine negritos recorded by Hanihara, but not at all to the Aeta recorded by von Bonin. As for Philippine negritos' overall similarities (Table 3, last column), all five closest populations are based in tropical East Asia (Malaya, the Philippines, Hainan, the Andamans, and Taiwan), suggesting a geographic affinity regardless of negrito/non-negrito status.

The findings presented here are supported by some but not all other studies on negrito craniometric affinities. A cluster comprising Andamanese and sub-Saharan African crania, based on Mahalanobis D^2 distances, was initially presented by Howells (1973b). However, when he applied statistical methods that adjusted for size differences, he obtained quite different results (Howells 1989: Figures 5b, 6b, 7b, 7c, 11, 12, 16, and 17). Andamanese either fell between sub-Saharan Africans and Europeans/Egyptians or else clustered with Europeans/Egyptians, or even clustered with East Asians/Guam. When South Asians and southwestern Asians were introduced to the comparisons, Wright (2002) found that Andamanese were closer to them than to sub-Saharan Africans, while Stock et al. (2007), adjusting for size, found that Andamanese clearly clustered with South Asians to the exclusion of other populations. On the other hand, Raghavan et al. (2013), also adjusting for size, find that Andamanese cluster with sub-Saharan Africans and are clearly distinct from South Asians. In sum, Andamanese crania show a wide range of affinities with Old World crania, apart from Southwest Pacific crania; however, a sub-Saharan African affinity is perhaps the most consistent result overall.

In the only other analysis that included sub-Saharan Africans in a study of Andamanese craniometrics, Uytterschaut (1983: Figure 12, Appendix 4) included Philippine negritos and three non-negrito Philippine populations but, regrettably, limited her number of variables to seven. While Philippine negritos and Andamanese both stood out as relatively isolated, Philippine negritos were closer to Mongoloid East Asians than any other populations, whereas the Andamanese were closer to the Dogon and Bushmen than any other populations.

Brace et al. (1991) have also examined Andamanese and Philippine negrito craniometrics, using 24 variables, and *C*-scores in order to register shape similarity. Whereas Andamanese clustered loosely with South Asians (Brace et al. 1991: Figure 3), Philippine negritos clustered with East Asian Mongoloids and most closely with those from the Philippines (Brace et al. 1991: 258; see also their Table 3). The authors did not like these results and so found a way to obtain the result they wanted, which was for Andamanese and Philippine negritos to cluster, and the negrito cluster to then join with Southwest Pacific groups (Brace et al. 1991: Figure 4). However, the methodology to obtain this result was flawed in such respects as combining indices and direct measurements in the same analysis, including an index based on two autocorrelated variables (effectively removing both variables from the analysis), and including an idiosyncratic index that related upper facial projection to midfacial breadth (Bulbeck et al. 2006: 127–128). Setting aside this last, methodologically flawed "result," we can conclude that their analysis reiterates the Mongoloid status of Philippine negrito craniometrics. It also confirms the

Andamanese–South Asian similarity found by some other studies, although in the context of excluding sub-Saharan Africans from the comparisons.

The single study that has compared all three negrito groups on their craniometrics also focused on shape, through derivation of the Penrose size and shape distances, based on 12 variables (Bulbeck 1996). Von Bonin's Philippine negritos clearly clustered with Southeast Asians, especially Javanese, in cranial shape, and also proved to have moderately large crania. Far removed from Philippine negritos was a cluster that included Andamanese and Semang along with coastal New Guinea crania and, at a further remove, Senoi and Tamils. Although this latter cluster was based on shape, these were also the five groups with the smallest crania. This cluster linked with the East Asian (including Philippine negrito) cluster but tended toward the cluster comprising Southwest Pacific groups with medium-size to large crania. Although this analysis excluded sub-Saharan Africans, it confirmed three important points noted above: Andamanese crania resemble those of the Semang and Senoi; Andamanese and Orang Asli crania are distinct from Mongoloid East Asian crania; and Philippine negritos have Mongoloid craniometrics, overall.

Negrito Cranial Morphology. As explained in "Materials and Methods," Boolean formulas were developed that discriminated most effectively between the cranial morphology of Mongoloid Indo-Malays and the three other groups (Australian Aborigines, Melanesians, and South Asians) for which comparable, cranial morphological data are available. The formulas (Tables 5–7) are expressed from the perspective of Indo-Malays—if a specimen evaluates as "True" for the expression, the specimen is classified as Indo-Malay, but if it evaluates as "False," it is classified with the non-Indo-Malay group. Also, three types of formulas were constructed. The most important formula is the one with the strongest discrimination, as measured by the difference of proportions score. The second formula correctly classifies all Indo-Malays that could be evaluated, and as large a proportion of the non-Indo-Malay group as possible. The logic here is that any specimen that does not classify as Indo-Malay falls outside the Indo-Malay range of variation. The third formula correctly classifies all specimens from the non-Indo-Malay group that could be evaluated and also as large a proportion of the Indo-Malays as possible. The logic here is that any specimen that does not classify with the non-Indo-Malay group falls outside the range of variation of the non-Indo-Malay group.

Australian Aborigines could be clearly distinguished from Indo-Malays on both the formula with the strongest discrimination (<10% of both Australians and Indo-Malays would be misclassified) and on the formula that successfully classifies all Indo-Malays (when <30% of Australians would have been classified as Indo-Malay). Melanesians and South Asians were reasonably distinguishable from Indo-Malays on the formulas with the strongest discrimination, when one-quarter or less of Indo-Malays, Melanesians and South Asians would be misclassified (Tables 5–7).

Original cranial morphological observations are available for 13 Andaman Islander males (11 by Johan Kamminga, 2 by the author), two Semang males (including

Table 5. Boolean Formulas Classifying Indo-Malay and Australian Male Crania

TYPE OF FORMULA	INDO-MALAY EXPRESSION (AUSTRALIAN EXPRESSION IS THE LOGICAL OPPOSITE)	CORRECTLY CLASSIFIED	
		INDO-MALAYS	*AUSTRALIANS*
Strongest discrimination	[(glabella not large OR supraorbital breadth not large) AND (sagittal keel indistinct OR nasofrontal articulation width narrow OR parietal bossing prominent) AND palate module ≤ 39] OR cranial index ≥ 75	113/117 (97%)	176/194 (91%)
All Indo-Malays	(palate module ≤ 39 OR cranial index ≥ 75) AND (glabella not large OR median frontal ridge indistinct OR sagittal keel indistinct)	117/117 (100%)	143/199 (72%)
All Australians	Cranial index ≥75 AND [orbital border sharp OR phaenozygy absent OR (nasofrontal articulation width narrow AND transverse occipital torus absent)]	54/117 (46%)	210/210 (100%)

Sources: Australians, Stanley Larnach Papers (South Australian Museum, Adelaide, Australia), Brown (1982); Indo-Malays, D. Bulbeck (unpublished data), J. Kamminga (unpublished data).

Table 6. Boolean Formulas Classifying Indo-Malay and Melanesian Male Crania

TYPE OF FORMULA	INDO-MALAY EXPRESSION (AUSTRALIAN EXPRESSION IS THE LOGICAL OPPOSITE)	CORRECTLY CLASSIFIED	
		INDO-MALAYS	*MELANESIANS*
Strongest discrimination	Orbital border sharp OR transverse occipital torus absent OR (cranial index ≥ 75 AND palate module ≤ 39 AND anterior nasal spine less than Broca 4)	83/112 (74%)	416/493 (84%)
All Indo-Malays	Cranial index ≥ 75 OR [palate module ≤ 39 AND (orbital border sharp OR supraorbital breadth not large OR frontal curvature index > 24.7)]	117/117 (100%)	200/492 (41%)
All Melanesians	(orbital border sharp OR transverse occipital torus absent) AND (phaenozygy absent OR parietal bossing prominent) AND [cranial index ≥ 75 OR (frontal curvature index > 24.7 AND supraorbital breadth not large AND supramastoid crest not slight)]	27/117 (23%)	525/525 (100%)

Sources: Melanesians, Green (1990), D. Bulbeck (unpublished data). J. Kamminga (unpublished data); Indo-Malays, D. Bulbeck (unpublished data), J. Kamminga (unpublished data).

Table 7. Boolean Formulas Classifying Indo-Malaysian and South Asian Male Crania

TYPE OF FORMULA	INDO-MALAY EXPRESSION (AUSTRALIAN EXPRESSION IS THE LOGICAL OPPOSITE)	CORRECTLY CLASSIFIED	
		INDO-MALAYS	*SOUTH ASIANS*
Strongest discrimination	(cranial index ≥ 75 OR parietal bossing prominent) AND (subnasal prognathism not large OR supraorbital breadth large) AND (glabella not large OR transverse occipital torus present)	63/85 (74%)	59/65 (91%)
All Indo-Malays	No such expression exists	N/A	N/A
All South Asians	Supraorbital breadth large AND (phaenozygy absent OR parietal bossing prominent OR subnasal prognathism not large) AND (glabella not large OR transverse occipital torus present)	17/106 (16%)	67/67 (100%)

Sources: D. Bulbeck (unpublished data), J. Kamminga (unpublished data).

the Pekan adolescent), and the Kinta Senoi male (Bulbeck 1981: 303). How well they classify as Indo-Malay compared with neighboring groups is summarized in Table 8. The negritos and Kinta Senoi are clearly distinguishable from Australians. They generally classify as Indo-Malays and are only ever classified as Australian (11 of 16) using the formula that also classifies half of the Indo-Malays as Australian in correctly classifying all of the Australians. However, the negritos and Kinta Senoi overall resemble Melanesians and South Asians in their cranial morphology more than they resemble Indo-Malays. With respect to the formulas with the strongest discrimination, 14 of 16 (88%) classify as Melanesian, and 10 of 16 (63%) classify as South Asian, compared with around one-quarter of Indo-Malays that would have classified as Melanesian or as South Asian with the same formulas. Negritos and the Kinta Senoi do not fall outside of the Indo-Malay range of variation in their cranial morphology—all would classify as Indo-Malay using the formulas sufficiently broad for Indo-Malay variation to correctly classify all Indo-Malays—but they fit better within the Melanesian and/or South Asian range of variation.

While the Semang show the same pattern of cranial morphological associations as do the Andamanese, so does the Kinta Senoi. Also, whether Andamanese and Orang Asli might be more similar to Africans than to Melanesians and South Asians in their cranial morphology (as in their craniometrics) is not currently known.

Discussion

Negritos have been recognized as an "entity" on the basis of sharing dark skin, frizzy hair, and small stature (Table 1), but other commonalities are not obvious (Table 9). The genetic evidence would refute any scenario that had negritos sharing

Table 8. Classification of Andamanese, Semang, and Kinta Senoi Male Crania in Terms of Cranial

COMPARISON/ TYPE OF FORMULA	INDO-MALAYS COMPARED WITH AUSTRALIANS		
	Strongest discrimination	*All Indo-Malays*	*All Australians*
Andamanese	13/13 Indo-Malay	13/13 Indo-Malay	8/13 Australian
Semang adult	Indo-Malay	Indo-Malay	Australian
Semang adolescent	Indo-Malay	Indo-Malay	Australian
Kinta Senoi	Indo-Malay	Indo-Malay	Australian

a common ancestry to the exclusion of neighboring populations. Dental morphology provides hints of similarities between different negrito groups, but these are less convincing than the similarities these negrito groups show with various non-negrito groups. Craniometrics and cranial morphology find a certain degree of negrito homogeneity in cranial form, but in this case convergent evolution is likely to be a factor. This is because Malay Peninsula Hoabinhian and Neolithic crania eschew any metrical affinities with the Andamanese in deference to Tasmanian, Zulu, and Easter Island classifications. Also, the Malay Peninsula Hoabinhian (although not the Neolithic) cranial morphology is more Australian than Melanesian-like (Bulbeck 2005; Bulbeck and Adi 2005; Bulbeck and Zuraina 2007). Thus, while all negrito groups can trace a substantial proportion of their ancestry to the Late Pleistocene *Homo sapiens* colonists of the Asia-Pacific, their ancestral lineages appear to have evolved largely independently of each other (Figure 1).

In contrast to the lack of evidence for negritos' shared unique ancestry, there is considerable evidence for shared unique ancestry between the Semang and Senoi (Table 9). Dental metrical shape analysis is the only aspect where the Semang and Senoi do not resemble each other. In addition, the Senoi appear to be at least as similar to Philippine negritos and Andamanese as the Semang are, as in the analysis of nuclear DNA markers that clustered the Senoi with Philippine negritos (Tan 2001), and the Andamanese metrical classification of two Senoi crania (Table 4). It is as though the Mongoloid traits of light skin and nonfrizzy hair had been absorbed by a non-Mongoloid population.

Philippine negritos clearly outrank the Senoi in their tendency to associate with Mongoloid Southeast Asians, notably those in the Philippines. Although Philippine negritos evince sporadic non-Mongoloid associations, to a large degree it is as though the traits of dark skin and frizzy hair had been absorbed by a Mongoloid population.

The clue to understanding the situation may be to recognize the existence of marital exchange between negrito and non-negrito neighbors. This predominantly involved non-negrito men marrying into negrito communities or negrito women marrying into non-negrito communities, at least in Palawan (Schebesta

Morphology

INDO-MALAYS COMPARED WITH MELANESIANS			INDO-MALAYS COMPARED WITH SOUTH ASIANS	
Strongest discrimination	*All Indo-Malays*	*All Melanesians*	*Strongest discrimination*	*All South Asians*
11/13 Melanesian	13/13 Indo-Malay	13/13 Melanesian	9/13 South Asian	13/13 South Asian
Melanesian	Indo-Malay	Melanesian	Indo-Malay	South Asian
Melanesian	Indo-Malay	Melanesian	South Asian	South Asian
Melanesian	Indo-Malay	Melanesian	Indo-Malay	South Asian

Table 9. Summary of Investigations into Negrito Genetic and Osteological Affinities

BIOLOGICAL INDICATOR	EVIDENCE THAT NEGRITOS SHARE A UNIQUE COMMON ANCESTRY?	NEGRITO AFFINITIES WITH "MONGOLOID" SOUTHEAST ASIANS?	NEGRITO AFFINITIES WITH OUTSIDE POPULATIONS?
Mitochondrial DNA	None evident	Semang with Senoi; Philippine negritos with Philippine non-negritos	Andamanese with South Asians
Nuclear DNA	No, although evidence is consistent with gene flow between negrito lineages	Semang with Senoi; Philippine negritos with Philippine non-negritos	Andamanese with South Asians
Dental morphology	Inconsistent hints	Semang with Senoi; Batak with Mongoloid Southeast Asians (both inconsistently)	Andamanese with South Asians; Semang with New Guinea and Europe
Dental metrical shape	None evident	Philippine negritos with Mongoloid East Asians	Andamanese and Semang with Southwest Pacific groups
Craniometrics	Semang and one Philippine negrito sample similar to Andamanese	Semang similar to Senoi; Philippine negritos with Malays and Philippine non-negritos	Andamanese, Semang, and one Philippine negrito sample with Africans
Cranial morphology	Andamanese and Semang not clearly different	Semang not clearly different from Senoi	Andamanese and Semang with Melanesians and South Asians

and Lebzelter 1928; Scholes et al. 2011). A child of a negrito mother may be predominantly negrito in appearance. In this case, membership with the mother's natal community may be easier to achieve than with the father's natal community, especially if there are any doubts as to the child's paternal ancestry. Alternatively, the child's way into the father's natal community may be paved by predominantly non-negrito looks. Any traits whose genetic basis is not linked to hair form or skin color—all of those reviewed in this study, to my knowledge—would freely pass between negrito and non-negrito communities even while these communities tended to retain their distinctive physical looks. After a certain point, however, the generation of too many individuals of intermediate appearance would break down the physical distinction and lead to populations with highly variable physical looks, such as the Saoch and the Mamanwa.

This scenario may be appropriate for ethnographic situations where negrito foragers and non-negrito communities (predominantly horticulturalists in ethnographic times) coexist, but what about the swathes of Indo-Malaysia where negritos have not been documented? Curiously, the large equatorial islands with the greatest expanses of rainforest fall in the latter category: Borneo and Sumatra, with their "Mongoloid" rainforest foragers, and Sulawesi, where rainforest foragers have not been recorded (see Grimes and Grimes 1987; Bulbeck 2006). Useful biological data on the Penan of Borneo and the Kubu of Jambi are to my knowledge unavailable for a satisfactory investigation of their biological affinities. What can be stated with confidence is that their population densities are low, like those of negrito (and non-negrito) rainforest foragers to their north, and they are facing the same problems of losing their rainforest habitat to the incursions of logging companies and swidden farmers.

Intriguingly, the distribution of the B4a1a* paragroup includes Borneo and Jambi as well as Taiwan, the Philippines and North Maluku. Soares et al. (2011) estimate a terminal Pleistocene to early Holocene antiquity for the B4ala clade and an early-middle Holocene for its dispersal, more likely to than from Taiwan. Borneo has also produced Indo-Malaysia's largest collection of biometrically analyzed pre-Neolithic and Neolithic burials, at Niah Cave. Manser's (2007) analysis of these burials demonstrates their Southeast Asian craniodental osteology, particularly the pre-Neolithic burials. Care should be taken in reconstructing demographic expansion on the basis of the distribution of haploid loci. Nonetheless, the typically Mongoloid craniodental affinities of Philippine negritos may reflect a very long period of genetic interaction between populations stretching from Jambi to Taiwan, with the derivation of Mongoloid craniodental features discernible in Borneo by the early Holocene. This scenario would be in accord with the regional diversification hypothesis rather than the two-layer hypothesis. The potential relevance of the B4a1a* paragroup distribution can be seen from the fact that the Andaman Islands and Malaya lie outside it, and here we see that the negritos (as well as the Senoi) are clearly distinguishable from predominant Mongoloid patterns. In addition, human remains in Malaya retain resolutely non-Mongoloid affinities till at least the Neolithic (Bulbeck 2011a).

Certainly, attempts to frame the two-layer hypothesis in terms of a mid-Holocene incursion of Mongoloid farmers into Southeast Asia lack certification. Proponents of this view disagree on whether the major site of Khok Phanom Di in south-central Thailand represents complex maritime foragers, comparable to the Da But sites in North Vietnam (Higham this issue), or the early expansion of mainland Southeast Asian farmers (Bellwood and Oxenham 2008). Archaeological evidence for the spread of agriculture associated with the expansion of the Malayo-Polynesian branch of Austronesian, from the Taiwan region into Indo-Malaysia, is ambiguous (Bellwood 2011). Whereas the osteological evidence for a demic diffusion from China to Southeast Asia associated with the Neolithic (however that is defined) is, to say the least, uncertain, historical records document the flow of immigrants from China into Southeast Asia for over 2,000 years, notably during the second millennium CE (Rae and Witzel 2008; Wikipedia 2012). This would be the only form of the "two-layer hypothesis" supported by the investigations summarized here, although I would prefer to interpret it as a version of the "regional diversification hypothesis" accompanied by significant north-to-south gene flow during the late Holocene (Figure 1C).

Major historical inflow of genes from China into Southeast Asia is also suggested by Chinese accounts of individuals of negrito appearance across a wider area than attested by ethnographic records. In the third century CE, K'ang T'ai wrote of the inhabitants of the early Southeast Asian state of Funan, near the Mekong Delta, that they were black and frizzy haired (Hall 1977: 27). Writing in the late seventh century CE, I-Tsing described the *K'un-lun* inhabitants of maritime Southeast Asia as having black skin and curly hair (Wolters 1967: 200). There are even Chinese accounts of small, dark-skinned people with curly hair as far north as Taiwan (Quartly 2004).

From the foregoing discussion, there would be no basis for assuming that, at 5 kya, Taiwan was populated by light-skinned, straight-haired individuals, whether or not they had Mongoloid craniodental characters. Nor would there be a basis to assume that their contemporaries to the southwest were uniformly dark skinned, woolly haired, or craniodentally non-Mongoloid. Nor would there be a basis to assume that Neolithic émigrés from Taiwan overran the pre-Neolithic Indo-Malaysians and, in so doing, directly established the numerical dominance (as observed ethnographically) of inhabitants of Mongoloid appearance. The dispersal of Malayo-Polynesian across Indo-Malaysia was certainly accompanied by significant genetic input, accounting for up to 20% of present-day Indo-Malaysian mtDNA, according to Hill et al. (2007). This linguistic dispersal would correspond to one or several of the population injections into Indo-Malaysia depicted in Figure 1C. However, the extent of its impact on Indo-Malaysians' physical features and skeletal characters would be a matter of conjecture.

Anyway, by the ethnographic present, negritos were restricted to circumscribed habitats, either the islands of the Andaman chain or remnant forest tracts in Malaya and the Philippines. This restriction to circumscribed habitats is the likely root cause for their shared features of small stature and a gracile (albeit not always "Mongoloid") cranial form.

Conclusions

Genetic evidence reveals that much of the ancestry of negrito populations is deeply rooted, reaching back to when *Homo sapiens* dispersed from Africa to colonize tropical Asia and Australia/New Guinea in the Late Pleistocene. The dark skin and woolly hair of negritos are also parsimoniously interpreted as retentions of archaic traits of these early colonists. However, none of this provides a basis for recognizing the negritos as a single lineage characterized by shared ancestry exclusive of other non-African lineages. On the contrary, in both their genetics and their craniodental osteology, negrito affinities are inconsistent both with respect to other negritos and in relation to the non-negrito populations of South Asia, Southeast Asia, and the Southwest Pacific. Cranial form (metrics and morphology) alone hints at a similarity covering Andaman Islanders, the Semang, and to some degree Philippine negritos. But in this case convergent evolution may be suspected, because the presumed ancestors of the Semang show quite different cranial affinities.

Andaman Islander external affinities lie mainly with South Asians but not consistently so. The Semang resemble their Senoi neighbors in numerous respects, and both could be viewed as "non-Mongoloid" in their associations. The Philippine negritos, on the other hand, often demonstrate affinities with Mongoloid populations, notably those in the Philippines. A model is proposed whereby the offspring of negrito/non-negrito marriages would tend to have been accepted in the negrito or non-negrito community based on looks, allowing the ready cross-flow of genes that do not code for physical looks. Also, the distribution of the B4a1a* paragroup is proposed as important for understanding the appearance of Mongoloid craniodental features in Island Southeast Asia/Taiwan, as the Philippines lie within this distribution whereas Malaya and the Andamans lie outside of it.

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